



Species diversity of fiddler crabs, genus *Uca* Leach, 1814 (Crustacea: Ocypodidae), from Taiwan and adjacent islands, with notes on the Japanese species

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Abstract

The fiddler crabs, genus *Uca* Leach, 1814 (Decapoda, Ocypodidae) of Taiwan, including the offshore islands of Penghu (Pescadores), Kinmen (Quemoy), Matsu (Matzu), and Dongsha (Pratas), are revised, with the recognition of five subgenera and 15 species, viz. *Uca* (*Austruca*) Bott, 1973: *U. lactea* (De Haan, 1835), *U. perplexa* (H. Milne Edwards, 1837), *U. triangularis* (A. Milne-Edwards, 1873); *U. (Gelasimus)* Latreille, 1817: *U. borealis* Crane, 1975, *U. jocelynae* Shih, Naruse & Ng, 2010, *U. tetragonon* (Herbst, 1790), *U. vocans* (Linnaeus, 1758); *U. (Paraleptuca)* Bott, 1973: *U. crassipes* (White, 1847), *U. splendida* (Stimpson, 1858); *U. (Tubuca)* Bott, 1973: *U. acuta* (Stimpson 1858), *U. arcuata* (De Haan, 1835), *U. coarctata* (H. Milne Edwards, 1852), *U. dussumieri* (H. Milne Edwards, 1852), *U. paradussumieri* (Bott, 1973); and *U. (Xeruca)* Shih, 2015: *U. formosensis* Rathbun, 1921. Among them, *U. acuta*, *U. paradussumieri*, and *U. vocans* are confirmed to be distributed in Taiwan. *Uca formosensis* is endemic to Taiwan. The *Uca* species of the main islands of Japan are also listed. Four species (*U. arcuata*, *U. lactea*, *U. crassipes* and *U. borealis*) are known, but the recent additional records of *U. perplexa* and *U. vocans* need further confirmation. Except *U. acuta*, *U. borealis*, *U. formosensis*, *U. lactea*, and *U. paradussumieri*, other 10 Taiwanese species can be found from the Ryukyus too. Only one endemic species, *U. boninensis*, is reported from the Ogasawara (Bonin) Islands. A key to the 18 species of *Uca* found in East Asia is also provided in this study.

Key words: Ryukyus, new records, taxonomy

Introduction

The islands on the eastern margin of Asia include Taiwan and adjacent islands (Fig. 1), the Ryukyus (= Ryukyu Islands), Ogasawara (Bonin) Islands, and the main islands of Japan. The main ocean currents of this region include the Kuroshio Current, which runs from south to north mainly along the eastern side of these islands, and the China Coast and South China Sea currents on the western side (Jan *et al.* 2002; Shih 2012a) can influence the larval dispersal of many marine organisms (e.g., see Chan *et al.* 2007 for barnacles). Fiddler crabs, genus *Uca* Leach, 1814 (Decapoda: Ocypodidae) are dominant among the intertidal benthos of tropical and subtropical mudflats (Crane 1975). The fiddler crab fauna of Taiwan and Japan was listed by Crane (1975) but some new records, new species, and a new subgenus have been added from this region during the decades (see Shih 1994, 2015; Yoshigou 2001; Shih *et al.* 2010a, b, 2012).

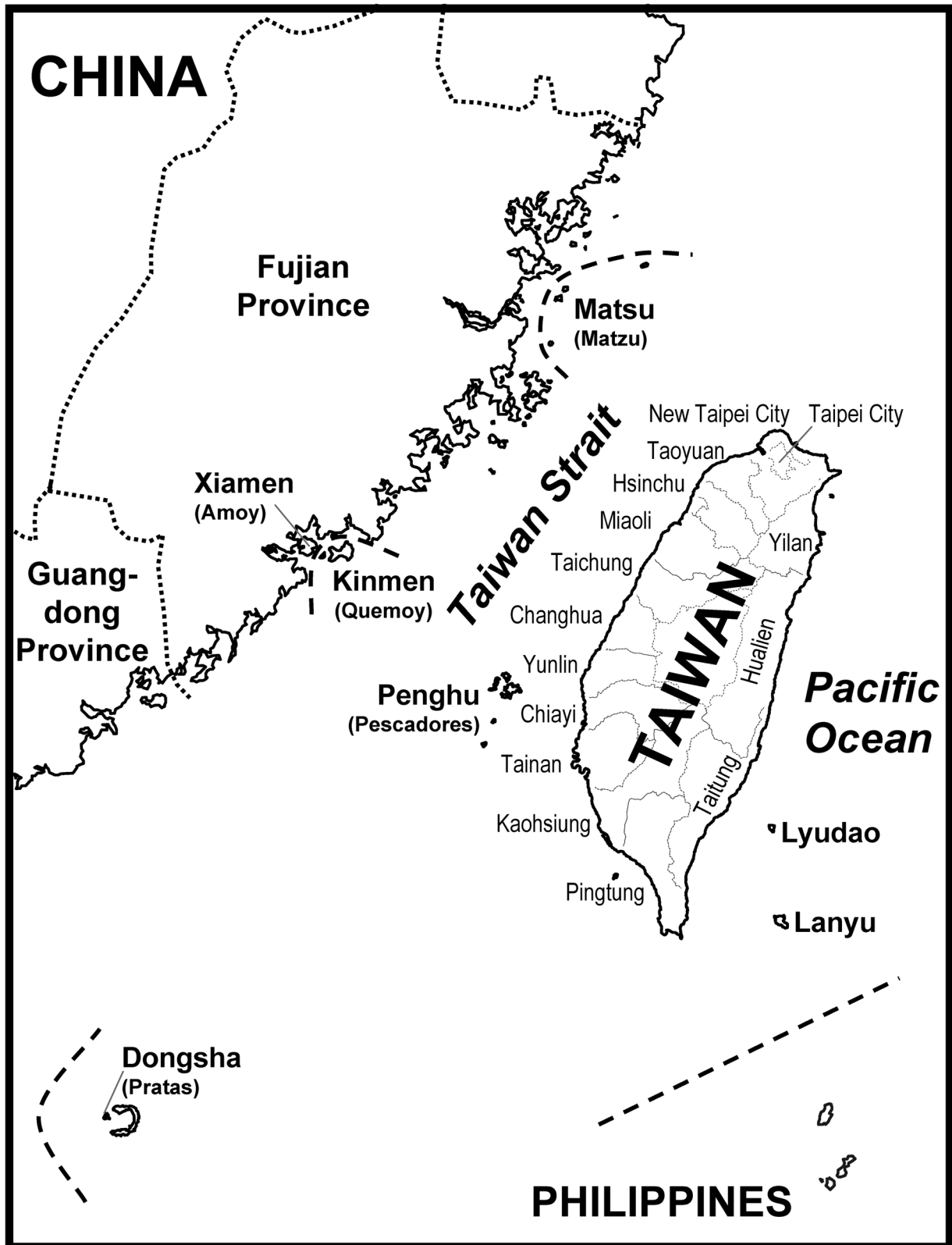


FIGURE 1. Taiwan and offshore islands, including Penghu, Kinmen, Matsu, Dongsha, Lanyu, and Lyudao.

Five species of *Uca* had been recorded from Taiwan before 1945, viz. *U. arcuata* (De Haan, 1835), *U. borealis* Crane, 1975, *U. crassipes* (White, 1847), *U. formosensis* Rathbun, 1921, and *U. lactea* (De Haan, 1835) (Maki & Tsuchiya 1923; Sakai 1939; Horikawa 1940; review by Shih 1994). The study of fiddler crabs then nearly stopped for about 40 years. Wang (1984) and Fukui *et al.* (1989) listed two new records, *U. triangularis* (A. Milne-

Edwards, 1873), and *U. perplexa* (H. Milne Edwards, 1837), respectively, from the Baoli River estuary, Pingtung. Huang *et al.* (1989) added two new records, *U. coarctata* (H. Milne Edwards, 1852), and *U. dussumieri* (H. Milne Edwards, 1852), from the same area, and Ho *et al.* (1993) recorded *U. tetragonon* (Herbst, 1790) from northern, eastern, and southern Taiwan. Shih (1994) revised the *Uca* species of Taiwan, compiling these records and related information of the ten species known from Taiwan. Although *U. acuta* (Stimpson 1858), has been recorded from Taiwan (Yamaguchi 1994), it is not confirmed and never collected again from the main island of Taiwan since Robert Swinhoe's collection in 1850s.

Uca jocelynae Shih, Naruse & Ng, 2010, was published recently, ranging from the islands of East Asia and Southeast Asia. Its type locality is Penghu Islands, central Taiwan Strait (Fig. 1; Shih *et al.* 2010a). *Uca splendida* (Stimpson, 1858), has been synonymized as *U. crassipes* since Crane (1975), but was reinstated by Shih *et al.* (2012). It is widely distributed from western Taiwan, southeastern China (including Hainan and Hong Kong), and Vietnam. The subgenus of the Taiwan endemic *U. formosensis* was established as new, *Uca (Xeruca)* Shih, 2015.

Shih *et al.* (2008) recorded *U. coarctata* from the Penghu Islands, showing that the *Uca* species of Penghu and the main island of Taiwan were the same. The *Uca* species from the small islands off Taiwan were nevertheless poorly known. Wang & Liu (1996b) collected *U. arcuata*, *U. borealis*, and *U. lactea* from Kinmen (Quemoy), and Shih (2012b) recorded *U. crassipes*, *U. jocelynae*, *U. perplexa*, *U. splendida*, and *U. tetragonon* from Dongsha (Pratas) Island, but no record from Matsu (Mazu) (Chen & Wu 2001; Ng *et al.* 2001).

The *Uca* species from Taiwan (including Penghu, Kinmen, Matsu and Dongsha) is herein revised, with the confirmation of three additional records for Taiwan. A key for the 18 species from East Asia is provided and the fiddler crabs from Japan (including the Ryukyus and Ogasawara Islands) are also briefly reviewed.

Material and methods

Specimens of fiddler crabs were collected from the coasts of main island of Taiwan, Penghu, Kinmen, Matsu, and Dongsha (Fig. 1). Additional specimens from the main islands of Japan and the Ryukyus were included. They were preserved in 70–95% alcohol after collection. Most specimens have been deposited in the Department of Life Science, National Chung Hsing University (NCHUZOO). The specimens deposited in British Museum of Natural History, London, UK (BM); National Museum of Natural Science, Taichung, Taiwan (NMNS); National Taiwan Museum, Taipei, Taiwan (TMCD); and Institute of Zoology, Academia Sinica, Taipei (ASIZ) were also examined. Measurements, in millimeters (mm), are of the carapace width (CW). The abbreviation G1 is used for the male first gonopod. The subgenera of fiddler crabs follow Ng *et al.* (2008), with an update from Shih *et al.* (2013) and Shih (2015). The synonymies listed for each species are mainly for the records from Taiwan and Japan.

Systematics

Family Ocypodidae Ortmann, 1894

Genus *Uca* Leach, 1814

Subgenus *Austruca* Bott, 1973

Uca (Austruca) lactea (De Haan, 1835)

(Fig. 2A, B)

Ocypode (Gelasimus) lactea De Haan, 1835: 54, pl. 15(5) [type locality: Japan].

Gelasimus lacteus—Stimpson 1858: 100; 1907: 108; Cano 1889: 92, 234; Sakai 1934: 320; 1939: 619, text-fig 93a–c, pl. 72(1); 1940: 32 [list]; Horikawa 1940: 28 [list]; Lin 1949: 26 [list].

Uca lactea—Parisi 1918: 92; Balss 1922: 143; Maki & Tsuchiya 1923: 211, pl. 24(9, 10); Sakai 1934: 320; 1935: 212, fig. 112, pl. 59(1); Miyake 1936: 511; Sakai 1939: 618; Takeda 1982: 209, 1 unnumbered fig.; Huang *et al.* 1989: 197, fig. 6, pl. 3D–F; Ho *et al.* 1993: 20 (part?); Okutani 1994b: 260, fig. 1; Yamaguchi 1994: 165; Wang & Liu 1996a: 58, 7 unnumbered figs.; Hung 2000: 140–1, figs. 434–435; Lee 2001: 103, 2 unnumbered figs.; Ng *et al.* 2001: 37 [list]; Yoshigou, 2001: 4, fig. 2, pl. 1L, M; Society of the Nature Records of Kagoshima 2002: 340, 3 unnumbered figs; Wang & Liu 2003: 79, figs.

77–83; Shen & Jeng 2005: 165, 1 unnumbered fig.; Liu & Wang 2010: 27, 39, 8 unnumbered figs.; Japanese Association of Benthology 2012: 215, 1 unnumbered fig., pl. 1(17); Shih 2012b: 14, figs. 12; Watanabe 2014: 103, 4 unnumbered figs. *Uca (Celuca) lactea lactea*—Crane 1975: 300, figs. 19A, 54J–JJ, 69E, pl. 40A, B; Sakai 1976a: 608, pl. 209(1) (part); Miyake 1983: 162, pl. 54(5); Wang 1984: 42; Dai et al. 1986: 425, fig. 236(1), pl. 59(2); Shih 1994: 103, figs. 68, 70, 71; Ho & Hung 1997: 61, 7 unnumbered figs. *Uca (Celuca) lactea*—Su & Lue 1984: 63, fig. 3; Dai & Yang 1991: 466, fig. 236(1), pl. 59(2). *Uca lactea lactea*—Fukui et al. 1989: 227; Chen 2001: 207, 2 unnumbered figs. *Uca (Paraleptuca) lactea*—Ng et al. 2008: 241 [list]; Toyota & Seki 2014: 225, 4 unnumbered figs. *Uca (Austruca) lactea*—Naderloo et al. 2010: 19, figs. 10a–f, 11a–c, 14a, 15a, 18a, b.

Material examined. Taiwan: 1 ♂ (13.1 mm), 1 ♀ (12.6 mm) (ASIZ), Lanyang R. estuary, Yilan (= Ilan), 25 July 2004; 1 ♂ (17.8 mm) (ASIZ), Lanyang R. estuary, Yilan, 27 July 2004; 2 ♀♀ (10.1, 11.1 mm) (NCHUZOOOL 14670), Lanyang R. estuary, Yilan, 5 Nov. 2011; 3 ♂♂ (10.2–13.7 mm), 2 ♀♀ (9.1, 9.7 mm) (NCHUZOOOL 14659), Hemei, New Taipei City, coll. H.-T. Shih, 20 Nov. 1995; 1 ♂ (18.4 mm) (NCHUZOOOL 14673), Jhuwei, New Taipei City, coll. H.-T. Shih, 30 June 2006; 3 ♂♂ (15.1, 16.0 mm, 1 broken), 2 ♀♀ (12.5, 13.5 mm) (NCHUZOOOL 14655), Wazaiwei, New Taipei City, coll. H.-T. Shih, 6 Nov. 1995; 2 ♂♂ (9.1, 16.1 mm), 2 ♀♀ (8.8, 11.3 mm) (NCHUZOOOL 14665), Wazaiwei, New Taipei City, coll. H.-T. Shih, 18 June 1996; 2 ♂♂ (10.0, 15.8 mm) (NMNS 003135-00035), Shezhidao, New Taipei City, coll. K.-S. Lee & H.-T. Hung, 12 Apr. 1999; 2 ♀♀ (10.0, 11.0 mm) (NCHUZOOOL 14666), Haishangu, Hsinchu City, coll. H.-T. Shih, 29 Apr. 1996; 2 ♂♂ (6.7, 11.1 mm), 2 ♀♀ (7.1, 9.1 mm) (NMNS 001737-00176), Houlong R. estuary, Miaoli, coll. P.-W. Hsueh, 7 Dec. 1992; 4 ♂♂ (4.7–12.2 mm) (NMNS 001737-00160), 2 ♂♂ (6.5, 11.3 mm), 2 ♀♀ (4.0, 11.5 mm) (NMNS 001737-00162), Dajia R. estuary, 9 Dec. 1993; 2 ♂♂ (5.7, 11.1 mm), 2 ♀♀ (9.2, 9.6 mm) (NMNS 001673-00010), Dajia R. estuary, 19 Jan. 1994; 1 ♂ (13.9 mm) (NCHUZOOOL 13216), Gaomei, Taichung, 14 June 2006; 1 ♂ (16.9 mm) (NCHUZOOOL 14657), Gaomei, Taichung, 10 Aug. 2007; 2 ♂♂ (11.9, 15.3 mm) (NMNS 003046-00057), Shengang, Changhua, coll. S.-M. Chao, 12 Nov. 1997; 1 ♂ (15.4 mm) (NCHUZOOOL 13213), Shengang, Changhua, coll. H.-T. Hung, 23 July 2003; 1 ♂ (13.9 mm), 3 ♂♂ (10.3–10.9 mm) (NCHUZOOOL 14669), coll. H.-T. Shih, 14 June 2014; 2 ♂♂ (11.3, 17.5 mm), 1 ♀ (9.1 mm), (NMNS 001491-00056), Bajhang R. estuary, Chiayi, coll. J.-D. Lee, 21 Oct. 1993; 3 ♂♂ (14.4–16.3 mm) (NCHUZOOOL 14667), Haomeiliao, Chiayi, 20 Sep. 2008; 1 ♂ (15.8 mm), 1 ♀ (13.2 mm) (NCHUZOOOL 14661), Dongshih Bridge, Chiayi, coll. H.-T. Shih, 6 Mar. 1996; 1 ♂ (15.8 mm), 1 ♀ (13.1 mm) (NCHUZOOOL 14660), Dongshih mangroves, Chiayi, coll. H.-T. Shih, 23 Apr. 1996; 3 ♂♂ (12.2–13.0 mm) (NCHUZOOOL 14643), Yanshuei R. estuary, Tainan, coll. J.-H. Lee et al., 4 Aug. 2009; 2 ♂♂ (16.4, 16.7 mm), 1 ♀ (13.8 mm) (NCHUZOOOL 14656), Cigu, Tainan, coll. H.-T. Shih, 21 Oct. 1996; 2 ♂♂ (16.0, 16.1 mm) (NCHUZOOOL 14664), Zengwen R. estuary, Tainan, coll. H.-T. Shih, 29 Mar. 1996; 1 ♀ (13.1 mm) (NCHUZOOOL 14640), Dapengwan, Pingtung, 20 July 2007. **Penghu Islands:** 2 ♂♂ (17.2, 18.9 mm) (NCHUZOOOL 14671), Cingluo, coll. H.-T. Shih, 14 Aug. 1996; 2 ♀♀ (15.6, 18.7 mm) (NCHUZOOOL 13489), Cingluo, coll. H.-T. Shih et al., 27 June 2006; 1 ♂ (16.9 mm) (NCHUZOOOL 14668), Cingluo, 18 Aug. 2009; 2 ♂♂ (19.3, 20.4 mm) (NCHUZOOOL 14662), Citou, coll. H.-T. Shih, 17 Aug. 1996; 1 ♂ (19.3 mm), 1 ♀ (14.3 mm) (NCHUZOOOL 14676), Chihsi, Siyu, coll. H.-T. Shih, 19 May 2007. **Kinmen Islands:** 2 ♂♂ (8.7, 13.7 mm) (NCHUZOOOL 13999), Wujiang R. estuary, J.-H. Lee, 30 Mar 2004; 3 ♂♂ (7.5–11.0 mm), 3 ♀♀ (8.5–10.6 mm), 3 juv. (NCHUZOOOL 13993), Wujiang R. estuary, H.-T. Shih & Y.-H. Wang, 7 Mar. 2008; 1 ♂ (14.4 mm), Wujiang R. estuary, coll. Y.-H. Wang, 16 Aug. 2011; 2 ♂♂ (10.0, 13.7 mm) (NCHUZOOOL 14746), Coastal Avenue, Lieyu, coll. P.-Y. Hsu, 23 June 2013. **Matsu Islands:** 3 ♂♂ (10.7–15.8 mm), 2 ♀♀ (11.7, 12.3 mm) (NCHUZOOOL 14609), Cingshuei, J.-H. Li, 9 July 2005; 2 ♂♂ (11.0, 14.9 mm) (NCHUZOOOL 14750), Jhuluo Harbor, Nangan, 29 Aug. 2011. **Main Japan islands:** 2 ♂♂ (15.9, 16.4 mm), 2 ♀♀ (17.1, 17.9 mm) (NCHUZOOOL 14658), Kotsuki R., Miyazaki, coll. H. Suzuki, 9 Oct. 2008.

Ecology. The male may build a hood to attract females during courtship (see Crane 1975).

Distribution. Main Japanese islands, Korea, China (including Hainan), Taiwan (including Penghu, Kinmen, Matsu), and Vietnam.

Remarks. *Uca lactea* and *U. perplexa* are sympatric in several regions of Taiwan, including Yilan, Tainan and Penghu (this study). Both species can be distinguished by a suite of characters. Anterolateral angles of *U. lactea* triangular (acute in *U. perplexa*); major pollex of *U. lactea* without or with small predistal triangular tooth in gape (with moderate to large predistal triangular tooth in *U. perplexa*); major dactylus of *U. lactea* arched throughout (arched only distally in *U. perplexa*); G1 of *U. lactea* with thumb long, reaching well beyond flange base, flange wider than long (with thumb moderately long, reaching flange base, flange wider than long in *U. perplexa*).

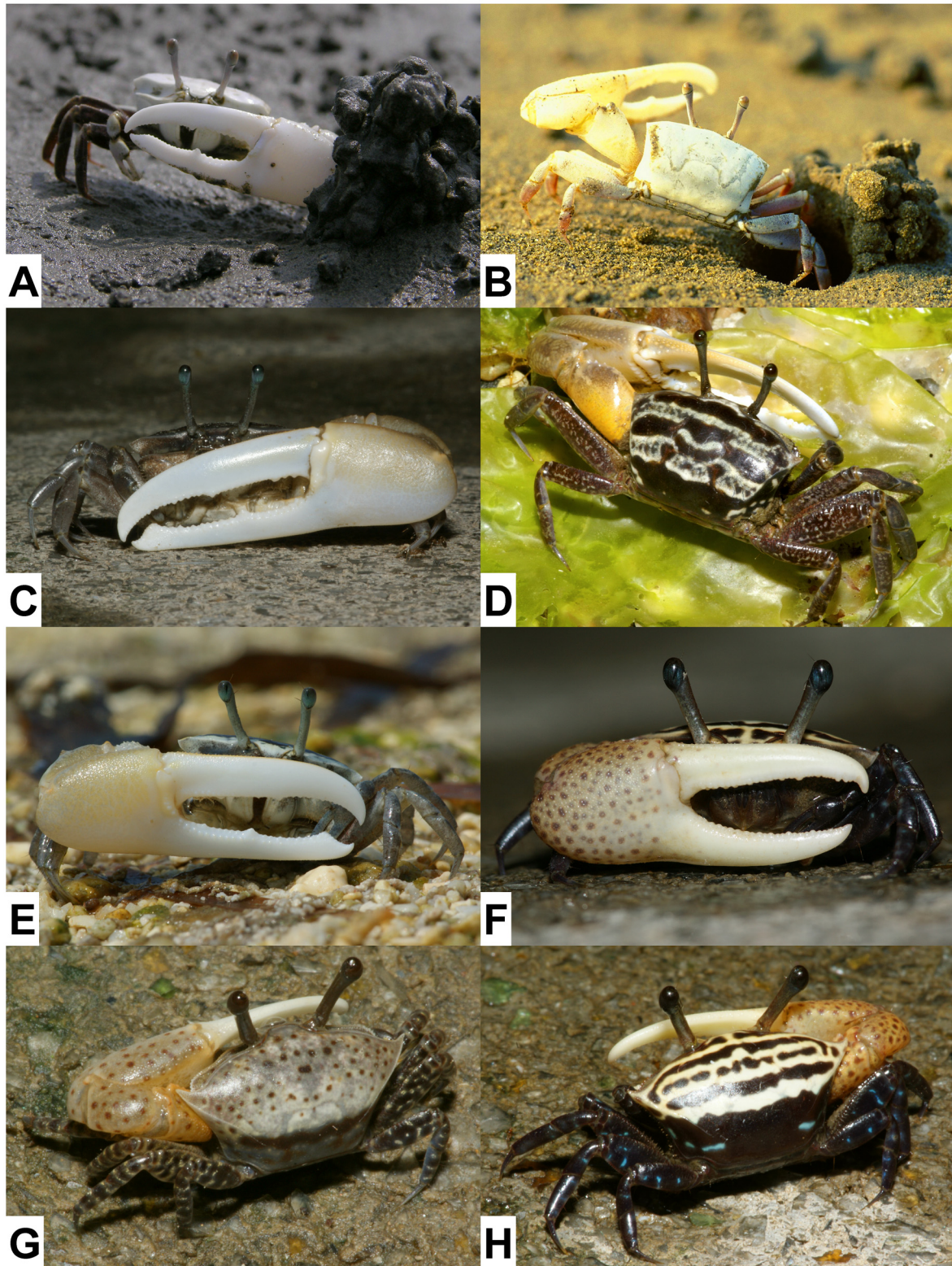


FIGURE 2. Species of the subgenus *Uca* (*Austruca*) from Taiwan. A, B, *Uca lactea* (De Haan, 1835), two males with hood from Gaomei, Taichung and Dongshih, Chiayi, respectively; C–E, *U. perplexa* (H. Milne Edwards, 1837), three males from the Yanshuei River estuary, Tainan (C), from Siyu, Penghu (D), and from Dongsha Island (E); F–H, *U. triangularis* (A. Milne-Edwards, 1873), males from the Yanshuei River estuary, Tainan.

Uca lactea is very common on the coasts of western Taiwan and Penghu, as well as Kinmen and Matsu. It is also found in Korea and the main islands of Japan. There are no records from northeastern China (north of Zhejiang; see Chen 1991; Shih *et al.* 2010b) and the Ryukyus (also see Remarks under *U. borealis*).

***Uca (Austruca) perplexa* (H. Milne Edwards, 1837)**

(Fig. 2C–E)

Gelasimus perplexus H. Milne Edwards 1852: 150, pl. 4(18) [type locality: Java].

Uca (Celuca) lactea perplexa—Crane 1975: 300, figs. 18D–F, 19B–H, 20A–C, 26D, 31E, 54K, 69C, pl. 39E–F; Miyake 1983: 163, pl. 55(1); Nagai & Nomura 1988: 55, 1 unnumbered fig.; Shih 1994: 103, figs. 69.

Uca (Celuca) lactea lactea—Sakai 1976a: 608 (part); Wang, 1984: 42 (not *Ocypode (Gelasimus) lactea* De Haan, 1835).

Uca lactea perplexa—Fukui *et al.* 1989: 227; Chen 2001: 208, 1 unnumbered fig.; Nakasone & Irei 2003: 269, fig. 31F.

Uca lactea—Ho *et al.* 1993: 20 (part?).

Uca perplexa—Ho *et al.* 1993: 20; Okutani 1994a: 214, fig. 1; Yamaguchi 1994: 165; Wang & Liu 1996a: 61, 2 unnumbered figs.; Hung 2000: 140-1, figs. 438–439; Lee 2001: 103, 3 unnumbered figs.; Ng *et al.* 2001: 37 [list]; Yoshigou 2001: 4, fig. 2, pl. 1N; Wang & Liu 2003: 82, figs. 84–86; Shen & Jeng 2005: 166, 1 unnumbered fig.; Katsu 2007: 92, 5 unnumbered figs.; Liu & Wang 2010: 41, 3 unnumbered figs.; Shih 2012b: 66, figs. 94–96; Fujita & Uyeno 2015: 95, fig. 2A, B.

Uca (Paraleptuca) perplexa—Ng *et al.* 2008: 241 [list]; Toyota & Seki 2014: 226, 4 unnumbered figs.

Uca (Austruca) perplexa—Naderloo *et al.* 2010: 24, figs. 16a–g, 17a, b, 18c–f.

Material examined. Taiwan: 1 ♂ (13.5 mm) (NCHUZOOOL 14647), Lanyang R. estuary, Yilan, 25 July 2004; 4 ♂♂ (16.6–17.6 mm) (NCHUZOOOL 14677), 1 ♀ (13.7 mm) (NCHUZOOOL 14643), Yanshuei R. estuary, Tainan, coll. J.-H. Lee *et al.*, 4 Aug. 2009; 2 ♂♂ (14.4, 15.6 mm), 1 ♀ (14.5 mm) (NCHUZOOOL 14637), Dingtouer Shoal, Cigu, Tainan, coll. J.-H. Lee, 14 Aug. 2009; 2 ♂♂ (14.3, 17.2 mm), 1 ♀ (15.7 mm) (NCHUZOOOL 14645), Gaoping R. estuary, Kaohsiung, coll. H.-T. Shih, 29 Apr. 1998; 1 ♂ (14.5 mm), 1 ♀ (12.0 mm) (NCHUZOOOL 14640), Dapengwan, Pingtung, 20 July 2007; 2 ♂♂ (9.3, 11.8 mm), 1 ♀ (12.9 mm) (NCHUZOOOL 13252), 1 ♂ (10.6 mm) (NCHUZOOOL 13253), Baoli R. estuary, Pingtung, coll. H.-T. Shih, 7 July 2001; 1 ♂ (14.0 mm), 1 ♀ (12.1 mm) (NCHUZOOOL 14641), Fengcuesha, Kenting, Pingtung, 18 May 2001; 3 ♂♂ (14.2–17.2 mm) (NTOU), Dulanwan, Taitung, coll. P.-H. Ho, 7 Apr. 2001. **Penghu Islands:** 1 ♂ (20.7 mm) (NCHUZOOOL 14662), Citou, coll. H.-T. Shih, 17 Aug. 1996; 1 ♂ (15.1 mm) (NCHUZOOOL 14675), Shiheyan, 21 June 2006; 2 ♂♂ (13.3, 16.5 mm) (NCHUZOOOL 14639), Chihsi, Siyu, 18 May 2007; 3 ♂♂ (15.8–16.4 mm) (NCHUZOOOL 14649), Chihsi, Siyu, 19 May 2007. **Dongsha Island:** 3 ♂♂ (12.2–17.5 mm), 2 ♀♀ (10.4, 15.1 mm), coll. C.-Y. Chung & Y.-H. Huang, 7 June 2011; 1 ♂ (16.6 mm) (NCHUZOOOL 14651), 19 Nov. 2011; 1 ♂ (17.6 mm) (NCHUZOOOL 14644), 26 May 2012. **Ryukyus:** 1 ♂ (15.8 mm) (NCHUZOOOL 14652), Oura Bay, Okinawa, 13 Nov. 1975; 3 ♂♂ (9.6–15.1 mm), 1 ♀ (7.9 mm) (NCHUZOOOL 14654), Yuhi R., Okinawa, 19 Mar. 1992; 1 ♂ (7.1 mm), 2 ♀♀ (6.5, 10.6 mm) (NCHUZOOOL 14650), Okinawa, 9 July 2009; 4 ♂♂ (11.0–14.2 mm) (NCHUZOOOL 14642), Sashiki, Okinawa, 28 Dec. 2011; 2 ♂♂ (13.4, 16.2 mm) (NCHUZOOOL 14752), Nagura, Ishigaki, coll. T. Naruse, 23 June 2004.

Distribution. Widely distributed in the western Pacific (Ryukyus, Taiwan [including Penghu and Dongsha], Philippines, New Guinea, Australia, New Caledonia, Indonesia, Borneo, Peninsular Malaysia, Thailand, Cambodia), eastern Indian Ocean (Nicobar Islands), western and central Pacific Ocean.

Remarks. See Remarks under *U. lactea* for the morphological comparison between *U. lactea* and *U. perplexa*, and Discussion for the distribution of *U. perplexa* in Japan.

***Uca (Austruca) triangularis* (A. Milne-Edwards, 1873)**

(Fig. 2F–H)

Gelasimus triangularis A. Milne-Edwards, 1873: 275 [type locality: New Caledonia].

Uca (Celuca) triangularis triangularis—Crane 1975: 290, figs. 50, 51, 59B, C, 68D, E, pl. 38F–L; Sakai 1976a: 607, text-fig. 333; Wang 1984: 42; Dai *et al.* 1986: 427, fig. 237(1–3), pl. 59(4); Shih 1994: 100, fig. 67.

Uca triangularis—Takeda 1982: 208, 1 unnumbered fig.; Fukui *et al.* 1989: 227, fig. 4; Huang *et al.* 1989: 192, fig. 1, pl. 1A–D; Ho *et al.* 1993: 20; Yamaguchi 1994: 178, fig. 13; Wang & Liu 1996a: 56, 2 unnumbered figs.; Hung 2000: 140-1, figs.

426–427; Ng *et al.* 2001: 37 [list]; Yoshigou 2001: 4, fig. 2, pl. 1K; Shen & Jeng 2005: 169, 2 unnumbered figs.; Liu & Wang 2010: 44, 2 unnumbered figs.; Japanese Association of Benthology 2012: 216, 1 unnumbered fig.; Fujita & Uyeno 2015: 99, fig. 4C, D.

Uca (Celuca) triangularis—Dai & Yang 1991: 467, fig. 237, pl. 59(4).

Uca triangularis triangularis—Nakasone & Irei 2003: 269, fig. 31A, B, D.

Uca (Paraleptuca) triangularis—Ng *et al.* 2008: 241 [list]; Toyota & Seki 2014: 227, 4 unnumbered figs.

Material examined. Taiwan: 2 ♂♂ (10.2, 11.5 mm), 1 ♀ (11.9 mm) (NCHUZOOOL 14709), Lanyang R. estuary, Yilan, 25 July 2004; 3 ♂♂ (11.4–13.0 mm) (NCHUZOOOL 14745), Yanshuei R. estuary, Tainan, 4 Aug. 2009; 1 ♀ (8.7 mm) (NCHUZOOOL 14711), Yanshuei R. estuary, Tainan, 18 Oct. 2011; 2 ♂♂ (9.1, 12.5 mm), 2 ♀♀ (8.8, 12.3 mm) (NCHUZOOOL 14710), Baoli R. estuary, Pingtung, 14 Sep. 1997; 1 ♂ (13.2 mm), 1 ♀ (5.2 mm) (NCHUZOOOL 14712), Baoli R. estuary, Pingtung, 20 July 2011; 5 ♂♂ (5.3–11.0 mm), 6 ♀♀ (5.0–8.4 mm), 3 juv. (TMCD), Beijyunjei, Taitung, 24 Apr. 1993.

Distribution. Western Pacific (Ryukyus, Taiwan [including Penghu], Guangdong in China, Philippines, Borneo, Indonesia, New Guinea).

Subgenus *Gelasimus* Latreille, 1817

Uca (Gelasimus) borealis Crane, 1975

(Fig. 3A–D)

Uca marionis—Maki & Tsuchiya 1923: 107, pls. 23(6), 24(8).

Uca marionis nitidus—Sakai 1935: 213, pl. 58(3).

Gelasimus marionis nitidus—Sakai 1934: 319; Horikawa 1940: 28 [list]; Sakai 1940: 32 [list]; Lin 1949: 27 [list]

Uca (Thalassuca) vocans borealis Crane, 1975: 90, figs. 64A, 99 [type locality: Hong Kong]; Su & Lue 1984: 63; Dai *et al.* 1986: 424, pl. 58(8); Dai & Yang 1991: 464, pl. 58(8); Shih 1994: 86, figs. 60–62; Ho & Hung 1997: 59, 4 unnumbered figs.

Uca (Thalassuca) vocans vocans—Sakai 1976a: 605 (part); Su & Lue 1984: 64, fig. 6 (not *Cancer vocans* Linnaeus, 1758).

Uca vocans borealis—Fukui *et al.* 1989: 227; Chen 2001: 203, 2 unnumbered figs. (part).

Uca borealis—Huang *et al.* 1989: 198, fig. 7, pl. 4A–C; Wang & Liu 1996a: 52, 7 unnumbered figs.; Hung 2000: 140–1, 2 unnumbered figs. (part); Lee 2001: 102 (part); Ng *et al.* 2001: 37 [list]; Wang & Liu 2003: 75, figs. 71–73; Shen & Jeng 2005: 158, 2 unnumbered figs. (part); Liu & Wang 2010: 32, 3 unnumbered figs.

Uca (Gelasimus) borealis—Ng *et al.* 2008: 240 [list]; Toyota & Seki 2014: 231, 1 unnumbered fig.

Material examined. Taiwan: 1 ♂ (18.1 mm) (NCHUZOOOL 13169), Yilan, coll. S. Huang, 31 May 1996; 1 ♂ (26.6 mm) (NCHUZOOOL 13170), Yilan, coll. S. Huang, 31 May 1996; 1 ♂ (22.0 mm) (NCHUZOOOL 13208), Wazaiwei, New Taipei City, coll. H.-T. Shih, 17 Nov. 1995; 3 ♂♂ (15.4–22.3 mm), 1 ♀ (18.4 mm), 2 ovig. ♀♀ (14.8, 17.9 mm) (NCHUZOOOL 13209), Wazaiwei, New Taipei City, coll. H.-T. Shih, 18 June 1996; 1 ♂ (18.4 mm), 1 ♀ (14.2 mm) (TMCD CHCD 227), Haishangu, Hsinchu, 16 Mar. 1991; 1 ovig. ♀ (19.9 mm) (TMCD CHCD 29), Haishangu, Hsinchu, 22 Mar. 1991; 1 ♂ (16.1 mm) (NCHUZOOOL 14743), 1 ♂ (23.6 mm) (NCHUZOOOL 14744), Haishangu, Hsinchu, coll. H.-T. Shih, 11 July 1998; 2 ♂♂ (19.4, 23.7 mm) (NCHUZOOOL 14740), Houlong R. estuary, Miaoli, 30 May, 2014; 1 ♂ (26.2 mm) (NCHUZOOOL 14742), Gaomei, Taichung, 22 Sep. 2006; 3 ♂♂ (18.3–29.5 mm), 1 ovig. ♀ (16.9 mm) (TMCD CHCD 1237), Shengang, Changhua, coll. H.-C. Liu, 4 June 1996; 4 ♂♂ (14.1–20.9 mm) (TMCD CHCD 391), Santiaolun, Yunlin, coll. H.-C. Liu, 24 May 1994; 1 ♂ (25.1 mm), 1 ovig. ♀ (22.2 mm) (TMCD), Haomeiliao, Budai, Chiayi, coll. C.-H. Wang, 13 July 1996; 4 ♂♂ (18.4–22.7 mm) (NCHUZOOOL 14741), Yanshuei R. estuary, Tainan, 4 Aug. 2009; 1 ♂ (24.5 mm) (NCHUZOOOL 14737), Yanshuei R. estuary, Tainan, 26 Apr. 2014; 1 ♂ (26.5 mm) (NCHUZOOOL 13220), Cigu, Tainan, coll. H.-T. Shih, 31 May 1996; 2 ♂♂ (12.5, 13.1 mm), 1 ♀ (16.1 mm), 1 ovig. ♀ (13.7 mm) (NCHUZOOOL 14739), Dingtouer Shoal, Cigu, Tainan, coll. J.-H. Lee, 14 Aug. 2009; 1 ♂ (22.6 mm) (NCHUZOOOL 13173), 1 ♂ (17.9 mm) (NCHUZOOOL 13174), Gaoping R. estuary, Kaohsiung, coll. H.-T. Shih, 29 Apr. 1998. **Penghu Islands:** 1 ♂ (27.1 mm) (NCHUZOOOL 13178), Cingluo, coll. H.-T. Shih, 15 Aug. 1996; 1 ♀ (18.6 mm) (NCHUZOOOL 14725), Citou, coll. H.-T. Shih *et al.*, 11 Aug. 2010; 1 ♀ (15.4 mm) (NCHUZOOOL 14722), Chihsi, Siyu, coll. H.-T. Shih *et al.*, 12 Aug. 2010. **Kinmen Islands:** 6 ♂♂ (17.0–27.0 mm), 2 ♀♀ (18.5, 20.3 mm) (TMCD CHCD 853), Wujiang R. estuary, coll. H.-C. Liu & C.-H. Wang, 9–12 Oct. 1995; 2 ♂♂ (21.4, 27.7 mm), 2 ♀♀ (16.8, 17.8 mm) (NCHUZOOOL

13991), Wujiang R. estuary, coll. J.-H. Lee, 30 May 2004; 1 ♂ (29.8 mm), 1 ovig. ♀ (23.1 mm) (NCHUZOOL 14601), Wujiang R. estuary, coll. Y.-H. Wang, 16 Aug, 2011; 4 ♂♂ (18.8–26.6 mm) (NCHUZOOL 14000), Mashan, Jinsha, coll. Y.-H. Wang, 17 Aug. 2011; 2 ♂♂ (22.3, 28.1 mm), 2 ♀♀ (18.9, 20.0 mm), 1 ovig. ♀ (19.4 mm) (TMCD CHCD 874), Yangcuo, Lieyu, coll. H.-C. Liu & C.-H. Wang, 10 Oct. 1995; 3 ♂♂ (9.3–19.5 mm), 2 ♀♀ (10.8, 17.3 mm) (NCHUZOOL 14751), Coastal Avenue, Lieyu, coll. P.-Y. Hsu, 23 June 2013. **Matsu Islands:** 2 ♂♂ (12.9, 26.9 mm), 1 ♀ (20.1 mm), 1 ovig. ♀ (20.1 mm) (NCHUZOOL 13165), Cingshuei, coll. J.-H. Li, 9 July 2005; 2 ♂♂ (10.8, 18.2 mm) (NCHUZOOL 14750), Jhuluo Harbor, Nangan, 29 Aug. 2011. **Main Japan islands:** 2 ♂♂ (23.5, 24.1 mm), 2 ♀♀ (15.4, 20.6 mm) (NCHUZOOL 13297), Hitotsuba Inlet, Miyazaki, coll. H. Suzuki, 11 Oct. 2008.

Distribution. Main Japanese islands, Taiwan (including Penghu, Kinmen, Matsu), China (including Hainan), and Vietnam.

Remarks. We confirm herein that there are three species of *U. vocans* species complex, viz. *U. borealis*, *U. jocelynae* and *U. vocans*, in Taiwan. Two or three species are sympatric in some localities, e.g. *U. borealis* and *U. jocelynae* (Yilan and Tainan); *U. jocelynae* and *U. vocans* (Pingtung [Hengchun Peninsula] and Taitung); and three species (Pingtung [Dapengwan] and Penghu).

The most reliable characters used to separate the three species are the shape of the dactylus and pollex of the major cheliped (Fig. 3A, C, E, G). Major cheliped of *Uca borealis* with pollex having a deep proximal depression and a shallow or without distal depression in gape, distal tooth small, dactylus slightly deeper than pollex only in young; *U. jocelynae* with pollex having a shallow proximal and a deep distal depressions in gape, distal tooth triangular, moderately large, dactylus deeper than pollex, especially basal half; *U. vocans* with pollex having both deep proximal and distal depressions in gape, distal tooth triangular, large, dactylus not deeper than pollex.

While the G1 of male is also a useful character to separate the three species (see Crane 1975: table 3, fig. 64A, B, F), it is difficult to identify the females by the external morphologies, although the morphologies of their vulvae (gonopores) are different (Crane 1975: table 3, fig. 64AA, BB, FF).

With regard to *U. borealis* from the main islands of Japan (Fig. 3C–D; Shih *et al.* 2010a), the morphologies of major chela and G1 (Fig. 3C, D) agree well with the characters of this species (Fig. 3A; Crane 1975; Shih *et al.* 2010a). Yamashita & Yamanishi (1999: fig. 9) reported *U. vocans* from Osaka Bay, but the chela of the young male specimens is more similar to *U. borealis*. It is noteworthy that there are no records of *U. borealis* from the Ryukyus. Such discontinued distribution is similar to *U. lactea* (see Remarks under *U. lactea*). The northern limit of distribution of *Uca borealis* in continental Asia is Fujian, China, but it is absent in other northern locations, including Korea (Shih *et al.* 2010b; this study). It is worthy studying the factors affecting the larval dispersal of the two species in this northern region of the East China Sea.

Uca (Gelasimus) jocelynae Shih, Naruse & Ng, 2010 (Fig. 3E, F)

Uca (Gelasimus) jocelynae Shih, Naruse & Ng, 2010a: 51, figs. 2–4 [type locality: Penghu, Taiwan]; Shih 2012b: 64, figs. 90–93; Toyota & Seki 2014: 221, 4 unnumbered figs. (see Shih *et al.* 2010a for list of citation of synonyms)
Uca jocelynae—Shih 2012b: 64, figs. 90–93; Fujita & Uyeno 2015: 98, fig. 3D–F.

Material examined. (See Shih *et al.* 2010a for specimens from Taiwan [including Penghu] and the Ryukyus) **Dongsha Island:** 1 ♂ (16.2 mm) (NCHUZOOL 14735), 1 ♂ (14.1 mm) (NCHUZOOL 14736), 3 Sep. 2011; 2 ♂♂ (14.9, 15.0 mm) (NCHUZOOL 14728), 19 Nov. 2011; 1 ♂ (18.1 mm) (NCHUZOOL 14729), 23 Mar. 2012; 1 ♂ (11.8 mm) (NCHUZOOL 14730), 24 Mar. 2012; 1 ♂ (17.5 mm) (NCHUZOOL 14734), 26 May 2012.

Distribution. Widely distributed on the western Pacific islands (Ryukyus, Taiwan [including Penghu and Dongsha], Guam, the Philippines, Sulawesi, Papua New Guinea, and Vanuatu).

Remarks. *Uca jocelynae* is found in the western part (west to Vanuatu) of the western Pacific, in contrast to the range of its sister species *U. neocultrimana* (east to Fiji) (Shih *et al.* 2010a: fig. 1). See Remarks under *U. borealis* for the morphological comparison of the three species of the *U. vocans* complex.

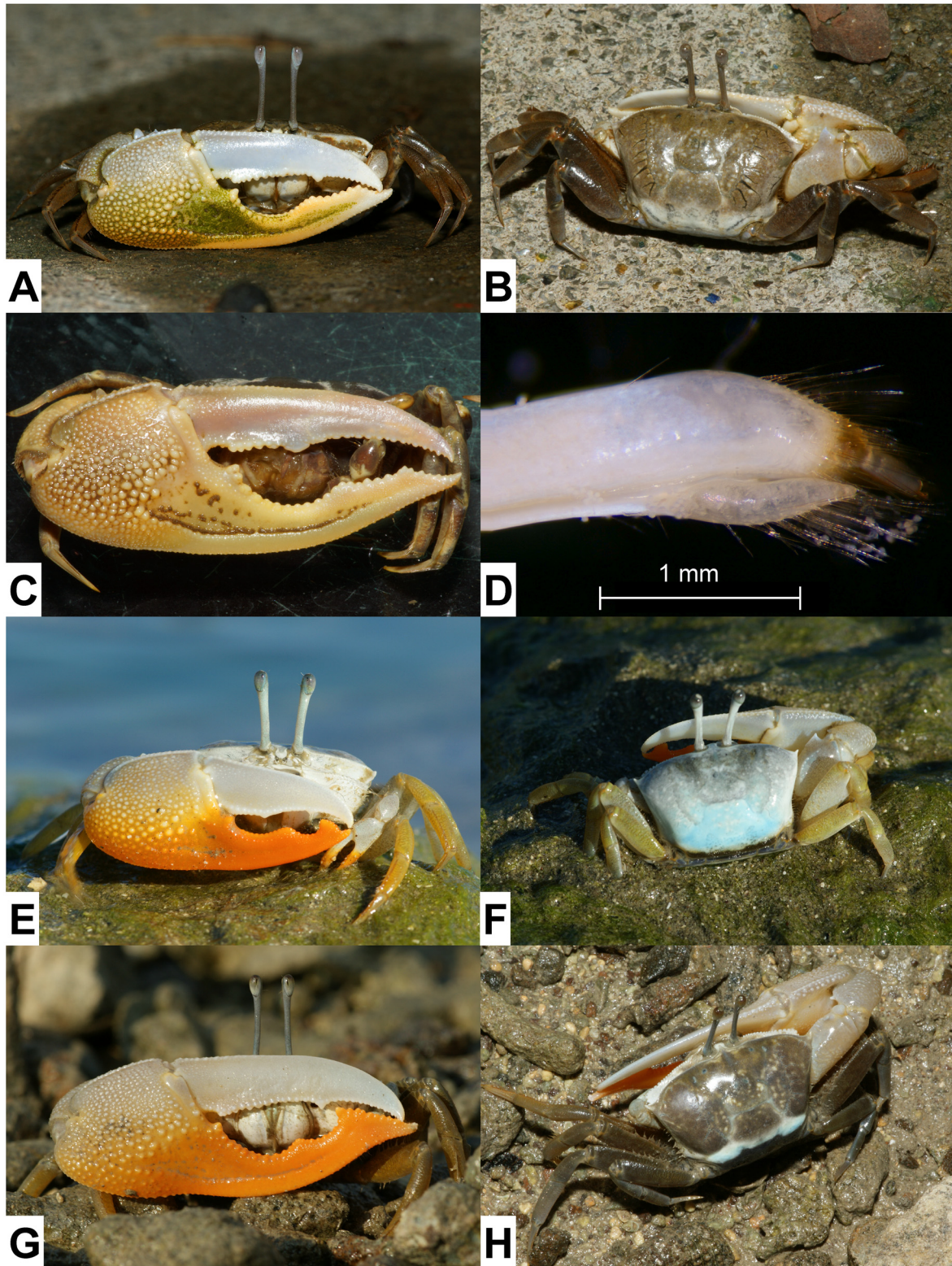


FIGURE 3. Species of the subgenus *Uca* (*Gelasimus*). A, B, *Uca borealis* Crane, 1975, male from Yanshuei River estuary, Tainan, Taiwan; C, *U. borealis*, male from Miyazaki, Japan, with G1 (D); E, F, *U. jocelynae* Shih, Naruse & Ng, 2010, males from Siyu, Penghu, Taiwan; G, H, *U. vocans* (Linnaeus, 1758), males from Cingluo, Penghu, Taiwan.

Uca (Gelasimus) tetragonon (Herbst, 1790)

(Fig. 4A, B)

Cancer tetragonon Herbst, 1790: 257, pl. 20(110) [type locality: Egypt].

Uca (Thalassuca) tetragonon—Crane 1975: 77, figs. 37D, 63A, B, 81F, 82E, 99, pl. 13; Sakai 1976a: 605, text-fig. 332a; Nagai & Nomura 1988: 53, 1 unnumbered fig.; Shih 1994: 78, figs. 51–55.

Uca tetragonon—Takeda 1973: 9, fig. 1; Takeda 1982: 208, 1 unnumbered fig.; Ho *et al.* 1993: 18, figs. 2, 3, 4d; Okutani 1994a: 214, figs. 4; Yamaguchi 1994: 177, 184; Wang & Liu 1996a: 48, 3 unnumbered figs.; Hung 2000: 140-1, figs. 430–431; Chen 2001: 205, 2 unnumbered figs.; Ng *et al.* 2001: 37 [list]; Yoshigou 2001: 4, fig. 2, pl. 1F, G; Nakasone & Irei 2003: 269, fig. 30; Wang & Liu 2003: 84, figs. 87–89; Shen & Jeng 2005: 167, 2 unnumbered figs.; Katsu 2007: 84, 9 unnumbered figs.; Liu & Wang 2010: 42, 3 unnumbered figs.; Japanese Association of Benthology 2012: 215, 1 unnumbered fig.; Shih 2012b: 70, figs. 99–101; Fujita & Uyeno 2015: 95, fig. 2C, D.

Uca (Gelasimus) tetragonon—Ng *et al.* 2008: 240 [list]; Toyota & Seki 2014: 222, 4 unnumbered figs.

Material examined. Taiwan: 2 ♂♂ (10.6, 25.2 mm), 1 ♀ (13.1 mm), 1 ovig. ♀ (18.1 mm), 1 juv. (7.2 mm) (TMCD CHCD 476), Houwan, Pingtung, coll. H.-C. Liu, 2 Aug. 1994; 2 ♂♂ (15.0, 18.9 mm), 5 ♂♂ (12.1–20.8 mm) (TMCD CHCD 491), 4 Aug. 1994; 3 ♂♂ (13.8–24.3 mm) (NCHUZOOL 14701), Wanlitong, Pingtung, coll. S.-H. Han, Oct. 1966; 2 ♂♂ (12.8, 13.6 mm), 1 ♀ (12.4 mm) (TMCD CHCD 526), Wanlitong, Pingtung, coll. H.-C. Liu & C.-H. Wang, 23 Sep. 1994; 2 ♂♂ (21.7, 23.5 mm), NCHUZOOL 14687, Wanlitong, Pingtung, coll. J.-H. Lee, 20 Aug. 2009; 3 ♂♂ (11.6–16.7 mm), 1 ♀ (16.4 mm) (TMCD), Beijyunjei, Taitung, 21 Apr. 1993; 2 ♂♂ (25.8, 30.2 mm) (NCHUZOOL 14696), Dulanwan, Taitung, 7 Apr. 2001; 4 ♂♂ (11.1–23.7 mm), 2 ♀♀ (9.7, 12.2 mm), 5 ovig. ♀♀ (16.7–23.8 mm) (NCHUZOOL 14695), 1 ♀ (17.0 mm) (NCHUZOOL 13666), Shanyuan, Taitung, coll. W.-C. Wang, 29 May 2004; 3 ♂♂ (18.4–23.6 mm), 1 ♀ (9.2 mm) (NCHUZOOL 14697), Shanyuan, Taitung, 27 July 2014; 1 ♀ (14.3 mm) (NCHUZOOL 14693), Dulanwan, Taitung, coll. H.-T. Hung, 2 Sep. 2004.

Penghu Islands: 1 ♂ (26.1 mm) (NCHUZOOL 13304), Citou, coll. H.-T. Shih, 17 Aug. 1996; 1 ovig. ♀ (26.9 mm) (NCHUZOOL 14686), Chihsi, Siyu, coll. H.-T. Shih, 19 May 2007. **Dongsha Island:** 1 ♂ (26.2 mm) (NCHUZOOL 14678), 1 ♂ (32.3 mm) (NCHUZOOL 14699), coll. Y.-C. Yang, 15 June 1997; 2 ♂♂ (21.3, 25.0 mm) (NCHUZOOL 14689), coll. D.-C. Jiang & J.-C. Fan-Jiang, 12 Sep. 2008; 3 ♂♂ (25.0–31.7 mm), 2 ♀♀ (18.5, 31.4 mm), 1 ovig. ♀ (25.6 mm) (NCHUZOOL 14688), coll. C.-Y. Chung & Y.-H. Huang, 7 June 2011; 1 ♂ (28.2 mm) (NCHUZOOL 14692), 3 Sep. 2011; 1 ♀ (31.0 mm) (NCHUZOOL 14684), 19 Nov. 2011; 1 ♂ (19.5 mm) (NCHUZOOL 14728), 19 Nov. 2011; 2 ♂♂ (18.3, 26.6 mm) (NCHUZOOL 13664), coll. H.-T. Shih, 22 Mar. 2012; 1 ♂ (21.4 mm) (NCHUZOOL 14694), coll. H.-T. Shih, 23 Mar. 2012; 1 ♂ (19.1 mm) (NCHUZOOL 14702), coll. H.-T. Shih, 24 Mar. 2012; 1 ♂ (29.0 mm) (NCHUZOOL 14698), 22 Sep. 2012. **Ryukyus:** 5 ♂♂ (19.1–26.9 mm), 2 ♀♀ (25.1, 26.9 mm) (TMCD 2739), Ootomo, Iriomote, coll. H. Ota, 26 Oct. 1991.

Distribution. Western Pacific (Ryukyus, Taiwan [including Penghu and Dongsha], Hainan in China, Philippines, Malay Peninsula, Borneo, Indonesia, New Guinea, Australia), Central and South Pacific, and Indian Ocean (Thailand, Middle East, East Africa).

Remarks. The species is common in eastern and southern Taiwan, as well as on the offshore islands of Penghu and Dongsha with habitats being mainly composed of coarse sand adjacent to coral reefs (Ho *et al.* 1993; Shih 2012b).

Uca (Gelasimus) vocans (Linnaeus, 1758)

(Fig. 3G, H)

Uca (Thalassuca) vocans vocans—Crane 1975: 92, figs. 38I, L, 56B, 60C–E, 64F, FF, pl. 14E–H; Sakai 1976a: 605, pl. 208(3) (part); Miyake 1983: 163, pl. 55(2); Dai *et al.* 1986: 423, fig. 234(1, 2), pl. 58(7); Nagai & Nomura 1988: 52, 1 unnumbered fig.; Dai & Yang 1991: 463, fig. 234, pl. 58(7).

Uca vocans—Takeda 1982: 207, 1 unnumbered fig.; Okutani 1994a: 214, fig. 5; Yamaguchi 1994: 181; Yoshigou 2001: 4, fig. 2, pl. 1H; Japanese Association of Benthology 2012: 216, 1 unnumbered fig.; Fujita & Uyeno 2015: 96, fig. 3A–C.

Uca borealis—Hung 2000: 140-1, figs. 428–429, 1 unnumbered figs. (part); Shen & Jeng 2005: 157, 1 unnumbered figs. (part) (not *Uca borealis* Crane, 1975).

Uca vocans vocans—Nakasone & Irei 2003: 269, fig. 31E; Katsu 2007: 94, 6 unnumbered figs.

Uca (Gelasimus) vocans—Ng *et al.* 2008: 240 [list]; Toyota & Seki 2014: 223, 4 unnumbered figs.

Material examined. **Taiwan:** 1 ovig. ♀ (19.2 mm) (NCHUZOO 14723), Yanshuei R. estuary, Tainan, 7 Apr. 2011; 1 ♂ (15.7 mm) (NCHUZOO 13168), Dapengwan, Pingtung, coll. H.-T. Shih, 9 Jan. 2001; 1 ♂ (12.7 mm) (TMCD CHCD 477), Houwan, Pingtung, coll. H.-C. Liu, 2 Aug. 1994; 1 ♂ (20.4 mm) (TMCD CHCD 792), Dulanwan, Taitung, 22 Apr. 1994. **Penghu Islands:** 5 ♂♂ (21.6–24.1 mm) (NCHUZOO 14733), Cingluo, 18 Aug. 2009; 1 ♀ (18.8 mm) (NCHUZOO 14724), Caiyuan, 11 Aug. 2010; 1 ♂ (24.2 mm) (TMCD CHCD 1516), Chihsi, Siyu, coll. H.-C. Liu, 6 Oct. 1997; 2 ♂♂ (16.4, 28.1 mm) (NCHUZOO 14731), Chihsi, Siyu, Penghu, coll. H.-T. Shih *et al.*, 28 June 2006; 2 ♂♂ (9.0, 26.1 mm) (NCHUZOO 14732), Chihsi, Siyu, Penghu, 11 Nov. 2007. **Ryukyus:** 4 ♂♂ (17.3–20.6 mm, 1 broken) (TMCD CHCD 711), Amami, coll. H.-C. Liu, 14 July 1995; 7 ♂♂ (11.4–19.1 mm), 5 ♀♀ (14.2–16.6 mm) (NCHUZOO 14706), Sashiki, Okinawa, 28 Dec. 2011; 4 ♂♂ (11.7–15.3 mm), 1 ♀ (17.5 mm), TMCD, Ishikawa, Yamada, Okinawa, 18 Mar. 1992; 13 ♂♂ (8.4–21.1 mm), 1 ♀ (13.5 mm), TMCD, Ishikawa, Yamada, Okinawa, 17 Apr. 1992; 3 ♂♂ (11.4–18.0 mm) (NCHUZOO 14708), Okukubi R., Okinawa, coll. T. Naruse, 25 Feb. 2002; 1 ♂ (11.6 mm) (NCHUZOO 14704), Yabuchi I., Okinawa, 29 May 2014; 6 ♂♂ (14.9–22.6 mm), 1 ♀ (19.6 mm) (TMCD CHCD 695), Nagura Bay, Ishigaki, coll. H.-C. Liu, 13 July 1995; 1 ♂ (22.1 mm), TMCD, Iriomote, coll. K. Wada, 17 Oct. 1982.

Distribution. Western Pacific and eastern Indian Ocean (Ryukyus, Taiwan [including Penghu] Hainan in China, Philippines, Borneo, Indonesia, Malay Peninsula, Thailand, Myanmar).

Remarks. See Remarks under *U. borealis* for a morphological comparison of the three species of *U. vocans* complex. And see Discussion for the distribution of *U. vocans* in Taiwan and Japan. This is a new record for Taiwan.

Subgenus *Paraleptuca* Bott, 1973

Uca (Paraleptuca) crassipes (White, 1847)

(Fig. 4C, D)

Gelasimus crassipes White, 1847a: 84 [type locality: Siquejor, Philippines]; White 1847b: 205; Adams & White 1848: 49.

Gelasimus gaimardi H. Milne Edwards, 1852: 150, pl. 4 fig. 17, 17a [type locality: Tongatabou]; Sakai 1939: 617 (part); 1940: 47 [list]; Lin 1949: 26 [list].

Gelasimus latreillei H. Milne Edwards, 1852: 150, pl. 4 fig. 20, 20a [type locality: Bora Bora]; Sakai 1939: 618; Sakai 1940: 47 [list].

Gelasimus pulchellus Stimpson, 1858: 100 [type locality: Tahiti]; 1907: 107, pl. 13(1).

Uca pulchella—Parisi 1918: 93 (part).

Uca latreillei—Balss 1922: 142.

Uca annulipes—Miyake 1936: 511; 1938: 109; Sakai 1936: 170 (not *Gelasimus annulipes* H. Milne Edwards, 1837).

Uca gaimardi—Miyake 1939: 222, 241; Yamaguchi 1994: 163.

Gelasimus annulipes—Sakai 1939: 616, pl. 104(4); 1940: 32 [list] (not *Gelasimus annulipes* H. Milne Edwards, 1837).

Uca (Amphiuca) chlorophthalmus crassipes—Crane 1975: 101, figs. 13A-1, 14, 26C, 37H, 39A, 56C, 60L-M, 68B, 81G, 82G, 83A, 99, pls. 15A-F, 46B (part); Sakai 1976a, text-fig. 332b, pl. 209(2-4) (part); Miyake 1983: 163, pl. 55(3); Wang 1984: 42; Nagai & Nomura 1988: 54, 1 unnumbered fig.; Shih 1994: 91, figs. 64-66 (part).

Uca (Paraleptuca) chlorophthalmus crassipes—Takeda & Nunomura 1976: 80.

Uca crassipes—Takeda 1982: 208, 1 unnumbered fig.; Huang *et al.* 1989: 193, fig. 2, pl. 1E-G (part); Ho *et al.* 1993: 20; Okutani 1994a: 214, figs. 2, 3; Wang & Liu 1996a: 54, 3 unnumbered figs.; Ng *et al.* 2001: 37 [list]; Katsu 2007: 88, 7 unnumbered figs.; Wang & Liu 2003: 77, figs. 74-76; Liu & Wang 2010: 28, 34, 3 unnumbered figs. (part); Japanese Association of Benthology 2012: 215, 1 unnumbered fig.; Shih 2012b: 15, 62, figs. 15, 87-89; Fujita & Uyeno 2015: 98, fig. 4A, B.

Uca chlorophthalmus crassipes—Chen 2001: 206, 2 unnumbered figs.; Yoshigou 2001: 4, fig. 2, pl. 11, J; Nakasone & Irei 2003: 269, fig. 31C.

Uca (Paraleptuca) crassipes—Ng *et al.* 2008: 241 [list]; Toyota & Seki 2014: 224, 4 unnumbered figs.

Material examined. See Shih *et al.* (2012) for specimens examined from Taiwan (including Penghu and Dongsha) and the Ryukyus.

Distribution. Western Pacific (Japan [including Ryukyus], Taiwan [including Penghu and Dongsha], Philippines, New Guinea, Australia), Central and South Pacific, and eastern Indian Ocean (Thailand).

Remarks. Shih *et al.* (2012) separated *U. splendida* (Stimpson, 1858) from *U. crassipes* and some old records *U. crassipes* have been revised (see Remarks under *U. splendida*).

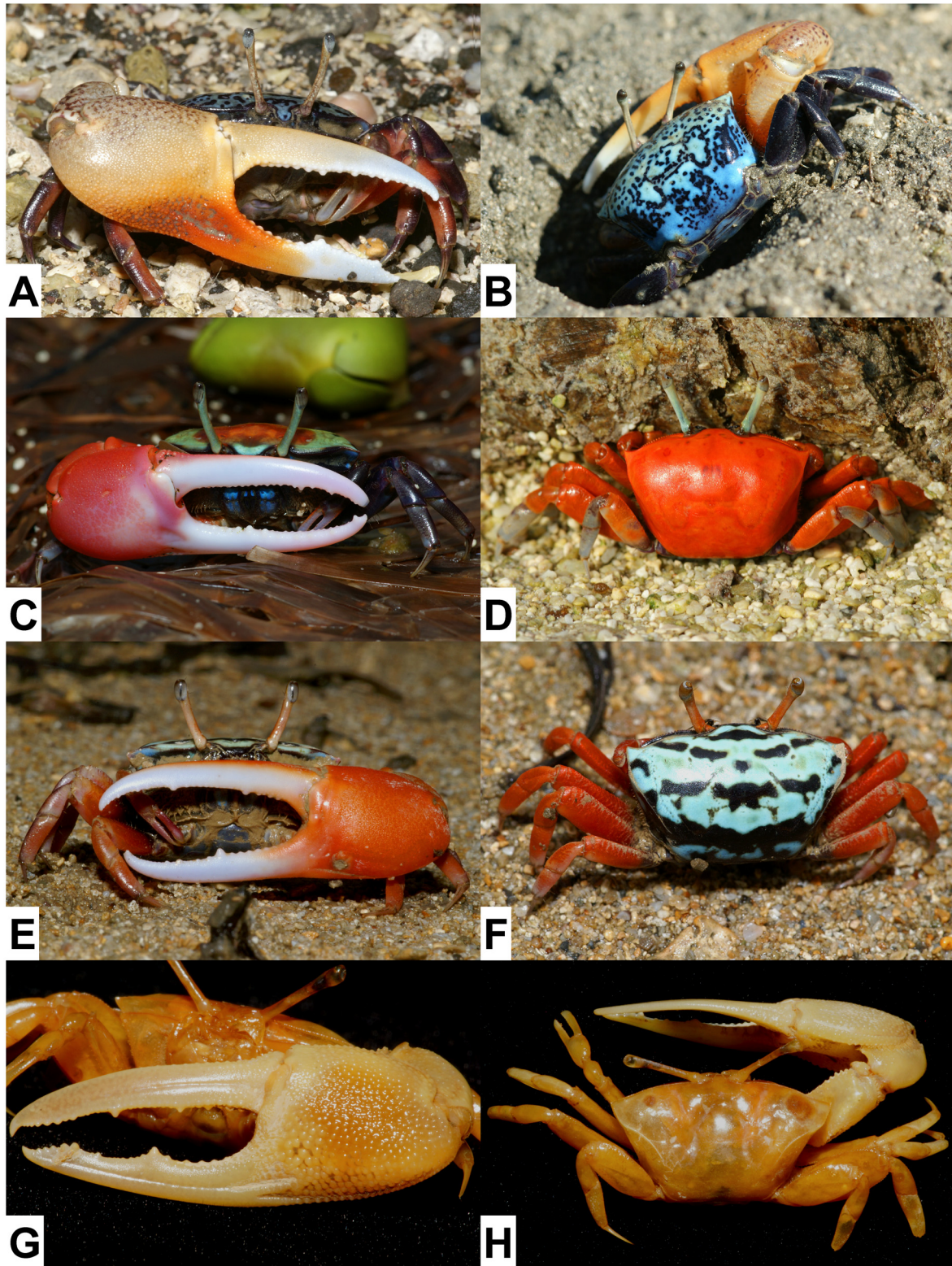


FIGURE 4. Species of the subgenera *Uca* (*Gelasimus*) (A, B), *U.* (*Paraleptuca*) (C–F), and *U.* (*Tubuca*) (G, H) from Taiwan. A, B, *Uca tetragonon* (Herbst, 1790), males from Siyu, Penghu; C, D, *U. crassipes* (White, 1847), male and female from Dongsha Island, respectively; E, F, *U. splendida* (Stimpson, 1858), male and female from Cingluo, Penghu; G, H, *U. acuta* (Stimpson, 1858), males from “Formosa Is.,” collected by R. Swinhoe (BM 58.162).

Parisi (1918) recorded *U. crassipes* (as *U. pulchella* (Stimpson, 1858)) from Misaki, Japan. Kudo & Yamada (2000) also mentioned a record from Wakayama, based on the communication with Dr. K. Wada. *Uca crassipes* is common in the Ryukyus. The record from “Tokaito coast: Oho Sima” deposited in the U.S. National Museum of Natural History, Washington DC, USA (USNM 22288) (Crane 1975) should be the island of Amami Oshima, in the central Ryukyus.

Previously the species from Ogasawara Islands has been identified as either *U. lactea*, *U. pulchella*, *U. annulipes* (H. Milne Edwards, 1837) or *U. crassipes* (see Shih *et al.* 2013), which was established as an endemic species, *Uca (Paraleptuca) boninensis* Shih, Komai & Liu, 2013. This species is similar to *U. crassipes*, but has a moderately acute and produced anteriorly anterolateral angles, and longer anterolateral margins (compared to *U. crassipes* with anterolateral angles strongly acute, produced anterolaterally, anterolateral margins short or absent) and a relatively stouter G1 (Shih *et al.* 2013).

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

(Fig. 4E, F)

Gelasimus splendidus Stimpson, 1858: 99 [type locality: Hong Kong]; 1907: 106, pl. 14(2) (see Shih *et al.* 2012 for list of citation of synonyms).

Uca crassipes—Aoki & Wada 2013: 791 (not *Gelasimus crassipes* White, 1847).

Uca (Paraleptuca) splendida—Shih *et al.* 2012: 34, figs. 2, 3, 4, 6, 7C.

Uca splendida—Shih 2012b: 68, figs. 97, 98.

Material examined. See Shih *et al.* (2012) for specimens from Taiwan (including Penghu and Dongsha).

Distribution. Ryukyus (Iriomote), Taiwan (including Penghu, Kinmen, Dongsha), China (including Hainan and Hong Kong), and Vietnam.

Remarks. Based on the molecular analyses and morphological comparison, Shih *et al.* (2012) resurrected *Uca splendida*, which was synonymized with *U. crassipes* by Crane (1975). It is easy to distinguish the two species by the morphologies of the carapace. The coloration is also useful for species identification, but juveniles sometimes show similar color patterns (Shih *et al.* 2012: figs. 4, 5). Whereas *U. crassipes* is widely distributed from the eastern Indian Ocean to the western Pacific, *U. splendida* is restricted to the continental coast, including Taiwan, southeastern China, and Vietnam.

The record of *Uca splendida* from Xiamen (Fujian, China) (Cano 1889: 92, 234) has been discussed by Shih *et al.* (2012: 43). An individual of this species from the adjacent islet, Lieyu (= Lesser Kinmen), has been observed and photographed (P.-Y. Hsu, personal communication), which supports the finding from Xiamen. It is possible that the northernmost limit of this species in the continental East Asia is the region of Xiamen and Kinmen.

In spite of the close proximity, no specimens of *U. splendida* have been reported from the Ryukyus. However, in the phylogeographic study of *U. crassipes*, using 504-bp mitochondrial control region sequences, Aoki & Wada (2013: appendix table 2) found specimens from Vietnam and Iriomote, with haplotypes (H75, H76 and H77) that are very different from those of other specimens. These haplotypes have been aligned and compared with sequences of *U. splendida* in Shih *et al.* (2012) that clearly support the occurrence of *U. splendida* in Iriomote, the Ryukyus (unpublished data). Nevertheless, it is likely that *U. splendida* is rare in Iriomote, as only three specimens were collected, compared with 19 specimens of *U. crassipes* from this island (Aoki & Wada 2013: table 1).

Subgenus *Tubuca* Bott, 1973

***Uca (Tubuca) acuta* (Stimpson, 1858)**

(Figs. 4G, H, 5, 6A, B)

Gelasimus acutus Stimpson, 1858: 99 [type locality: Macao]; 1907: 105, pl. 14(3).

Uca (Deltuca) [acuta] acuta acuta—Crane 1975: 25, fig. 61B, pl. 1E–H.

Uca acuta acuta—Yamaguchi 1994: 183.

Uca acuta—Jones & Morton 1994: fig. 1, pls. 1A, B, 2A, B.

Uca (Tubuca) acuta—Ng *et al.* 2008: 241 [list].

Material examined. Taiwan: 4 ♂♂ (18.1–20.2 mm), BM 58.162, “Formosa Is.,” coll. R. Swinhoe, 1850s. **Kinmen Islands:** 1 ♂ (21.2 mm) (NCHUZOO 13996), Wujiang R. estuary, coll. J.-H. Lee, 30 May 2004; 1 ♂ (18.8 mm) (NCHUZOO 13650), Wujiang R. estuary, coll. J.-H. Lee, 21 May 2005; 1 ♂ (11.4 mm) (NCHUZOO 14602), Wujiang R. estuary, H.-T. Shih & Y.-H. Wang, 7 Mar. 2008.

Distribution. China (including Hainan), Taiwan (including Kinmen), and Vietnam.

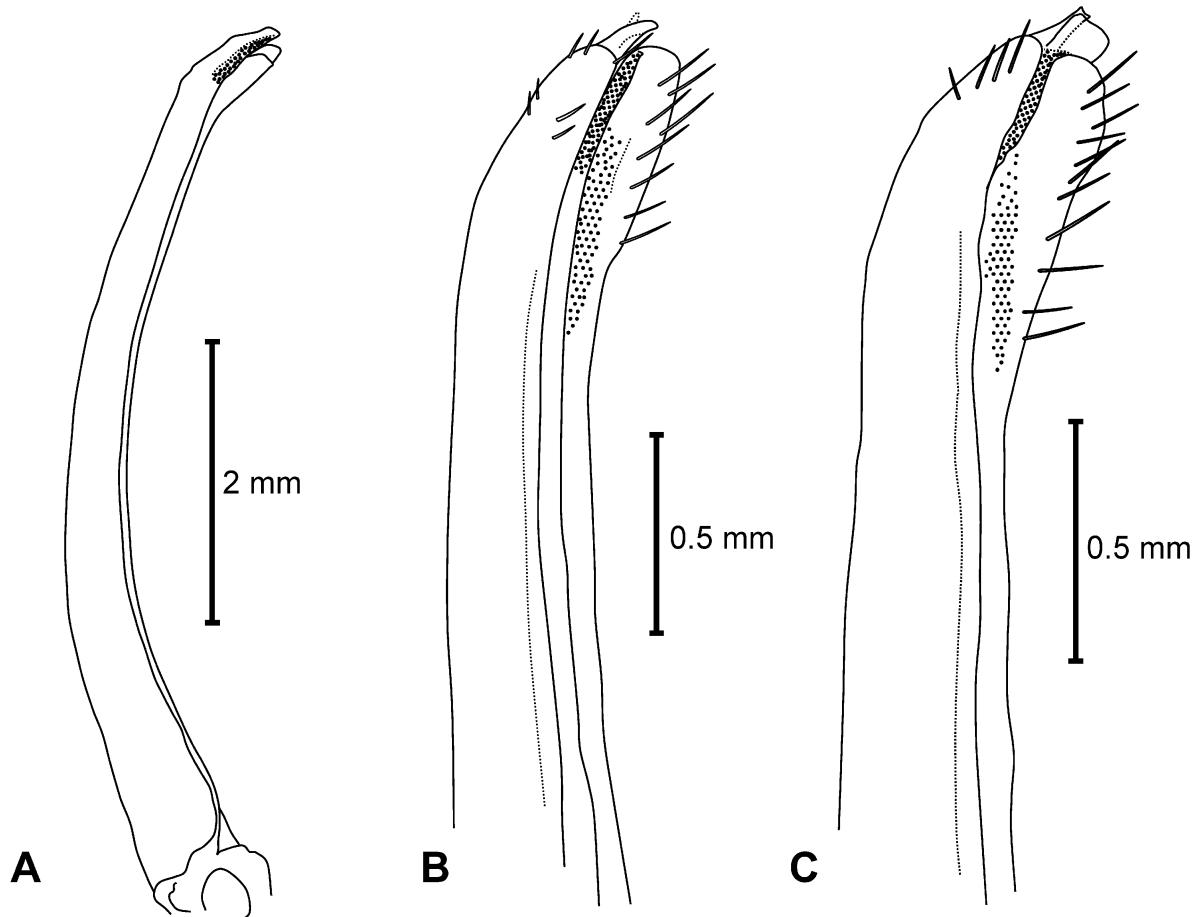


FIGURE 5. The G1s of specimens from Taiwan (A, B) and Kinmen (C). A, right G1, mesial view; B, C, distal part of right G1. A, B, male (CW 22.2 mm), BM 58.162, “Formosa Is.”; C, male (CW 18.8 mm), NCHUZOO 13650, Kinmen, Taiwan.

Remarks. Four male specimens of *Uca acuta* (BM 58.162) (Fig. 4G–H), collected by R. Swinhoe, with the locality as “Formosa Is.,” were examined and confirmed by J. Crane in 1963 (see Yamaguchi 1994: 183). Crane (1975), however, did not include this Taiwanese record in her monograph and there have been no additional reports from Taiwan until now (see below). In his visit to Tainan, southwestern Taiwan, in 1858 Swinhoe (1859: 148) mentioned “A species of crab, with one large white claw, dotted the mud like flowers. They were very quick, and off in an instant into their holes”, which is very likely referred to *U. acuta*, based on the white chela character and muddy habitat. The four specimens of *U. acuta* collected by R. Swinhoe in the 1850s, should be the oldest specimens of crabs recorded from Taiwan.

The G1 of the specimen from Taiwan (CW 22.2 mm, BM 58.162; Fig. 5A, B) with tip tapering; thumb subdistal, short, reaching base of anterior flange; inner process small, scarcely reaching flange base, agrees with that from Kinmen (CW 18.8 mm, NCHUZOO 13650; Fig. 6C) (also see Crane 1975: fig. 61B; Jones & Morton 1994: fig. 1). *Uca acuta* and *U. arcuata* are always sympatric in the field, e.g. Kinmen (this study), Hong Kong (Jones & Morton 1994), and Vietnam (Kosuge *et al.* 1997). It is easier to identify them based on the adult color pattern, but it is difficult to distinguish them after preservation. Crane (1975) and Jones & Morton (1994) have discussed the difference of morphology. Adults of *U. arcuata* is much larger than adults of *U. acuta*, with CW ~ 37 mm and ~20 mm, respectively. Compared to young individuals of *U. arcuata*, *U. acuta* do not have strongly arched

carapace but always with posterolateral stria on carapace. The major cheliped of *U. acuta* with thinner and longer fingers, more slender manus, and smaller tubercles on outer manus of male cheliped, when compared to *U. arcuata*.

***Uca (Tubuca) arcuata* (De Haan, 1835)**

(Fig. 6C–E)

Ocypode (Gelasimus) arcuata De Haan, 1835: 53, pl. 7(2) [type locality: Japan].

Gelasimus arcuatus—Sakai 1934: 320; Sakai 1939: 619, text-fig. 94a, pl. 72(2); Sakai 1940: 42 [list]; Horikawa 1940: 28 [list]; Lin 1949: 26 [list].

Uca arcuata—Parisi 1918: 93; Balss 1922: 143; Maki & Tsuchiya 1923: 209, pls. 23(5), 24(7); Sakai 1935: 212, pl. 59(2); Takeda 1982: 207, 1 unnumbered fig.; Fukui *et al.* 1989: 227; Huang *et al.* 1989: 196, fig. 5, pl. 3A–C; Hosoya *et al.* 1993: 43, fig. 2; Okutani 1994b: 259, figs. 9–10; Yamaguchi 1994: 154, 183, fig. 1; Wang & Liu 1996a: 44, 5 unnumbered figs.; Hung 2000: 140–1, figs. 436–437; Chen 2001: 201, 2 unnumbered figs.; Lee 2001: 99, 3 unnumbered figs.; Ng *et al.* 2001: 36 [list]; Yoshigou 2001: 4, fig. 2, pl. 1A; Wang & Liu 2003: 71, figs. 63–65; Shen & Jeng 2005: 157, 2 unnumbered figs.; Liu & Wang 2010: 28, 30, 10 unnumbered figs.; Japanese Association of Benthology 2012: 214, pl. 1(16), 1 unnumbered fig.; Shih 2012b: 14, figs. 11; Watanabe 2014: 101, 4 unnumbered figs.

Gelasimus formosensis—Wu *et al.* 1962: 198 (not *Uca formosensis* Rathbun, 1921).

Uca (Deltuca) arcuata—Crane 1975: 44, figs. 8C, 9C, 61J, 98, pl. 5A–F; Sakai 1976a: 601, text-fig. 328a, pl. 208(1); Miyake 1983: 161, pl. 54(3); Wang 1984: 42; Su & Lue 1984: 63, fig. 4; Dai *et al.* 1986: 420, fig. 232, pl. 58(5); Dai & Yang 1991: 460, fig. 232, pl. 58(5); Shih 1994: 69, figs. 44–47; Ho & Hung 1997: 50, 8 unnumbered figs.

Uca (Tubuca) arcuata—Ng *et al.* 2008: 241 [list]; Toyota & Seki 2014: 228, 4 unnumbered figs.

Material examined. Tainan: 4 ♂♂ (16.5–26.6 mm) (NCHUZOO 14625), Yilan, coll. S. Huang, 31 May 1996; 1 juv. (9.3 mm) (NCHUZOO 14620), Lanyang R. estuary, Yilan, coll. H.-T. Shih, 5 Nov. 2011; 2 juv. (4.0, 7.2 mm) (NCHUZOO 14626, 14627), Jhuwei, New Taipei City, coll. H.-T. Shih, 4 Oct. 1995; 1 ♂ (34.1 mm) (NCHUZOO 14617), Jhuwei, New Taipei City, coll. H.-T. Shih, 30 June 2006; 1 ♂ (31.8 mm) (NCHUZOO 14621), Hsinchu, coll. H.-T. Shih, 6 Jan. 1996; 1 ♂ (35.0 mm) (NCHUZOO 14613), Hsinchu, H.-T. Shih, 29 Jan. 1996; 1 ♂ (35.8 mm) (NCHUZOO 14635), Haishangu, Hsinchu, H.-T. Shih, 5 Jan. 1996; 1 ♂ (29.0 mm) (NCHUZOO 14614), Houlong, Miaoli, coll. H.-T. Shih, 8 Apr. 1995; 1 ♂ (23.2 mm) (NCHUZOO 14616), Yuanli, Miaoli, coll. M.-W. Chen, 5 Mar. 2006; 1 ♂ (36.9 mm) (NCHUZOO 14619), Wenliao, Taichung, coll. H.-T. Shih & H.-T. Hung, 20 Aug. 2002; 1 ♂ (19.0 mm) (NCHUZOO 14629), Gaomei, Taichung, coll. H.-T. Shih, 30 July 2007; 1 ♂ (38.2 mm) (NCHUZOO 13660), Shengang, Changhua, coll. H.-T. Hung, 5 Aug. 2002; 1 ♂ (23.5 mm), 1 ♀ (22.8 mm) (NCHUZOO 14615), Shengang, Changhua, coll. H.-T. Shih, 19 Feb. 2004; 2 ♂♂ (23.5, 33.2 mm) (NCHUZOO 14611), coll. H.-T. Shih, 13 Sep. 2005; 1 ♀ (26.8 mm) (NCHUZOO 14624), Shengang, Changhua, coll. B.-Y. Huang, 7 Oct. 2005; 1 ♂ (18.3 mm) (NCHUZOO 14634), Fusing, Hanbao, Changhua, coll. H.-T. Shih, 11 July 2001; 1 ♂ (29.6 mm) (NCHUZOO 14632), Wanggong, Changhua, coll. H.-T. Shih, 6 Sep. 2005; 1 ♂ (36.1 mm) (NCHUZOO 14618), Dongshih Bridge, Chiayi, coll. H.-T. Shih, 30 May 1996; 4 ♂♂ (24.0–30.0 mm) (NCHUZOO 14612), Cigu, Tainan, coll. H.-T. Shih, 31 May 1996; 2 ♂♂ (21.5, 29.2 mm) (NCHUZOO 14630), Caiguniang Temple, Tainan, coll. H.-T. Shih, 26 Mar. 1998. **Penghu Islands:** 1 ♂ (30.6 mm) (NCHUZOO 14631), Cingluo, H.-T. Shih, 14 Aug. 1996; 1 ♂ (22.1 mm) (NCHUZOO 14628), coll. H.-T. Shih, 21 June 2006; 1 ♂ (40.2 mm) (NCHUZOO 14663), Shuanhuyuan, coll. students from HTS's laboratory, 30 Aug. 2014. **Kinmen Islands:** 1 ♂ (16.1 mm) (NCHUZOO 13992), 1 ♂ (15.3 mm) (NCHUZOO 14604), 1 ♂ (13.6 mm) (NCHUZOO 14605), 1 ♂ (20.1 mm) (NCHUZOO 14607), 2 ♂♂ (11.5, 18.4 mm) (NCHUZOO 14622), 1 ♂ (11.6 mm), 1 ovig. ♀ (14.7 mm) (NCHUZOO 13998), 1 ♀ (14.6 mm) (NCHUZOO 13997), Wujiang R. estuary, coll. J.-H. Lee, 30 May 2004; 1 ♂ (32.1 mm) (NCHUZOO 13990), 2 ♂♂ (11.8, 21.5 mm), 1 ♀ (21.3 mm) (NCHUZOO 14608), 1 ♂ (13.1 mm) (NCHUZOO 14749), Wujiang R. estuary, coll. Y.-H. Wang, 16 Aug. 2011; 1 ♂ (soft carapace) (NCHUZOO 14747), Housha, Jinning, coll. Y.-H. Wang, 17 Aug. 2011. **Main Japan islands:** 2 ♂♂ (30.9, 33.6 mm), 2 ♀♀ (24.9, 27.1 mm) (NCHUZOO 14610), Kaeda R., Miyazaki, coll. H. Suzuki, 16 Oct. 2008. **Ryukyus:** 1 ♂ (11.0 mm) (NCHUZOO 14708), Okukubi R., Okinawa, coll. T. Naruse, 25 Feb. 2002.

Ecology. The typical habitat is the mudflat, especially in mangrove forests. Male and female *U. arcuata* build chimneys, with a height of about 3 cm, from material scraped from the surface of substrate near the burrows (see Shih *et al.* 2005).

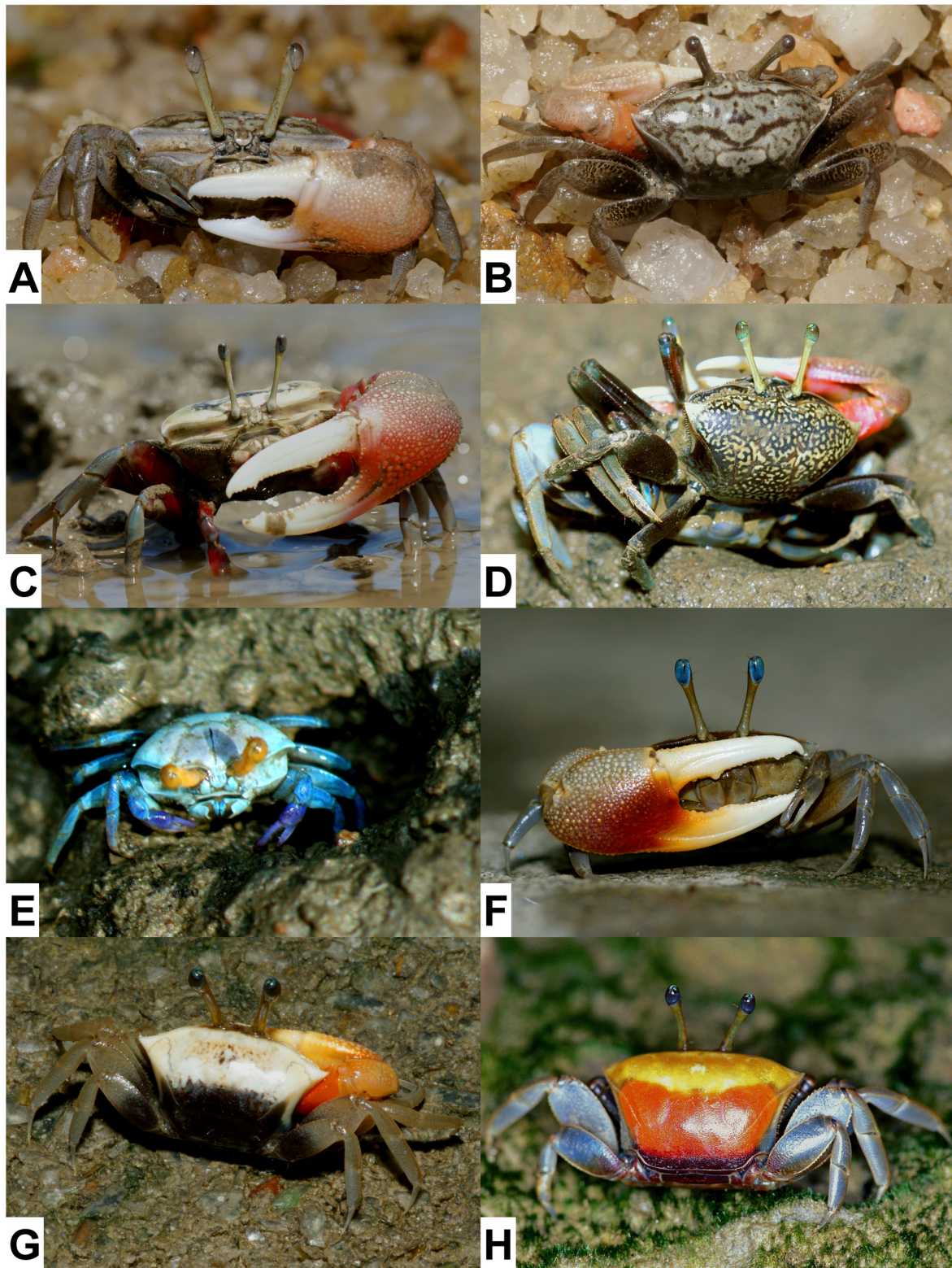


FIGURE 6. Species of the subgenus *Uca* (*Tubuca*) from Taiwan. A, B, *Uca acuta*, male from Kinmen; C–E, *U. arcuata* (De Haan, 1835), adult male and juvenile from Guandu, Taipei City (C, E), mating pair from Shengang, Changhua (D); F–H, *U. coarctata* (H. Milne Edwards, 1852), male from the Yanshuei River estuary, Tainan (F, G) and female from the Baoli River estuary, Pingtung (H).

Distribution. Korea, China (including Hainan), Japan (including Ryukyus), Taiwan (including Penghu and Kinmen), Vietnam.

Remarks. *Uca arcuata* is one of the most abundant fiddler crabs in East Asia, especially near mangroves. This species is very abundant in Taiwan near introduced mangroves (e.g. *Kandelia obovata* and *Avicennia marina*), which were planted artificially (Wester 1988).

The juveniles of *U. arcuata* in Taiwan show a blue carapace and orange eyestalks (J.-T. Shih 1990; J.-T. Shih *et al.* 1991) (Fig. 6E). The blue juveniles of *Uca* from Ishigaki and Iriomote (Yamaguchi & Takeda 1973: 13; Yoshigou 2001: pl. 1D) need further study, because there is no record of *U. arcuata* from the southern Ryukyus.

***Uca (Tubuca) coarctata* (H. Milne Edwards, 1852)**
(Fig. 5F–H)

Gelasimus coarctatus H. Milne Edwards, 1852: 146 [type locality: “Odessa”]; A. Milne-Edwards 1873: 272.

Uca dubia—Sakai 1974: 10, 13; Sakai 1976b: 38.

Uca (Deltuca) coarctata coarctata—Crane 1975: 52, figs. 9B, 26A, 31A, 36B, 37C, 38M–P, 62A–C, 81D, 82H, pl. 6E–H, 7, 46C–D; Sakai 1976a: 603, text-figs. 328, 330, pl. 208(2); Sakai 1976b: 32, 38, frontispiece fig. 2; Shih 1994: 73, figs. 48–50.

Uca coarctata—Fukui *et al.* 1989: 227, fig. 2; Huang *et al.* 1989: 194, fig. 3, pl. 2A–D; Yamaguchi 1994: 159; Wang & Liu 1996a: 46, 2 unnumbered figs.; Lee 2001: 101, 5 unnumbered figs.; Ng *et al.* 2001: 37 [list]; Yoshigou 2001: 4, fig. 2, pl. 1E; Liu & Wang 2010: 33, 2 unnumbered figs.; Japanese Association of Benthology 2012: 214, 1 unnumbered fig.; Fujita & Uyeno 2015: 99, fig. 5A–C.

Uca coarctata coarctata—Yamaguchi 1994: 183; Nakasone & Irei 2003: 269, fig. 29C, D.

Uca dussumieri—Katsu 2007: 82, 4 unnumbered figs (not *Gelasimus dussumieri* H. Milne Edwards, 1852).

Uca crassipes—Katsu 2007:90, 1 unnumbered fig.

Uca (Tubuca) coarctata—Ng *et al.* 2008: 241 [list]; Toyota & Seki 2014: 229, 4 unnumbered figs.

Material examined. **Taiwan:** 1 ♀ (16.8 mm) (ASIZ), Lanyang R. estuary, Yilan, coll. H.-C. Liu, 25 July 2004; 2 ♂♂ (12.7, 18.6 mm) (NCHUZOOL 14679), Yanshuei R. estuary, Tainan, 4 Aug. 2009; 1 ♀ (18.4 mm) (NCHUZOOL 14685), Yanshuei R. estuary, Tainan, 18 Oct. 2011; 1 ♂ (17.5 mm), 1 ♀ (21.7 mm) (TMCD 2026), Baoli R. estuary, Pingtung, 26 Apr. 1983; 1 ♂ (18.4 mm) (TMCD CHCD 780), Baoli R. estuary, Pingtung, coll. H.-C. Liu, 20 Apr. 1995; 2 ♂♂ (13.5, 14.5 mm), 3 ♀♀ (12.7–15.0 mm) (TMCD CHCD 810), 4 ♂♂ (12.1–19.2 mm), 2 ♀♀ (8.8, 13.3 mm) (TMCD CHCD 812), 6 ♂♂ (12.0–24.4 mm), 1 ♀ (14.2 mm) (TMCD CHCD 813), Baoli R. estuary, Pingtung, 14 June 1995; 1 ♂ (22.4 mm) (NCHUZOOL 14683), 1 ♀ (20.0 mm) (NCHUZOOL 14681), Baoli R. estuary, Pingtung, coll. H.-T. Shih, 12 Jan. 2000; 2 ♂♂ (13.2, 13.2 mm) (NCHUZOOL 14682), Baoli R. estuary, Pingtung, coll. H.-T. Shih, 20 July 2011. **Penghu Islands:** 1 ♀ (21.0 mm) (NCHUZOOL 13231), Citou, coll. H.-T. Shih & Y.-H. Wang, 19 May 2007.

Distribution. Western Pacific (Ryukyus, Taiwan [including Penghu], China (?), Philippines, Indonesia [including Sumatra], New Guinea, Australia).

Remarks. Crane (1975) examined specimens of *U. coarctata* from Luzon, Philippines, which was the northernmost record in the western Pacific in her monograph. Sakai (1976a, b), however, identified his “*U. dubia*” (Sakai 1974) as *U. coarctata*, although *Gelasimus dubius* Stimpson, 1858, had been confirmed by Crane (1975) as *U. dussumieri* (see below). The two species can be distinguished by the morphology of orbital floor and major fingers: *U. coarctata* has the orbital floor with a row of tubercles (without tubercles in *U. dussumieri*) and the dactylus of the major cheliped with 1 groove (with two grooves in adult *U. dussumieri*).

The first records of this species in Taiwan are those of Fukui *et al.* (1989) and Huang *et al.* (1989). Shih *et al.* (2008) confirmed it from Penghu. Katsu (2007) identified a female from Amami, central Ryukyus, as “*U. dussumieri*”, but it is *U. coarctata* because there is a row of tubercles on the floor of the orbit.

***Uca (Tubuca) dussumieri* (H. Milne Edwards, 1852)**
(Fig. 7A–C)

Gelasimus dussumieri H. Milne Edwards, 1852: 148, pl. 4(12) [type locality: Java].

Gelasimus dubius Stimpson, 1858: 99 [type locality: Ryukyus]; 1907: 104; Sakai 1939: 621; Sakai 1940: 47 [list].

Uca dussumieri—Sakai 1974: 10, 13; Takeda 1982: 207, 1 unnumbered fig.; Huang *et al.* 1989: 195, fig. 4, pl. 2E–H; Ho *et al.* 1993: 20; Okutani 1994a: 215, figs. 6; Yamaguchi 1994: 161; Wang & Liu 1996a: 42, 3 unnumbered figs.; Hung 2000: 140–1, figs. 432–433; Lee 2001: 100, 4 unnumbered figs.; Ng *et al.* 2001: 37 [list]; Yoshigou 2001: 4, fig. 2, pl. 1B, C.; Shen & Jeng 2005: 162, 2 unnumbered figs.; Katsu 2007: 80, 4 unnumbered figs.; Liu & Wang 2010: 26, 36, 3 unnumbered figs.; Fujita & Uyeno 2015: 100, fig. 5D–F.

Uca dubia—Sakai 1936, 170; Miyake 1936: 511; 1938: 109; 1939: 222.

Uca dussumieri dussumieri—Miyake 1963: 70; Yamaguchi 1994: 184; Ho 1996: 9, figs. 1–7; Chen 2001: 204, 2 unnumbered figs.; Nakasone & Irei 2003: 269, fig. 29A, B.

Uca (Deltuca) dussumieri dussumieri—Crane 1975: 37, figs. 5, 8A, 9A, 34A, 36A, 37B, 52A–BB, 54C, 61F, 74A–K, pls. 2E–F, 3; Sakai 1976a: 602, text-figs. 328b, 329; Sakai 1976b: 32, 38, frontispiece fig. 3; Miyake 1983: 162, pl. 54(4); Nagai & Nomura 1988: 51, 1 unnumbered fig.; Shih 1994: 66, figs. 41–43.

Uca (Tubuca) dussumieri—Ng *et al.* 2008: 242 [list]; Toyota & Seki 2014: 230, 4 unnumbered figs.

Material examined. **Taiwan:** 6 ♂♂ (15.3–25.0 mm), 1 ♀ (21.5 mm) (NCHUZOOL 14716), Yanshuei R. estuary, Tainan, coll. J.-H. Lee *et al.*, 4 Aug. 2009; 1 ovig. ♀ (21.5 mm) (NCHUZOOL 14720), Yanshuei R. estuary, Tainan, 2 July 2012; 1 ♂ (18.5 mm) (TMCD), Dapengwan, Pingtung, coll. C.-H. Wang, 14 July 1996; 1 ♀ (19.0 mm) (NCHUZOOL 14718), Dulanwan, Taitung, 7 Apr. 2001. **Penghu Islands:** 1 ♀ (24.4 mm) (NCHUZOOL 14717), Cingluo, coll. H.-T. Shih, 14 Aug. 1996; 1 ovig. ♀ (17.3 mm) (NCHUZOOL 14719), Cingluo, coll. H.-T. Shih, 15 Aug. 1996; 1 ♂ (23.7 mm) (NCHUZOOL 14715), Citou, coll. H.-T. Shih *et al.*, 19 Aug. 2009; 1 ♂ (15.8 mm) (NCHUZOOL 14721), Chihsu, Siyu, coll. H.-T. Shih, 19 May 2007. **Ryukyus:** 4 ♂♂ (11.5–14.5 mm), 1 ♀ (broken) (TMCD), Yuhi R., Okinawa, 16 Apr. 1992; 2 ♂♂ (18.6, 29.8 mm), 1 ♀ (24.2 mm) (TMCD CHCD 718), Ishigaki, coll. H.-C. Liu, 13 July 1995.

Distribution. Western Pacific (Ryukyus, Taiwan [including Penghu], China (?), Philippines, Indonesia [including Sumatra], New Guinea).

Remarks. *Gelasimus dubius* Stimpson, 1858 is a synonym of *U. dussumieri* (Miyake 1963; Crane 1975), but Sakai (1974, 1976a, b) considered the species a synonym of *U. coarctata* (see Discussion).

Uca (Tubuca) paradussumieri (Bott, 1973)

(Fig. 7D, E)

Mesuca (Latuca) paradussumieri Bott, 1973: 317, fig. 10 [type locality: Bengal, India] (see Shih *et al.* 2010b for list of citation of synonyms).

Uca sp.—Lai 2009: 61, 1 unnumbered fig.

Material examined. **Taiwan:** 1 ♂ (34.5 mm) (NCHUZOOL 14713), Houlong R. estuary, Miaoli, coll. J.-H. Lee, 28 May, 2012; 2 ♂♂ (33.0, 33.2 mm) (NCHUZOOL 14714), Houlong R. estuary, Miaoli, coll. J.-H. Lee, 16 July, 2012. **Kinmen Islands:** 2 ♂♂ (20.2, 22.6 mm) (NCHUZOOL 13995), Wujiang R. estuary, coll. J.-H. Lee, 21 May 2005; 1 ♂ (31.8 mm) (NCHUZOOL 13994), Wujiang R. estuary, coll. H.-T. Shih & Y.-H. Wang, 7 Mar. 2008; 2 ♂♂ (27.8, 36.3 mm) (NCHUZOOL 14606), 1 ♂ (21.8 mm) (NCHUZOOL 14748), Wujiang R. estuary, coll. Y.-H. Wang, 16 Aug. 2011.

Distribution. Western Pacific and eastern Indian Ocean (Taiwan [including Kinmen], China [including Hainan], Vietnam, Thailand, Malay Peninsula, Borneo, Sumatra, Myanmar, Bengal).

Remarks. *Uca paradussumieri* and *U. dussumieri* are very similar in morphology, but the coloration of adult individuals is different, with *U. paradussumieri* having carapace pale brown or greyish brown and major cheliped deep yellow or yellow brown (Fig. 6D, E), but *U. dussumieri* has carapace dark brown or black and major cheliped deep orange red (Fig. 6A–C).

This species is distributed widely from the coast of eastern and southeastern China, Hainan, Vietnam, Borneo, and both sides of Peninsular Malaysia (Shih *et al.* 2010b). The finding from Kinmen was expected because this species has been recorded in adjacent Xiamen (Shih *et al.* 2010b). The records from Taiwan, however, seem unusual. One photograph in Lai (2009), taken from Dajhongmiao, Tainan (W.-C. Lai, personal communication), is confirmed to be *U. paradussumieri* by the yellow brown major cheliped and long fingers. Three large specimens were also collected from the Miaoli mudflats, northwestern Taiwan in 2012 (this study), with at least 20 individuals in this area (JHL, personal observation). This species should be very rare in Taiwan but more surveys are needed (see Discussion).

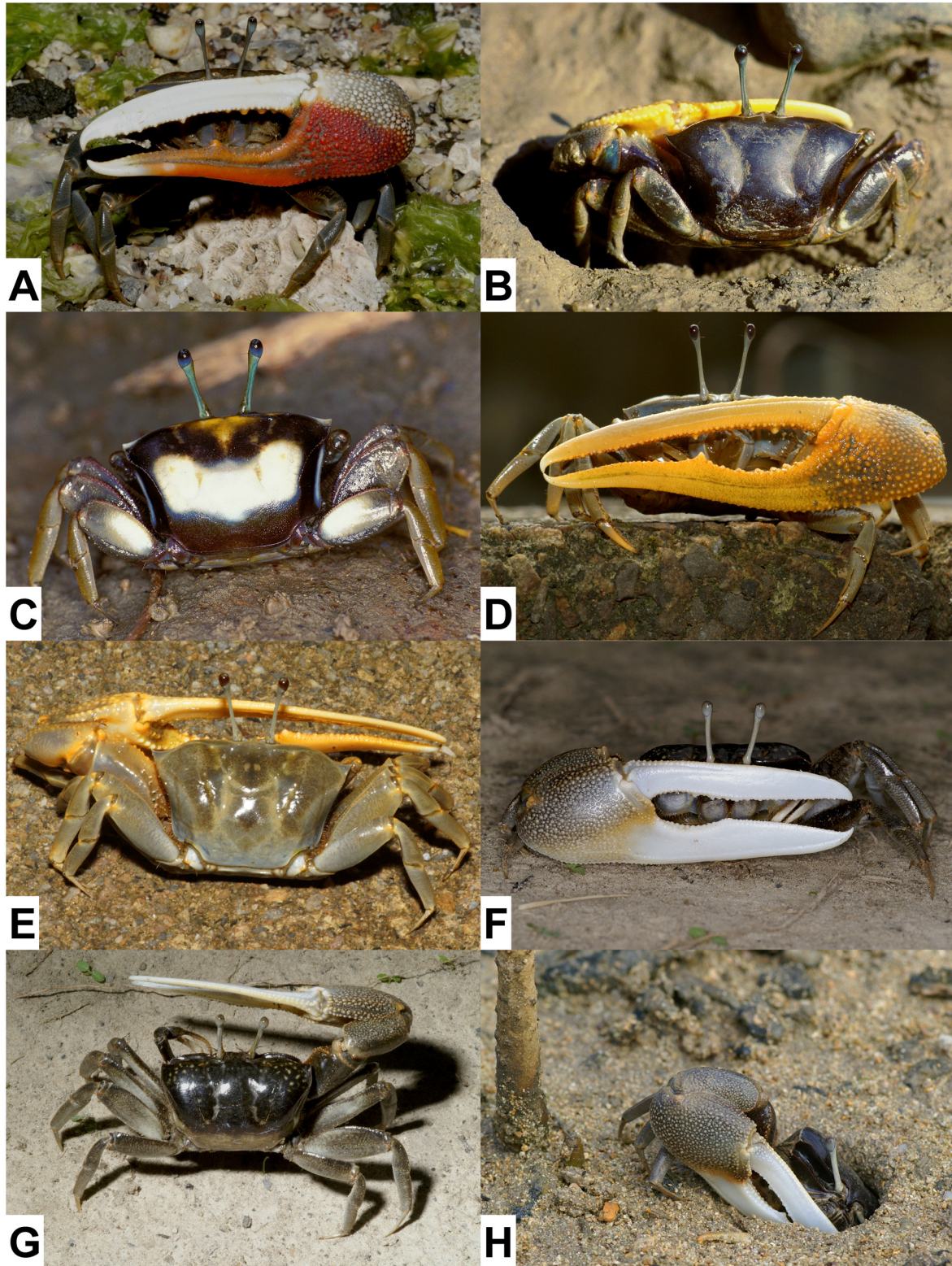


FIGURE 7. Species of the subgenera *Uca* (*Tubuca*) (A–E) and *Xeruca* (F–H) from Taiwan. A–C, *Uca dussumieri* (H. Milne Edwards, 1852), male from Siyu, Penghu (A), male and female from the Baoli River estuary, Pingtung (B, C); D, E, *U. paradussumieri* Bott, 1973, male from the Houlong River estuary, Miaoli; F–H, *U. formosensis* Rathbun, 1921, males from Haishangu, Hsinchu (F, G), male from Cingluo, Penghu (H).

Subgenus *Xeruca* Shih, 2015

Uca (Xeruca) formosensis Rathbun, 1921 (Fig. 7F–H)

Uca formosensis Rathbun, 1921: 155 [type locality: Lugang, Changhua, Taiwan] (see Shih 2015 for list of synonyms).

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

Uca (Xeruca) formosensis—Shih 2015: 162, figs. 2, 3, 4A, 5A, 6, 7.

Material examined. See Shih (2015) for material from Taiwan (including Penghu).

Ecology. A chimney is built by the male after attracting a female into his burrow during the neap tide (see Shih *et al.* 2005).

Distribution. Endemic to Taiwan (including Penghu).

Remarks. Based on morphological and molecular evidence, Shih (2015) established a new subgenus *Xeruca* for this endemic species to solve its uncertain position. *Xeruca* is also a subgenus with the smallest distribution among the subgenera of *Uca*. Detailed information on the history, morphology, coloration, and distribution can be found in Shih *et al.* (1999) and Shih (2015). Shih *et al.* (2005) also investigated the possible function of chimney building and its ecology. The conservation of this endemic species has become important and critical due to the diminishing populations (e.g. in Penghu, Fig. 7H) because the sediment has been changed by the introduced mangroves, and by being less competitive than *U. arcuata*, which is dominant in mangrove habitats (Shih *et al.* 1999; Hsieh *et al.* 2004; Shih 2015).

Key to the 18 East Asian species of *Uca*

1. Front narrow; outer major manus with tubercles 2
- Front wide; outer major manus smooth. 11
2. Anterolateral margin long; merus of first 3 ambulatories wide 3
- Anterolateral margin short; merus of first 3 ambulatories slender 5
3. Fourth ambulatory merus slender; fingers of major cheliped without gape in distal half, outer surface without or with faint groove *U. formosensis*
- Fourth ambulatory merus wide; fingers of major cheliped with large gape, outer surface with one clear groove on dactylus and pollex. 4
4. Carapace strongly arched; posterolateral stria absent; large size (up to CW ~ 37 mm) *U. arcuata*
- Carapace not strongly arched; posterolateral stria on carapace always present; small size (up to CW ~ 20 mm) *U. acuta*
5. Outer major dactylus without groove; suborbital crenellations large and distinct 6
- Outer major dactylus with 1 or 2 grooves; suborbital crenellations small and indistinct 8
6. Outer major manus with small tubercles; fingers narrow and thick; outer pollex without groove; female with pile posteriorly on carapace sides *U. 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. 7
7. Major pollex with a deep proximal depression and a shallow or without distal depression in gape, dactylus deeper than pollex only in young; oblique ridge of inner major manus low; carapace without dorsolateral margins in adult male *U. borealis*
- Major pollex with a shallow proximal and a deep distal depressions in gape, dactylus deeper than pollex; oblique ridge of inner major manus high; carapace with dorsolateral margins in adult male *U. jocelynae*
- Major pollex with both deep proximal and distal depressions in gape, dactylus not deeper than pollex; oblique ridge of inner major manus high; carapace without dorsolateral margins in adult male *U. vocans*
8. Floor of orbit with a row of tubercles; outer surface of major cheliped fingers with one groove 9
- Floor of orbit without a row of tubercles; outer surface of major cheliped fingers with two grooves 10
9. Floor of orbit with a long row of tubercles (often ≥ 15); outer surface of major cheliped fingers with one shallow groove; female without large tooth on either finger in gape *U. typhoni*
- Floor of orbit with a short row of tubercles; outer surface of major cheliped fingers with one deep groove; female with a large tooth at least on one finger in gape *U. coarctata*
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) *U. paradussumieri*
- Front almost without discernible median groove; G1 with distal blunt chitinous process; female always with a large tooth on both fingers in gape; medium size (up to CW ~ 27 mm) *U. dussumieri*
11. A shallow, triangular depression outside major pollex base; fourth ambulatory merus broad, its dorsal margin convex 12
- No triangular depression outside major pollex base; fourth ambulatory merus slender, its dorsal margin straight. 14

12. Anterolateral angles strongly acute, produced anterolaterally, anterolateral margins short or absent *U. crassipes*
 - Anterolateral angles moderately acute, produced anteriorly, anterolateral margins longer. 13
 13. Anterolateral margins almost straight, G1 with terminal process more truncate distally *U. splendida*
 - Anterolateral margins slightly diverging, G1 with terminal process gradually tapering distally. *U. boninensis*
 14. Outer major dactylus with two grooves; posterior carapace moderately narrow; orbits very oblique. *U. triangularis*
 - Outer major dactylus without groove; posterior carapace slightly narrow; orbits not oblique. 15
 15. Anterolateral angles triangular; major pollex without or with small predistal triangular tooth in gape; major dactylus arched throughout; G1 with thumb long, reaching well beyond flange base, flange wider than long. *U. lactea*
 - Anterolateral angles moderately acute; major pollex with moderate to large predistal triangular tooth in gape; major dactylus arched only distally; G1 with thumb moderately long, reaching flange base, flange wider than long. *U. perplexa*
 - Anterolateral angles strongly acute; major pollex with small to moderate predistal triangular tooth in gape; major dactylus arched throughout; G1 with thumb short, not reaching flange base, flange remarkably long *U. annulipes*

Discussion

There are 18 species of *Uca* recorded from East Asia (China, Korea, Japan, and Taiwan) (Sakai 1976a; Dai *et al.* 1986; Dai & Yang 1991; Shih 1994; Yoshigou 1999; Shih *et al.* 2010a, b, 2012, 2013; this study). Except the tropical *U. annulipes* and *U. typhoni* Crane, 1975, recorded from southern Hainan Island in China (Dai *et al.* 1986: 426; Dai & Yang 1991: 467; Shih *et al.* 2010b), the remaining 16 species are found from the islands of eastern Asia, viz. Taiwan, the Ryukyus, Ogasawara Islands, and the main islands of Japan (Table 1).

TABLE 1. The records of 18 *Uca* species from East Asia (Taiwan, Japan, China and Korea); n, total species number; ?, questionable record. Also see Remarks for each species and Shih *et al.* (2010b).

	Taiwan (n=15)					Japan (n=13)			China (n=11)		Korea (n=2)
	Taiwan	Penghu	Kimmen	Matsu	Dongsha	main islands of Japan	Ryukyus	Bonin Islands	continental China	Hainan	
<i>U. acuta</i>	*		*						*	*	
<i>U. annulipes</i>										*	
<i>U. arcuata</i>	*	*	*			*	*		*	*	*
<i>U. boninensis</i>								*			
<i>U. borealis</i>	*	*	*	*		*			*	*	
<i>U. coarctata</i>	*	*					*			?	
<i>U. crassipes</i>	*	*			*	*	*				
<i>U. dussumieri</i>	*	*					*		?		
<i>U. formosensis</i>	*	*									
<i>U. jocelynae</i>	*	*			*		*				
<i>U. lactea</i>	*	*	*	*		*			*	*	*
<i>U. paradussumieri</i>	*		*						*	*	
<i>U. perplexa</i>	*	*			*	?	*				
<i>U. splendida</i>	*	*	?		*		*		*	*	
<i>U. tetragonon</i>	*	*			*		*			*	
<i>U. triangularis</i>	*	*					*		*		
<i>U. typhoni</i>										*	
<i>U. vocans</i>	*	*				?	*		?	*	
Total species number	15	13	5 (6?)	2	5	4 (6?)	10	1	7 (9?)	10 (11?)	2

Taiwan fiddler crabs. Twelve species of *Uca* were reported from the Taiwanese territory previously (Shih 1994; Shih et al. 2010a, 2012). Three additional three species (*U. acuta*, *U. paradussumieri* and *U. vocans*) are confirmed herein. All 15 species are recorded from the main island of Taiwan, with fewer species from adjacent islands, viz. Penghu, Kinmen, Matsu, and Dongsha, which makes the species richness of this region (Fig. 1) the highest in East Asia (Table 1).

Uca vocans is widely distributed in the western Pacific and found in the South China and East China seas (Crane 1975; Shih et al. 2010a). Its distribution in Taiwan, between the Ryukyus and Philippines, is not surprising because of the effect of the Kuroshio Current and the Kuroshio Branch on larval dispersal (Shih 2012a). The occurrence of *Uca paradussumieri* in Taiwan may be due to unstable oceanic currents that transported larvae from southeastern China. With a similar habitat to *U. paradussumieri*, the record of *U. acuta* from southwestern Taiwan in the 1850s was probably also caused by the unstable currents, although there were no additional record afterwards.

There are 13 species of *Uca* in Penghu (Table 1), but their habitats are mainly coarse coral sand, sparsely distributed by introduced mangroves (Shih 2008), different from the mudflat or mangroves of western Taiwan and coastal China. The dominant species of Penghu are *U. splendida* and *U. vocans* complex, which are different from the dominant *U. arcuata* and *U. lactea* in Taiwan (Shih 1997, 2008; Hung 2000; Shen & Jeng 2005; Shih et al. 2010a; this study). In addition to the insular environment of Penghu, its exclusive *Uca* composition is most possibly influenced by the Kuroshio Branch, which flows from the southern tip of Taiwan, while the main Kuroshio Current runs from the Philippines, through eastern Taiwan, to the Ryukyus (Jan et al. 2002; Shih 2012a).

Because Crane (1975) confirmed *U. borealis* (as *U. vocans borealis*) from northwestern Taiwan, all records of this species complex in the past were identified as *U. borealis* (Shih 1994; Ng et al. 2001). Based on Shih et al. (2010a) and this study, three species (*U. borealis*, *U. jocelynae*, and *U. vocans*) are recorded from Taiwan, being sympatric in some areas (see Remarks under *U. borealis*), which makes field identification difficult, especially for males with regenerated chela as well as females (see Crane 1975). Lu et al. (1997) studied the genetic structure of allozymes among four populations of *U. borealis* from Taiwan, viz. Jhuwei, Taipei; Siangshan (= Haishangu), Hsinchu; Mashagou, Tainan, and Toucheng, Yilan (cf. Fig. 1). They found that the three populations from western Taiwan were very close compared with the population from Yilan. The percentage of polymorphic loci from Yilan population was also the highest (71.4%). Because both *U. borealis* and *U. jocelynae* have been recorded from Yilan (Shih et al. 2010a; this study), it is possible that the two species were confused in the Yilan population.

The distributions of the three species of the *U. vocans* complex are also different in the Taiwanese territory. *Uca borealis* is found from northeastern region (Yilan), through western Taiwan, to southwestern region (e.g. Dapengwan in Pingtung) of Taiwan, as well as on the offshore islands of Penghu, Kinmen, and Matsu. In contrast, *U. jocelynae* is mainly found in eastern Taiwan, from Yilan, through eastern and southern Taiwan, to southwestern Tainan, as well as on the offshore islands of Penghu and Dongsha. The distribution of *Uca vocans* is similar, but narrower, to that of *U. jocelynae*, recorded from southern (Pingtung) and eastern Taiwan (Taitung), as well as from Penghu.

Only three species, *U. arcuata*, *U. borealis* and *U. lactea* were recorded previously from Kinmen (Wang & Liu 1996b; Ng et al. 2001). Our study confirms the distribution of *U. acuta* and *U. paradussumieri*, which increases the species number to five. The species composition of fiddler crabs between Kinmen and Xiamen (Fujian, China) are identical (Shih et al. 2010b; this study) since both areas are separated by a very narrow channel (width ca. 4.5 km) (Fig. 1).

No fiddler crab was recorded from Matsu Islands previously (Chen & Wu 2001; Ng et al. 2001). In our study, specimens of *Uca borealis* and *U. lactea* were collected from the mudflat in Cingshuei, Nangan, Matsu. These two species are also common in coastal region of China and Taiwan (Shih 1994; Dai et al. 1986; Dai & Yang 1991).

Ng et al. (2001) revised the crab fauna from the shallow water around Dongsha Island, but little known for the intertidal crabs of this island. In Shih's (2012b) guide book, five species of fiddler crabs, *U. crassipes*, *U. jocelynae*, *U. perplexa*, *U. splendida* and *U. tetragonon*, have been reported.

Japan fiddler crabs. Two species, *U. arcuata* and *U. lactea* were listed by De Haan (1835). Parisi (1918) added the records "*U. vocans*" (= *U. borealis*, see Remarks under *U. borealis*) and *U. pulchella* (= *U. crassipes*) from Misaki. Sakai (1934, 1935) reported *U. arcuata*, *U. lactea*, and *U. marionis nitidus* (= *U. borealis*) from Nagasaki, Kyushu. Crane (1975) listed the records of species from the main Japanese islands. The record of *U. vocans* from Wakayama (Yamashita & Yamanishi 1999) is likely to be *U. borealis* instead (see Remarks under *U. borealis*). Similarly, Kudo & Yamada (2000) mentioned *U. perplexa* was found in Wakayama based on personal

communication with Prof. Keiji Wada, which needs confirmation because this species is morphologically similar to *U. lactea* (see Remarks under *U. lactea*).

The *Uca* fauna of the Ryukyus is more diverse than that of the main Japanese islands. Stimpson (1858, 1907) listed two species, *Gelasimus vocans* (= *U. vocans*) and *U. dubius* (= *U. dussumieri*, see Remarks under *U. dussumieri*) from the Ryukyus. Balss (1922) reported *U. latreillei* (= *U. crassipes*), *U. marionis nitidus* (= *U. vocans*), and *U. arcuata* from Miyako Island. Miyake (1936) listed four species from Ishigaki, viz. *U. annulipes* (= *U. crassipes*), *U. lactea* (= *U. perplexa*), *U. dubia* (= *U. dussumieri*) and *U. marionis nitidus* (= *U. vocans*). Miyake (1963) added *U. triangularis* from the Ryukyus, and confirmed *U. dubia* is a synonym of *U. dussumieri*. Takeda (1973) listed a new record of *U. tetragonon* from Iriomote, with a list of seven known species from the Ryukyus. Sakai (1974) separated “*U. dubia*” from *U. dussumieri*, and later (Sakai 1976a, b) considered “*U. dubia*” is *U. coarctata*, not *U. dussumieri* in Crane (1975) (but see below and Remarks under *U. dussumieri*). Crane (1975) confirmed *U. dubia* as *U. dussumieri* as suggested by Miyake (1963), and also determined that “*U. lactea*” from the Ryukyus is actually *U. perplexa*, but she did not include the record of *U. arcuata* of Balss (1922). Yamaguchi (1994) mentioned “*U. neocultrimana*” from Ishigaki and Iriomote, which later identified as *U. jocelynae* by Shih *et al.* (2010a).

There is only one species of fiddler crab from Ogasawara Islands, *U. boninensis* Shih, Komai & Liu, 2013, which is endemic (see Remarks under *U. crassipes*).

Although Sakai (1976a) revised the fiddler crabs mainly based on Crane (1975), taxonomy of some species seem to be not well reflected. Crane (1975) treated *Gelasimus dubius* Stimpson, 1858 as a synonym of *U. dussumieri*, based on the description and figures of Stimpson (1858, 1907) and specimens of *G. dubius* in Sakai (1934, 1939, 1940), which agreed with Miyake’s (1963) identification. Sakai (1974, 1976a, b) nevertheless considered his “*U. dubia*” as a synonym of *U. coarctata*, not *U. dussumieri*. Based on the figures of the chela and carapace of *U. dubia* in Stimpson (1907: pl. 14), we agree it is *U. dussumieri* instead of *U. coarctata*.

Crane (1975) identified *Uca perplexa* from the Ryukyus, different from *U. lactea* from the main Japanese island and Taiwan. However, Sakai (1976a, b) have cited Crane (1975) but only used the name “*U. lactea lactea*”, for the species from the main Japanese islands, the Ryukyus and Taiwan. This may be a careless mistake, because all Japanese literature after Crane (1975) is using *U. perplexa* (e.g. Takeda 1982; Miyake 1983; Yoshigou 2001; Nakasone & Irei 2003; Fujita & Uyeno 2015).

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