Zoological Studies **61**:64 (2022)
doi:10.6620/ZS.2022.61-64

Zoological Studies

Special issue: Systematics and Biogeography of Fiddler Crabs

Open Access

Systematics and Biogeography of Fiddler Crabs – A Special Issue in *Zoological Studies*

Hsi-Te Shih[1] and Benny K. K. Chan[2,*]

[1]*Department of Life Science and Research Center for Global Change Biology, National Chung Hsing University, Taichung 402, Taiwan. E-mail: htshih@dragon.nchu.edu.tw (Shih)*
[2]*Biodiversity Research Center, Academia Sinica, Taipei 115, Taiwan. *Correspondence: E-mail: chankk@gate.sinica.edu.tw (Chan)*

Received 7 September 2022 / Accepted 9 September 2022 / Published 16 November 2022
Communicated by Ryuji Machida

Special issue: Systematics and Biogeography of Fiddler Crabs (articles 64–71). Editors: Hsi-Te Shih and Benny K. K. Chan

Fiddler crabs are a fantastic group of intertidal brachyuran crabs, and the research fields focused on their biodiversity, phylogeography, phylogenomics, and larval biology are still in developing stages. In this special issue, seven articles are included focusing on the diversity, phylogeography, mitogenome phylogeny and larval morphology of fiddler crabs, covering the regions of the Indo-West Pacific and Americas. Results from this special issue open up further opportunities to study new species identification based on an integrative taxonomy approach, genomic-level phylogeny and larval morphology, especially in regards to the mitogenomes in the genera *Cranuca*, *Gelasimus*, *Paraleptuca*, and *Uca* for filling up the knowledge gap of fiddler crabs in the world.

Key words: Fiddler crabs, Systematics integrative taxonomy, Mitogenomes, Larval biology, Phylogeny.

Fiddler crabs are a fantastic group of intertidal brachyuran crabs that have attracted attracting a lot of naturalists' focus on their natural history, including taxonomy, phylogeny, evolution, behavior, ecology, etc. (Crane 1975; Shih et al. 2016; Pardo et al. 2020; Perez et al. 2020). Among the literature, "Fiddler Crabs of the World" (Crane 1975) remains an important monograph influencing the modern studies of fiddler crabs (von Hagen 1976). With respect to systematics, Crane (1975) divided the fiddler crabs into nine subgenera, seven of which were erected by her. However, Bott (1973) published a revision of fiddler crabs which divided fiddler crabs into 10 genera with two additional subgenera. As a result, most of Crane's (1975) subgeneric names needed to be replaced by the generic names in Bott (1973), according to the priority of nomenclature (von Hagen 1976). In Beinlich and von Hagen (2006), the systematics of fiddler crabs was revised into eight subgenera, including a new subgenus *Cranuca* Beinlich & von Hagen (2006); the subgenus *Gelasimus* Latreille, 1817 has priority over *Mesuca* Bott, 1973; the subgenus *Uca* Latreille, 1817 including *Afruca* Crane, 1975; and the subgenus *Paraleptuca* Bott, 1973 including *Austruca* Bott, 1973, which were followed by the checklist of extant brachyuran crabs of the world (Ng et al. 2008).

New modern taxonomy and systematics involve both morphological and molecular approaches to study species lineages and can be applied to fiddler crabs. Levinton et al. (1996) and Sturmbauer et al. (1996) studied the phylogeny of fiddler crabs by using mitochondrial 16S rDNA (*16S*) from 27 species and concluded that fiddler crabs comprise the "Ancestral America Clade", "Derived American Clade" and "Indo-West Pacific Clade". However, few molecular studies of fiddler crabs were conducted between then and 2009, although the above two references have been cited and discussed in the revisions of Rosenberg (2001) and Beinlich and von Hagen (2006).

By using the mitochondrial *16S* and cytochrome oxidase subunit I (*COI*) and nuclear 28S rDNA (*28S*), Shih et al. (2016) revised the family Ocypodidae

Citation: Shih HT, Chan BKK. 2022. Systematics and biogeography of fiddler crabs – a special issue in *Zoological Studies*. Zool Stud **61**:64. doi:10.6620/ZS.2022.61-64.

from 78 species of fiddler crabs and 13 ghost crabs (genus *Ocypode*). The molecular phylogeny of fiddler crabs showed the group was paraphyletic, which was hardly accepted by most traditional naturalists, but the molecular phylogenetic results largely agreed with Levinton et al. (1996: fig. 2), *i.e.*, one clade formed the subfamily Gelasiminae, but *Ocypode* and another formed the subfamily Ocypodinae. The latest revision in fiddler crabs based on molecular evidence raised all the subgenera of fiddler crabs to 11 full genera, except *Australuca* Crane, 1975, which has been synonymized with *Tubuca* Bott, 1973. The latest systematics and phylogenetic trees established by Shih et al. (2016) have been applied for the evolution of synchronous waving behaviors (Backwell 2019; Perez et al. 2020) and above-ground sedimentary structures (Pardo et al. 2020).

An alternative taxonomic grouping of fiddler crabs proposed by Rosenberg (2019) adopted the subfamily Ucinae Dana, 1851 and grouped species into tribes and subgenera. However, this system was not supported consistently by the current available genetic data (Shih et al. 2016) and was not followed by later taxonomic studies (*e.g.*, Shih and Poupin 2018; Sasaki 2019; Michie et al. 2021; Shih et al. 2021) and the World Register of Marine Species (WoRMS 2022).

Since 2009, a series of phylogenetic or taxonomic papers using mitochondrial and nuclear markers (*e.g.*, Shih et al. 2009 2013b) have been published and have supported two new subgenera (*Uca* (*Petruca*) Shih, Ng & Christy, 2015 and *Uca* (*Xeruca*) Shih, 2015) (Shih 2015; Shih et al. 2015a), six new species (*Austruca citrus* Shih & Poupin, 2020, *Austruca occidentalis* (Naderloo, Schubart & Shih, 2016), *Gelasimus jocelynae* (Shih, Naruse & Ng, 2010), *Minuca osa* (Landstorfer & Schubart, 2010), *Paraleptuca boninensis* (Shih, Komai & Liu, 2013), *Tubuca alcocki* Shih, Chan & Ng, 2018) (Landstorfer and Schubart 2010; Shih et al. 2010 2013a 2018; Naderloo et al. 2016; Shih and Poupin 2020), and two resurrected species (*Paraleptuca splendida* (Stimpson, 1858) and *Austruca variegata* (Heller, 1862)) (Shih et al. 2012 2019) (Fig. 1). Many studies on the phylogeography of fiddler crabs were reported from the Indo-West Pacific (Silva et al. 2010; Aoki and Wada 2013; Shih et al. 2015b; Fratini et al. 2016; Nehemia and Kochzius 2017; Tokuyama et al. 2020; Hardianto et al. 2022) and Atlantic-East Pacific regions (Sanford et al. 2006; Wieman et al. 2013; Staton et al. 2014; Laurenzano et al. 2012 2013 2016; Thurman et al. 2018 2021). With regard to the mitogenomes, 10 species of fiddler crabs and three species of *Ocypode* are available (see Liu and Shih 2022). The fields of study of fiddler crab biodiversity, phylogeography, larval morphology and mitogenomes are still in the developing stages.

In this special issue, seven articles are included focusing on regional fauna, phylogeography, mitogenome phylogeny and larval morphology, covering the regions of the Indo-West Pacific and Americas. Two articles about the diversity of fiddler crabs from around the Arabian Sea (Shih et al. 2022a) and Vietnam (Shih et al. 2022b), confirmed by the DNA barcoding analyses, reveal the composition of faunas with biogeographical discussion. Two phylogeographic articles of *Letpuca thayeri* (Rathbun, 1900) and *Uca maracoani* (Latreille, 1803) along the tropical West Atlantic (Marochi et al. 2022), as well as *Tubuca arcuata* (De Haan, 1835) in East Asia and Vietnam (Shih et al. 2022c), contribute to the understanding of the potential mechanisms of population composition. A phylogeny based on the mitogenomes of the Taiwan endemic *Xeruca formosensis* (Rathbun, 1921) and other members of the Ocypodidae (Liu and Shih 2022) further confirms the systematics of this family established by Shih et al. (2022). The complete larval stages of *Austruca albimana* (Kossmann, 1877) from the Red Sea (Kumar and Al-Aidaroos 2022) and the first zoeal stage of 15 species from Taiwan (Zhang and Shih 2022) show the importance of larval morphology to the taxonomy and systematics of fiddler crabs.

For the future studies of taxonomy and systematics of fiddler crabs, the following topics are suggested. First, more species, either new or resurrected species, supported by molecular evidence, will be published (personal communication and unpublished by HT Shih) to contribute to the diversity of fiddler crabs. Second, although a preliminary phylogenetic analysis based on multiple markers, viz. *16S*, *COI* and *28S*, as well as a nuclear histone 3, showed the same pattern with Shih et al. (2016) (unpublished data by HT Shih), using more genetic markers, mitogenomes, or even whole genomes, of fiddler crabs, especially species of the genera *Uca* and *Afruca*, as well as *Ucides* Rathbun, 1897, will strengthen the systematics of the Ocypodidae. Third, by analyzing the phylogeographic patterns of more species, we will be able to understand the underlying mechanisms of the species distribution within a region. Finally, more studies of species with complete larval stages, especially the species of the genera *Cranuca*, *Gelasimus*, *Paraleptuca*, and *Uca*, may reveal more reliable larval characters to provide additional morphological evidence to taxonomy and systematics.

We thank Dr. Ryuji Machida for helping process manuscripts and all the reviewers for helping improve the manuscripts of this issue. The photographs provided by Patricia Backwell, Meng-Hsien Chuang, Taisuke Iwano and Mani Prema are appreciated.

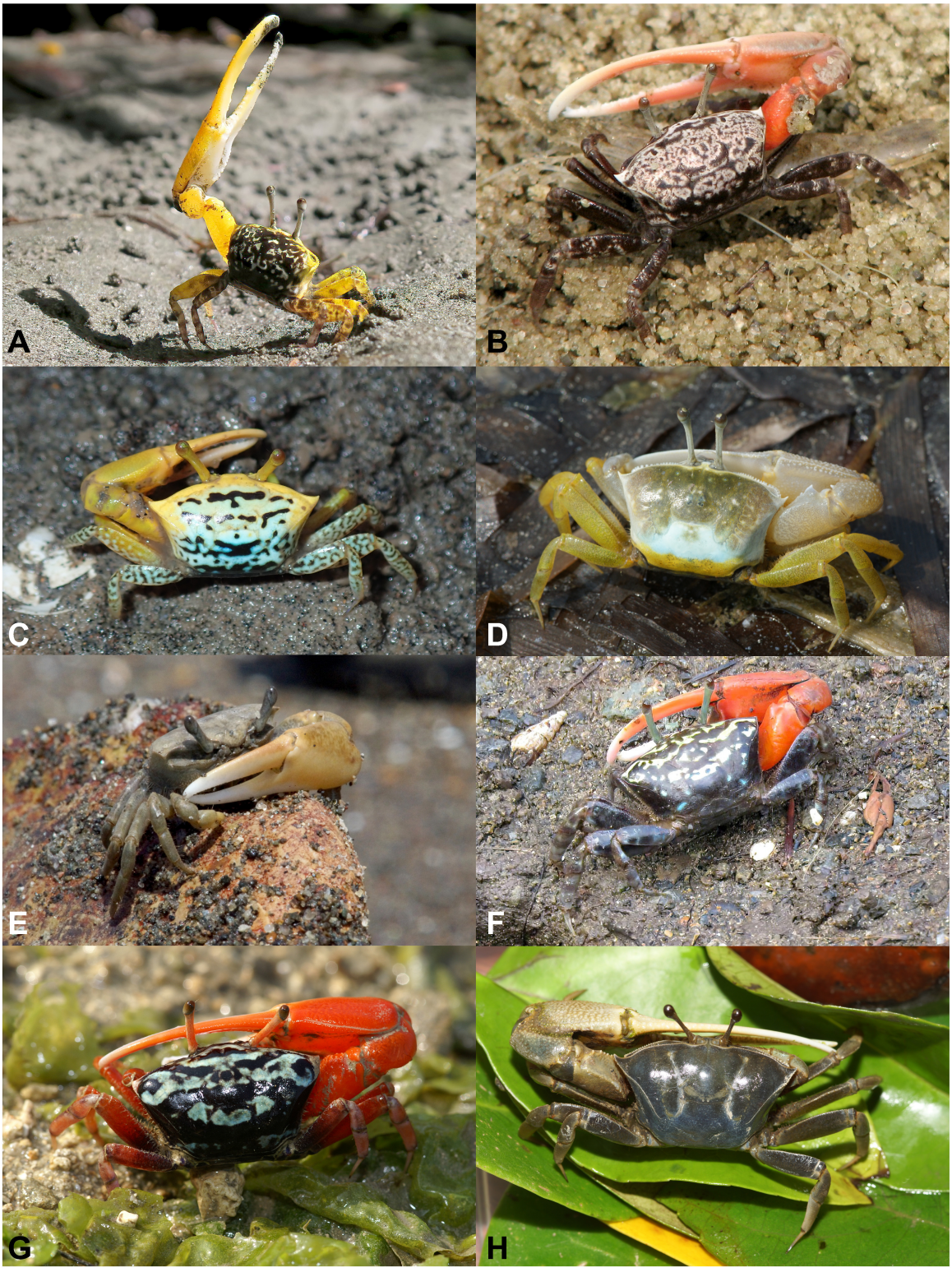

Fig. 1. Photographs of some taxa of fiddler crabs published as new or resurrected recently. A, *Austruca citrus* Shih & Poupin, 2020 (Fiji); B, *Austruca occidentalis* Naderloo, Schubart & Shih (Inhaca, Mozambique); C, *Austruca variegata* (Heller, 1862) (Vellar River estuary, Tamil Nadu, India); D, *Gelasimus jocelynae* (Shih, Naruse & Ng, 2010) (Dongsha Island, Taiwan); E, *Petruca panamensis* (Stimpson, 1859) (Panama); F, *Paraleptuca boninensis* (Shih, Komai & Liu, 2013) (Ogasawara Islands, Japan); G, *Paraleptuca splendida* (Stimpson, 1858) (Penghu, Taiwan); H, *Tubuca alcocki* Shih, Chan & Ng, 2018 (Ranong, Thailand). Photographs courtesy of T. Iwano (A), P. Backwell (B, E), M. Prema (C) and M.-H. Chuang (F).

REFERENCES

Aoki M, Wada K. 2013. Genetic structure of the wide-ranging fiddler crab *Uca crassipes* in the West Pacific region. J Mar Biol Assoc UK **93:**789–795. doi:10.1017/S0025315412001178.

Backwell PRY. 2019. Synchronous waving in fiddler crabs: a review. Curr Zool **65:**83–88. doi:10.1093/cz/zoy053.

Beinlich B, Hagen HO von. 2006. Materials for a more stable subdivision of the genus *Uca* Leach. Zool Meded Leiden **80:**9–32.

Bott R. 1973. Die verwandtschaftlichen Beziehungen der *Uca*-Arten. Senck Biol **54:**315–325.

Crane J. 1975. Fiddler Crabs of the World (Ocypodidae: Genus *Uca*). Princeton University Press, Princeton, New Jersey, 23+736 pp.

Fratini S, Ragionieri L, Cannicci S. 2016. Demographic history and reproductive output correlates with intraspecific genetic variation in seven species of Indo-Pacific mangrove crabs. PLoS ONE **11:**e0158582. doi:10.1371/journal.pone.0158582.

Hagen HO von. 1976. Review of Jocelyn Crane: Fiddler Crabs of the World. Ocypodidae: Genus *Uca*. Crustaceana **31:**221–224. doi:10.1163/156854076X00314.

Hardianto E, Wijayanti DP, Shy JY, Mather P, Hughes J, Imai H. 2022. Molecular ecology of the fiddler crab *Austruca perplexa* (H. Milne Edwards, 1852): genetic divergence along a major biogeographical barrier, Wallace's Line. Biological J Linn Soc **135:**310–321. doi:10.1093/biolinnean/blab142.

Kumar AAJ, Al-Aidaroos AM. 2022. Larval development of the mangrove fiddler crab *Austruca albimana* (Kossmann, 1877) (Crustacea: Brachyura: Ocypodidae) under laboratory conditions. Zool Stud **61:**70. doi:10.6620/ZS.2022.61-70.

Landstorfer RB, Schubart CD. 2010. A phylogeny of Pacific fiddler crabs of the subgenus *Minuca* (Crustacea, Brachyura, Ocypodidae: *Uca*) with the description of a new species from a tropical gulf in Pacific Costa Rica. J Zool Syst Evol Res **48:**213–218. doi:10.1111/j.1439-0469.2009.00554.x.

Laurenzano C, Costa TM, Schubart CD. 2016. Contrasting patterns of clinal genetic diversity and potential colonization pathways in two species of Western Atlantic fiddler crabs. PLoS ONE **11:**e0166518. doi:10.1371/journal.pone.0166518.

Laurenzano C, Farías NE, Schubart CD. 2012. Mitochondrial genetic structure of two populations of *Uca urugayensis* fails to reveal an impact of the Rio de la Plata on gene flow. Nauplius **20:**15–25. doi:10.1590/S0104-64972012000100003.

Laurenzano C, Mantelatto FLM, Schubart CD. 2013. South American homogeneity versus Caribbean heterogeneity: population genetic structure of the western Atlantic fiddler crab *Uca rapax* (Brachyura, Ocypodidae). J Exp Mar Biol Ecol **449:**22–27. doi:10.1016/j.jembe.2013.08.007.

Levinton JS, Sturmbauer C, Christy J. 1996. Molecular data and biogeography: resolution of a controversy over evolutionary history of a pan-tropical group of invertebrates. J Exp Mar Biol Ecol **203:**117–131. doi:10.1016/0022-0981(96)02573-7.

Liu MY, Shih HT. 2022. The complete mitogenome of *Xeruca formosensis* (Rathbun, 1921) (Crustacea: Brachyura: Ocypodidae), a fiddler crab endemic to Taiwan, with its phylogenetic position in the family. Zool Stud **61:**69. doi:10.6620/ZS.2022.61-69.

Marochi MZ, Tangerina M, Rodrigues R, Laurenzano C, Vilegas W, Costa TM, Schubart CD. 2022. Phylogeographic structure within the fiddler crabs *Leptuca thayeri* and *Uca maracoani* (Brachyura, Ocypodidae) along the tropical West Atlantic. Zool Stud **61:**67. doi:10.6620/ZS.2022.61-67.

Michie LA, Barnes RSK, Clark PF, Bennett WA, Cragg SM. 2021. Distinguishing ten sympatric species of fiddler crab (Decapoda: Ocypodidae) using a suite of phenotypic characteristics. Zootaxa **5026:**480–506. doi:10.11646/zootaxa.5026.4.2.

Naderloo R, Schubart CD, Shih HT. 2016. Genetic and morphological separation of *Uca occidentalis*, a new East African fiddler crab species, from *Uca annulipes* (H. Milne Edward, 1837) (Crustacea: Decapoda: Brachyura: Ocypodidae). Zool Anz **262:**10–19. doi:10.1016/j.jcz.2016.03.010.

Nehemia A, Kochzius M. 2017. Reduced genetic diversity and alteration of gene flow in a fiddler crab due to mangrove degradation. PLoS ONE **12:**e0182987. doi:10.1371/journal.pone.0182987.

Ng PKL, Guinot D, Davie PJF. 2008. Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. Raffles Bull Zool Suppl **17:**1–296.

Pardo JCF, Stefanelli-Silva G, Christy JH, Costa TM. 2020. Fiddler crabs and their above-ground sedimentary structures: a review. J Ethol **38:**137–154. doi:10.1007/s10164-020-00647-1.

Perez DM, Crisigiovanni EL, Pie MR, Rorato AC, Lopes SR, Araujo SBL. 2020. Ecology and signal structure drive the evolution of synchronous displays. Evolution **74:**434–446. doi:10.1111/evo.13841.

Rosenberg MS. 2001. The systematics and taxonomy of fiddler crabs: a phylogeny of the genus *Uca*. J Crustacean Biol **21:**839–869. doi:10.1163/20021975-99990176.

Rosenberg MS. 2019. A fresh look at the biodiversity lexicon for fiddler crabs (Decapoda: Brachyura: Ocypodidae). Part 1: taxonomy. J Crustacean Biol **39:**729–738. doi:10.1093/jcbiol/ruz057.

Sanford E, Holzman SB, Haney RA, Rand DM, Bertness MD. 2006. Larval tolerance, gene flow, and the northern geographic range limit of fiddler crabs. Ecology **87:**2882–2894. doi:10.1890/0012-9658(2006)87[2882:ltgfat]2.0.co;2.

Sasaki J. 2019. The species list of Decapoda, Euphausiacea, and Stomatopoda, all of the world, version 03-3.1. Local Independent Administrative Agency Hokkaido Research Organization, Resources Management and Enhancement Division, Abashiri Fisheries Research Institute, Fisheries Research Department, Hokkaido, Japan, 14644 pp. doi:10.13140/RG.2.2.22353.89446.

Shih HT. 2015. *Uca* (*Xeruca*), a new subgenus for the Taiwanese fiddler crab *Uca formosensis* Rathbun, 1921 (Crustacea: Decapoda: Ocypodidae), based on morphological and molecular evidence. Zootaxa **3974:**151–169. doi:10.11646/zootaxa.3974.2.1.

Shih HT, Chan BKK, Ng PKL. 2018. *Tubuca alcocki*, a new pseudocryptic species of fiddler crab from the Indian Ocean, sister to the southeastern African *T. urvillei* (H. Milne Edwards, 1852) (Crustacea, Decapoda, Brachyura, Ocypodidae). ZooKeys **747:**41–62. doi:10.3897/zookeys.747.23468.

Shih HT, Kamrani E, Davie PJF, Liu MY. 2009. Genetic evidence for the recognition of two fiddler crabs, *Uca iranica* and *U. albimana* (Crustacea: Brachyura: Ocypodidae), from the northwestern Indian Ocean, with notes on the *U. lactea* species-complex. Hydrobiologia **635:**373–382. doi:10.1007/s10750-009-9930-6.

Shih HT, Komai T, Liu MY. 2013a. A new species of fiddler crab from the Ogasawara (Bonin) Islands, Japan, separated from the widely-distributed sister species *Uca* (*Paraleptuca*) *crassipes* (White, 1847) (Crustacea: Decapoda: Brachyura: Ocypodidae). Zootaxa **3746:**175–193. doi:10.11646/zootaxa.3746.1.8.

Shih HT, Liu MY, Aoki M, Suzuki H. 2022. Phylogeography of the fiddler crab *Tubuca arcuata* (Crustacea: Brachyura: Ocypodidae) in East Asia and northern Vietnam. Zool Stud **61:**68. doi:10.6620/ZS.2022.61-68.

Shih HT, Low MEY, Ng PKL. 2021. The nomenclature, identity and

synonyms of *Cancer vocans minor* Herbst, 1782 and *Gelasimus caerulens* Adams, 1847 (Decapoda, Brachyura, Ocypodidae). Crustaceana **94:**207–225. doi:10.1163/15685403-bja10077.

Shih HT, Naruse T, Ng PKL. 2010. *Uca jocelynae* sp. nov., a new species of fiddler crab (Crustacea: Brachyura: Ocypodidae) from the Western Pacific. Zootaxa **2337:**47–62. doi:10.5281/zenodo.193214.

Shih HT, Ng PKL, Christy JH. 2015a. *Uca* (*Petruca*), a new subgenus for the rock fiddler crab *Uca panamensis* (Stimpson, 1859) from Central America, with comments on some species of the American broad-fronted subgenera. Zootaxa **4034:**471–494. doi:10.11646/zootaxa.4034.3.3.

Shih HT, Ng PKL, Davie PJF, Schubart CD, Türkay M, Naderloo R, Jones DS, Liu MY. 2016. Systematics of the family Ocypodidae Rafinesque, 1815 (Crustacea: Brachyura), based on phylogenetic relationships, with a reorganization of subfamily rankings and a review of the taxonomic status of *Uca* Leach, 1814, sensu lato and its subgenera. Raffles Bull Zool **64:**139–175.

Shih HT, Ng PKL, Liu MY. 2013b. Systematics of the Indo-West Pacific broad-fronted fiddler crabs (Crustacea: Ocypodidae: genus *Uca*). Raffles Bull Zool **61:**641–649.

Shih HT, Ng PKL, Ravichandran S, Prema M. 2019. Resurrection of *Gelasimus variegatus* Heller, 1862, a fiddler crab closely related to *Austruca bengali* (Crane, 1975) and *A. triangularis* (A. Milne-Edwards, 1873) (Decapoda, Brachyura, Ocypodidae), from the Bay of Bengal, Indian Ocean. Zool Stud **58:**12. doi:10.6620/ZS.2019.58-12.

Shih HT, Ng PKL, Wong KJH, Chan BKK. 2012. *Gelasimus splendidus* Stimpson, 1858 (Crustacea: Brachyura: Ocypodidae), a valid species of fiddler crab from the northern South China Sea and Taiwan Strait. Zootaxa **3490:**30–47. doi:10.11646/zootaxa.3490.1.2.

Shih HT, Poupin J. 2020. A new fiddler crab of *Austruca* Bott, 1973, closely related to *A. perplexa* (H. Milne Edwards, 1852) (Crustacea: Brachyura: Ocypodidae), from the South Pacific islands. Zool Stud **59:**26. doi:10.6620/ZS.2020.59-26.

Shih HT, Prema M, Kumar AJ, Saher NU, Ravichandran S, Odhano S, Paulay G. 2022. Diversity and distribution of fiddler crabs (Crustacea: Brachyura: Ocypodidae) around the Arabian Sea. Zool Stud **61:**64. doi:10.6620/ZS.2022.61-64.

Shih HT, Saher NU, Kamrani E, Ng PKL, Lai YC, Liu MY. 2015b. Population genetics of the fiddler crab *Uca sindensis* (Alcock, 1900) (Crustacea: Brachyura: Ocypodidae) from the Arabian Sea. Zool Stud **54:**1. doi:10.1186/s40555-014-0078-3.

Shih HT, Wong KJH, Chan BKK, Nguyen TS, Do VT, Ngo XQ, Hsu PY. 2022. Diversity and distribution of fiddler crabs (Crustacea: Brachyura: Ocypodidae) in Vietnam. Zool Stud **61:**65. doi:10.6620/ZS.2022.61-65.

Silva IC, Mesquita N, Paula J. 2010. Lack of population structure in the fiddler crab *Uca annulipes* along an East African latitudinal gradient: genetic and morphometric evidence. Mar Biol **157:**1113–1126. doi:10.1007/s00227-010-1393-9.

Staton JL, Borgianini SA, Gibson IB, Brodie RJ, Greig TW. 2014. Limited gene flow in *Uca minax* (LeConte 1855) along a tidally influenced river system. Cent Eur J Biol **9:**28–36. doi:10.2478/s11535-013-0200-7.

Sturmbauer C, Levinton JS, Christy J. 1996. Molecular phylogeny analysis of fiddler crabs: test of the hypothesis of increasing behavioral complexity in evolution. Proc Natl Acad Sci USA **93:**10855–10857. doi:10.1073/pnas.93.20.10855.

Thurman CL, Alber RE, Hopkins MJ, Shih HT. 2021. Morphological and genetic variation among populations of the fiddler crab *Minuca burgersi* (Holthuis, 1967) (Crustacea: Brachyura: Ocypodidae) from shores of the Caribbean Basin and western South Atlantic Ocean. Zool Stud **60:**19. doi:10.6620/ZS.2021.60-19.

Thurman CL, Hopkins MJ, Brase AL, Shih HT. 2018. The unusual case of the widely distributed fiddler crab *Minuca rapax* (Smith, 1870) from the western Atlantic: an exemplary polytypic species. Invertebr Syst **32:**1465–1490. doi:10.1071/IS18029.

Tokuyama T, Shy J-Y, Lin H-C, Henmi Y, Mather P, Hughes J, Tsuchiya M, Imai H. 2020. Genetic population structure of the fiddler crab *Austruca lactea* (De Haan, 1835) based on mitochondrial DNA control region sequences. Crustacean Res **49:**141–153. doi:10.18353/crustacea.49.0_141.

Wieman AC, Berendzen PB, Hampton KR, Jang J, Hopkins MJ, Jurgenson J, McNamara JC, Thurman CL. 2014. A panmictic fiddler crab from the coast of Brazil? Impact of divergent ocean currents and larval dispersal potential on genetic and morphological variation in *Uca maracoani*. Mar Biol **161:**173–185. doi:10.1007/s00227-013-2327-0.

WoRMS. 2022. Ocypodidae Rafinesque, 1815. Available at: https://www.marinespecies.org/aphia.php?p=taxdetails&id=106773. Accessed on 17 Aug. 2022.

Zhang YC, Shih HT. 2022. First zoeal stage of 15 species of fiddler crabs (Crustacea: Brachyura: Ocypodidae) from Taiwan. Zool Stud **61:**61. doi:10.6620/ZS.2022.61-61.