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

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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
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 bonimensis* (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 maracoanii* (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 *Australuca albimana* (Kossmann, 1877) from the Red Sea (Kumar and Al-Aidaroso 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.

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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 splendid*a (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).
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