A fresh look at the biodiversity lexicon for fiddler crabs (Decapoda: Brachyura: Ocypodidae). Part 1: Taxonomy

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ABSTRACT

Fiddler crabs (Ocypodidae) have gone through a gradual series of taxonomic revisions and refinements over the last 40 years, culminating most recently with an expansion from a single genus into eleven different genera. I examine the opportunities presented by these revisions with respect to establishing formal names for previously established clades at a variety of taxonomic levels that were otherwise previously impossible to name due to historical compression of these crabs into a single genus, including the establishment or reestablishment of three tribes (Ucini, Gelasimini, and Minucini) and ten subgenera: Uca (Uca), Uca (Acanthoplax), Gelasimus (Gelasimus), Gelasimus (Mesuca), Austruca (Austruca), Austruca (Ganuca), Austruca (Sinduca), Tubuca (Tubuca), Tubuca (Australuca), and Tubuca (Augustuca). A previously overlooked synonymy between Gelasimus excisa (Nobili, 1906) and G. neocultrimana (Bott, 1973) is discussed, and the former name is adopted as valid.

Key Words: Gelasimus, ghost crabs, new tribes, new subgenera, systematics, Uca

INTRODUCTION

Fiddler crabs (Ocypodidae Rafinesque, 1815) are well-known brachyuran crabs inhabiting shorelines worldwide across the tropics and well into the temperate zones. Despite their rather small size and somewhat shy nature around humans, their colorful markings, aggressive waving and fighting behaviors, and the seemingly absurd claw asymmetry found in males makes them a charismatic group, popular with both amateur naturalists as well as in scientific studies. As with many other groups of organisms, the taxonomy of fiddler crabs has gradually shifted over time as new studies, technologies, and scientific attitudes have led to new and different insights into the evolutionary history of these species. The last truly comprehensive revision and study of the taxonomy of fiddler crabs (Crane, 1975) has served as a benchmark for all subsequent works of Crane (1975) and Bott (1973); Crane’s names were more widely recognized, and the goal of this work is to consider the current status of fiddler crab taxonomy in light of these recent changes, identify opportunities in our current classification for better describing known and likely clades, clarify a taxonomic ambiguity that has been left unresolved, and highlight places where more work is necessary.

ABOVE AND BEYOND THE GENUS: THE HIGHER-LEVEL TAXONOMY

Fiddler crab species have usually been considered members of a single genus: Gelasimus Latreille, 1817 for most of the 19th century and Uca Leach, 1814 starting after 1897 when the priority of this name was recognized (Rathbun, 1897). Proposed subdivisions within the genus largely started with the split of the Eastern Pacific species into two subgenera by Bott (1954): Uca (the narrow-front species) and Minuca Bott, 1954 (the broad-front species). More widespread divisions of the genus began with the competing works of Crane (1975) and Bott (1973); Crane’s names were more

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widely recognized and thought to better represent true systematic clusters, but Bott’s names had taxonomic priority (von Hagen, 1976; Rosenberg, 2001). Since the mid-1990s, as additional morphological characterization and formal molecular phylogenetic methods were applied to the genus, a number of studies proposed to contract or expand the various subgenera (Rosenberg, 2001; Beilich & von Hagen, 2006; Spivak & Cuesta, 2009; Shih, 2015; Shih et al., 2015). Outside of a number of largely ignored, informal superspecies designations by Crane (1975), little additional effort was made to further subdivide the species within subgenera. Because Crane (1975) treated many of the now-recognized species as subspecies the subsequent literature often refers to the larger groups of formerly-single-species-under-Crane as semi-formally recognized taxa, e.g., the vocas species complex (Shih et al., 2010, 2016a; Rosenberg, 2013) or the lactea species complex (Shih et al., 2009, 2010; 2013b; Naderloo et al., 2010, 2016). Because all fiddler crabs were otherwise considered a single genus, higher-level taxonomic names only served to express relationships between fiddler crabs and closely related clades such as ghost crabs (Ocypode Weber, 1795) and mangrove crabs (Ucides Rathbun, 1897).

Shih et al. (2016b) upended this system with their conclusion that fiddler crabs were paraphyletic without the inclusion of ghost crabs. This paraphyly had been seen in earlier works with that fiddler crabs were paraphyletic without the inclusion of phylogenetically contained within another; see below). Shih all fiddlers (one of the former subgenera was abandoned as it was genus monophyly forced them to abandon the traditional concept of the higher-order names across fiddler crabs. The lack of fiddler crab error likely not reflecting the true evolutionary history of these crabs. With their larger data set and high phylogenetic support, Shih et al. (2016b) embraced this result and used it to reorganize higher-order names across fiddler crabs. The lack of fiddler crab monophyly forced them to abandon the traditional concept of the genus Uca as a single taxonomic name capturing all fiddler crabs; instead all but one of the former subgenera were raised to generic status and no single taxonomic name can be used to refer to all fiddlers (one of the former subgenera was abandoned as it was phylogenetically contained within another, see below). Shih et al. (2016b) organized these genera into two subfamilies: Ocypodinae Rafinesque, 1815 (containing the fiddler crab genera Uca and Afruca Crane, 1975 as well as the ghost crabs, predominantly the genus Ocypode) and the Gelasminae Miers, 1886 (containing the other nine fiddler crab genera) (Fig. 1). A third subfamily, Ucidinae Dana, 1851, contains the mangrove crab genus Ucides. The relationship between Uca, Afruca, and Ocypode was left unresolved by Shih et al. (2016b), such that it was not clear whether the two fiddler crab genera formed a clade separate from Ocypode. The World Register of Marine Species (WoRMS, 2019) currently assumes these two fiddler crab genera are a clade, represented by the subfamily Ucinae Dana, 1851, reserving Ocypodinae for just the ghost crabs (Fig. 1).

The hypothesis/result that fiddler crabs are paraphyletic with respect to ghost crabs is not without controversy. To many researchers (MSR, unpublished data), this result seems biologically implausible (although by no means impossible), as it appears to have written off the result as a taxonomic reconstruction (1996) and Sturmbauer et al. 2009, 2010; 2013b; Naderloo et al., 2010, 2016). Because all fiddler crabs were otherwise considered a single genus, higher-level taxonomic names only served to express relationships between fiddler crabs and closely related clades such as ghost crabs (Ocypode Weber, 1795) and mangrove crabs (Ucides Rathbun, 1897).

Figure 1. Outline of the phylogeny of fiddler, ghost, and mangrove crabs (after Shih et al., 2016), indicating subfamily designations as given in Shih et al. (2016b) and World Register of Marine Species (WoRMS) (5 April 2019).
It has long been accepted that fiddler crabs consist of three primary groups corresponding to broad geographic distributions (Levinton et al., 1996; Rosenberg, 2001). The first group to diverge consists of the Eastern Atlantic species ($Afriuca$) and the American narrow-front species ($Uca$) (equivalent to Ucinae above), combined into a clade with Oxypodidae by Shih et al. (2016b). The remaining fiddler crabs form a clade (Gelasiminae) with two major subclades: the American broad-front species and the Indian and Western Pacific oceans species (Indo-West Pacific, or IWP, region). The American broad-front and IWP clades have long been recognized (Levinton et al., 1996; Sturmbauer et al., 1996; Rosenberg, 2001) but remain formally unnamed, in part due to taxonomic limitations imposed by the tradition of treating all fiddler crabs as a single genus.

With the expansion of fiddler crab species to multiple genera and subfamilies and to aid in clarity of communication it seems clear that these latter two subclades should receive formal names, with tribe being the obvious rank. The American broad-front species should be referred to as the tribe Minucini tribus nov. with tribe being the obvious rank. The American broad-front species and the Indian and Western Pacific species (Indo-West Pacific, or IWP, region). The American broad-front and IWP clades have long been recognized (Levinton et al., 1996; Sturmbauer et al., 1996; Rosenberg, 2001) but remain formally unnamed, in part due to taxonomic limitations imposed by the tradition of treating all fiddler crabs as a single genus.

The American broad-front species form a clade (Gelasiminae) with two major subclades: the American broad-front species and the Indian and Western Pacific species (Indo-West Pacific, or IWP, region). The American broad-front and IWP clades have long been recognized (Levinton et al., 1996; Sturmbauer et al., 1996; Rosenberg, 2001) but remain formally unnamed, in part due to taxonomic limitations imposed by the tradition of treating all fiddler crabs as a single genus.

With the expansion of fiddler crab species to multiple genera and subfamilies and to aid in clarity of communication it seems clear that these latter two subclades should receive formal names, with tribe being the obvious rank. The American broad-front species should be referred to as the tribe Minucini tribus nov. (containing Minuca, Lepitca Bott, 1973 and Petruca Shih, Ng & Christy, 2015), and the IWP species should be referred to as the tribe Gelasmianes Miers, 1886 status nov. (containing Tubuca, Xeruca Shih, 2015, Gelasimus, Cranuca Beinlich & von Hagen, 2006, Paraleptuca Bott, 1973, and Austruca Bott, 1973). One could alternatively reserve Gelasmianes for just the IWP species and use Minucini for the American broad-front species, but that division would fail to recognize the clear relationship of those two clades relative to the Ucinae and Ocypodinae. For rank consistency across all of the groups, the tribe Ucini Dana, 1851 would contain Uca and Afruca (Fig. 2), following the WoRMS (2019) classification under the assumption that Uca and Afruca form a monophyletic group. The latter tribe was originally used by Pretzmann (1983) for all fiddler crabs when he accepted the multiple genera of Bott (1973) but would be restricted to only these two genera under the current system.

A clear advantage of these tribes is taxonomic stability as, unlike the subfamilies, the tribes would likely retain their identical meaning whether fiddler crabs are monophyletic or paraphyletic. If future studies find fiddler crabs to be monophyletic, Ucinae would have priority as the subfamily representing all fiddler crabs, with the subtribe Gelasmianes status nov., with the superfamilies Ucinae and Ocypodinae serving the role currently occupied by Ucinae.

**THE SUBGENERA ARE DEAD, LONG LIVE THE SUBGENERA**

With the former subgenera raised to generic status, there is now potentially room within the new genera for further delineation, which would seem useful in a few cases. Previous researchers have questioned the need for subgenera (e.g., von Hagen, 1976) and the majority of scientific publications since they were broadly introduced in the 1970s have tended to ignore them. It is fair to question whether increasing the complexity of our taxonomy by designating new subgenera is necessary now, when we have concluded splitting a single genus into multiple genera. In a few cases, I believe it is readily justified because we already use informal names to refer to some of these groups, e.g., the vocans species complex. Another important point to note is that the use of subgenera can be viewed as condition-dependent. Researchers can use them when they provide value or clarity but choose to ignore them when they do not.

For each genus discussed below, the initial designated subgenus is already a well-recognized group in the literature, with additional support from the phylogeny of Shih et al. (2016b). Additional subgenera are suggested as place-holders for the remaining species in the genus, generally based on strongly supported clades from that same phylogeny (exceptions will be noted).

**Gelasimus** currently consists of eight species; seven of these make up what has generally been referred to as the vocans species complex (Shih et al., 2010, 2016a; Rosenberg, 2013), defined as the subspecies grouped into a single species by Crane (1975). This group can be formally designated the subgenus Gelasimus Latreille, 1817 status nov., consisting of the species *G. bocarisi* (Crane, 1975), *G. damipi* (Crane, 1975), *G. excisa* (Nobili, 1906), *G. hesperia* (Crane, 1975), *G. jocelynae* (Shih, Naruse & Ng, 2010), *G. vocans* (Linnaeus, 1758), and *G. xeruca* (McNeill, 1920). The single remaining species in the genus, *G. tetragonon* (Herbst, 1790), is placed in the monotypic subgenus Mesuca Bott, 1973 status nov.

**Austruca** currently consists of 12 species; eight of these make up what has generally been referred to as the lactea species complex (Shih et al., 2009, 2010, 2013b; Naderloo et al., 2010, 2016), defined as the subspecies grouped into a single species by Crane (1975). This group can formally be designated the subgenus Austruca, consisting of *A. albimana* (Kossmann, 1877), *A. annulipes* (H. Milne Edwards, 1837), *A. crytica* (Naderloo, Türky & Chen, 2010; see Naderloo et al., 2010), *A. iranica* (Pretzmann, 1971), *A. lactea* (De Haan, 1835), *A. mjobergi* (Rathbun, 1924), *A. occidentalis* (Naderloo, Schubart & Shih, 2016), and *A. perplexa*.

![Figure 2](https://academic.oup.com/jcb/article-abstract/39/6/729/5614985/731)
The four other species in the genus can be divided among two additional new subgenera: Caneatoca subgen. nov., consisting of A. triangularis (A. Milne-Edwards, 1873), A. bengali (Crane, 1975), and A. variegata (Heller, 1862); and Sinduca subgen. nov., consisting of A. sindsensis (Alcock, 1900). The former is derived from the Latin for tapering (describing the sharppointing anterior-lateral angles of these species) and represents the pair of species formerly considered subspecies of Uca triangularis by Crane (1975) (the “triangularis-species complex” according to Shih et al., 2019), as well as A. variegata, a recently recognized (Shih et al. 2019) long-lost relative. In keeping with the current informal naming convention, Shih et al. (2019) suggest renaming this group the variegata species complex, demonstrating that a formal taxonomic name would be useful. Austruca sindensis is placed in its own subgenus because it occupies a basal division and does not appear to be closely related to any of the other species within the genus (Shih et al., 2016b); Sinduca derives its name from the same source as the type species, the Indus River where it was first found.

Tubuca also appears to be readily divisible into three subgenera based on Shih et al. (2016b): 1) subgenus Tubuca Bott, 1973 status nov., consisting of a clade of 11 species: T. alocoki Shih, Chan & Ng, 2018, T. arcuata (De Haan, 1833), T. capricornis (Crane, 1975), T. coerulata (H. Milne Edwards, 1832), T. demani (Ortmann, 1897), T. ducommieri (H. Milne Edwards, 1852), T. flammula (Crane, 1975), T. festipata (Adams & White, 1848), T. paradoxussaneri (Bott, 1973), T. typhoni (Crane, 1975) and T. uvariles (H. Milne Edwards, 1852); 2) subgenus Austruca Crane, 1975 status nov., consisting of a clade of seven species, T. bellator (White, 1847), T. elegans (George & Jones, 1982), T. hissitanus (George & Jones, 1982), T. longidigitum (Kingsley, 1880), T. polita (Crane, 1975), T. sessinella (Crane, 1975), and T. signata (Hess, 1865) (this subgenus was previously abandoned when Tubuca as a whole was considered a subgenus; with Tubuca now representing a full genus, the concept of Austruca can be reestablished within this new genus); and 3) subgenus Angustuca subgen. nov., consisting of three species, T. acuta (Stimpson, 1858), T. rhizophorae (Tweedie, 1950), and T. rosea (Tweedie, 1937). The phylogeny of Shih et al. (2016b) has these last three species basal to the remainder of the genus. In this tree (Shih et al., 2016b: fig. 2) these three species would be considered paraphyletic, but only due to a poorly-supported branch (as defined therein) under both Bayesian and Maximum Likelihood inference. I tentatively place them here in a single subgenus. The clustering of these three species is not novel; Crane (1975) treated them as the informal superspecies acuta, but since that is not particularly appropriate for a subgeneric designation (and would potentially confound and confuse older species/subspecies designations with subgenus/species designations), I propose the name Angustuca for the subgenus, derived from the Latin for “narrow” (and a synonym of “acute”).

The genus Uca has one clear, differentiated subgroup consisting of three species, which can be considered the subgenus Acanthophlos Milne Edwards, 1852: U. insignis (H. Milne Edwards, 1852), U. maracoani (Latreille, 1803), and U. ornata (Smith, 1870). These species are among the largest of all fiddler crabs and have uniquely shaped major claws, with extraordinarily wide and flat dactyl and pollex that more resembled pruningshears than the major claws of most other species. The remaining six species are tentatively placed in the subgenus Uca: U. heteroleuca (Smith, 1870), U. intermedia von Prahl & Toro, 1905, U. major (Herbst, 1702), U. monilifera Rathbun, 1915, U. princeps (Smith, 1870), and U. stylifera (H. Milne Edwards, 1852). The relationships among the species in this genus are generally not yet well enough known for confident subdivision.

Of the remaining seven genera, four are monospecific (Afruca, Canna, Xeruca, and Pituca); while the other three (Leftuca, Miuca, and Peraeuflexuca) currently lack the systematic clarity necessary for further subdivision.

**Species Taxonomic Notes**

As with many other groups, named species of fiddler crab have gone through waves of consolidation and expansion. Over the last few decades, the relationships among most of the historical names have largely stabilized with taxonomic advances mostly revolving around the recognition/discovery of cryptic species within formerly recognized single species (Novak & Salmon, 1974; Thurman, 1981; Naderoo et al., 2010, 2016; Shih et al., 2009, 2010, 2012, 2013a, 2018, 2019; Thurman et al., 2018); although a few purely novel species have been described as well (George & Jones, 1982; von Prahl & Toro, 1985; von Hagen, 1987; Landstorfer & Schubart, 2010).

One currently recognized species requires some discussion with respect to historical names and nomenclature: Gelasimus excisa (Nobili, 1906) versus G. neocultrimana (Bott, 1973).

Desmarest (1817) described a fossil crab under the Latin name Goneplax nitida (using “Goneplace huant” as a common name in French). Desmarest (1822) subsequently renamed this fossil Gelasima nitida, a reassignment later accepted by Milne Edwards (1837). Dana (1851) subsequently described a new species from Fiji as Gelasimus nitidus, apparently without reference or knowledge of Desmarest’s earlier name. Dana’s species became part of a complex of names, in particular with Uca marionis (Desmarest, 1823) and U. cultrimana (Adams & White, 1848), which were used for the same and/or very similar species or forms, all of which were eventually synonymized with Uca vocans by the 1970s.

Crane (1975) recognized six subspecies of Uca vocans, including a supposedly new subspecies, Uca vocans pacificiens Crane, 1975, found in Fiji. This name was later found to be a junior synonym of Metuca (Latuca) neocultrimana Bott, 1973, also described from Fiji (Rosenberg, 2004; Shih et al., 2010). Shih et al. (2016b) further sub-divided this species into two: U. neocultrimana with a range restricted to Fiji and nearby islands (American Samoa, Tuvalu, Tonga, Wallis and Futuna), and U. jocelynae, ranging throughout most of the Western Pacific islands west of Fiji, including Vanuatu, New Caledonia, Taiwan, the Philippines, Papua New Guinea, and the eastern half of Indonesia. The revision of Shih et al. (2016b) moved these species back to Gelasimus. Gelasimus neocultrimana is the only member of the group (subgenus Gelasimus as defined herein) found in Fiji; the other three or four species of fiddler crabs though to be found in Fiji are quite easily distinguished from G. neocultrimana.

Lost in all of these revisions was the fact that Dana’s (1851) Gelasimus nitidus was from Fiji. That being the case, Gelasimus nitidus should clearly be viewed as a synonym of G. neocultrimana and not a synonym of G. vocans. Gelasimus nitidus Dana 1851, however, cannot have priority because, as already mentioned, it is a junior homonym of Gelasima nitida Desmarest, 1822. This homonym was originally recognized by Nobili (1906: 313), who specifically and clearly suggested replacing Dana’s name nitida with the name excisa.

> “Le G. cultrimanus dans le sens de Kingsley et de Ortmann est identique avec le G. nitidus Dana. Ce dernier nom serait donc le nom de cette espèce ou variété, mais comme il y a déjà un Gelasimus nitidus Desmarest, espèce fossile, je propose pour cette forme le nom d’excisa.”

Of note is that Crane (1975) recognized that her name Uca vocans pacificiens could be a junior synonym of Dana’s species but felt that nitida should be avoided due to the confusion with Desmarest’s name. Crane (1975) also rejected use of excisa by Nobili (1906) as a replacement for nitida, because she claimed Nobili’s meaning was unclear and not tied to specific type specimens or locations. Her reasoning was unfortunately faulty as Nobili specifically suggested a replacement name for Dana’s species, thus inheriting his name-bearing type and type locality.
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*Gelasimus neocultrimana* (Bott, 1973) should therefore be recognized as a junior synonym of the senior name, *Gelasimus excisa* (Nobili, 1906).

**THE FUTURE OF FIDDLER-CRAB SYSTEMATICS**

While this work has been predominantly focused on taxonomy, three areas of inquiry with respect to the systematics of fiddler crabs stand out as critical to the next generation of studies.

1) What is the phylogenetic relationship between fiddler crabs and ghost crabs? Is it actually paraphyletic as suggested by Shih et al. (2016b) or was that result a data artifact?

2) What are the relationships of species within the genera and subgenera? A lot of progress has been made on understanding the broader relationships among the genera, but on the whole the species-level relationships are still quite uncertain, particularly within *Minuca* (18 species) and *Leptuca* (30 species).

3) Where will the next cryptic species be found? As molecular systematics have been more broadly applied to fiddler crabs, a number of geographically widespread species have recently been split into sets of more regional similar/cryptic species (Shih et al., 2009, 2010, 2012, 2018, 2019; Naderloo et al., 2010, 2016; Thurman et al., 2018), and it is likely more are waiting to be found. Species such as *Uca (Uca) princeps* (Crane, 1975; MSR, unpublished data), *Tabuca (Tabuca) forcipata* (MSR, unpublished data; H.T. Shih, personal communication), and *Minuca euad/onius* (Barnwell, 1968) have all been observed to encompass enough variation to raise questions as to whether they represent multi-species complexes currently hidden under a single name.

**OUTLINE OF THE TAXONOMIC HIERARCHY OF FIDDLER CRABS**

The lists of synonymous names and prior usages of each taxon are not included below as this outline, with the sole exception of *Gelasimus* (*Gelasimus*) excisa discussed above, does not change or challenge other recent revisions that otherwise contain identical such lists (e.g., Shih et al., 2016b). Species marked with † are only currently hidden under a single name.

**Family Ocypodidae** Rafinesque, 1815

**Subfamily Ucininae** Dana, 1851

**Tribe Ucini** Dana, 1851

*Type genus:* *Uca* Leach, 1814

**Genus Uca** Leach, 1814

*Type species:* *Uca (Uca) major* (Herbst, 1782)

See Shih et al. (2016b) for a recent diagnosis and description.

**Subgenus Uca (Uca) Leach, 1814**

*Type species:* *Uca (Uca) major* (Herbst, 1782)

Species included: *Uca (Uca) heteropleura* (Smith, 1870), *Uca (Uca) intermedia* von Prahl & Toro, 1985, *Uca (Uca) major* (Herbst, 1782), *Uca (Uca) monilifera* Rathbun, 1915, *Uca (Uca) oldroydi* Rathbun, 1926, *Uca (Uca) princeps* (Smith, 1870), *Uca (Uca) stylifera* (H. Milne Edwards, 1852)

*Diagnosis:* Medium to very large sized species (carapace breadth 25–50 mm); front narrow; dactyl, pollex of major chela of males somewhat broad, flat; dactyl with mildly convex upper margin, concave lower margin; upper margin of pollex often flat for half its length, but all species with clear gape when claw is closed.

**Remarks:** This subgenus is readily distinguished from subgenus *Acanthoplax* by the shape of the major chela, with the claws of *Uca* more similar to those of other fiddler crab species rather than the broad and flat shear-like shape of *Acanthoplax*. *Uca (Uca) monilifera* has a chela shape midway between the rest of the *Uca* and *Acanthoplax* making its placement within this subgenus tentative.

**Subgenus Uca (Acanthoplax)** H. Milne Edwards, 1852

*Type species:* *Uca (Acanthoplax) insignis* (H. Milne Edwards, 1852)

*Species included:* *Uca (Acanthoplax) antiqua* Brito, 1972, *Uca (Acanthoplax) insignis* (H. Milne Edwards, 1852), *Uca (Acanthoplax) maracoani* (Latreille, 1803), *Uca (Acanthoplax) mariae* Domínguez Alonso, 2008, *Uca (Acanthoplax) ornata* (Smith, 1870)

*Diagnosis:* Medium to very large sized species (carapace breadth 25–50 mm); front narrow; dactyl, pollex of major chela on males broad, flat; dactyl with strongly convex upper margin, markedly straight lower margin, generally with height exceeding that of pollex; upper margin of pollex also straight for 2/3 of its length, together leaving little-to-no gape when claw is closed.

**Remarks:** Among the largest fiddler crabs, the subgenus *Acanthoplax* is readily distinguished from the sister subgenus *Uca* by the unique shape of the major chela, with only *Uca (Uca) monilifera* having a shape approaching those of the *Acanthoplax*.

**Genus Afruca** Crane, 1975

*Type species:* *Afruca tangeri* (Eydox, 1835)

*Species included:* *Afruca miocenica* (Artal, 2008), *Afruca tangeri* (Eydox, 1835)

See Shih et al. (2016b) for a recent diagnosis and description.

**Subfamily Gelasiminae** Miers, 1886

**Tribe Gelasimini** Miers, 1886 *status nov.*

*Type genus:* *Gelasimus* Latreille, 1817

*Diagnosis:* Small-to-medium sized species (carapace breadth 10–40 mm); front narrow or broad; gastric mill without large brownish setae at base of posterior tooth plate; pleonal locking mechanism present or absent.

**Remarks:** The tribe Gelasimini is geographically restricted to the Indian and central-to-western Pacific oceans and includes all fiddler crab genera within these regions. It can be distinguished from its sister tribe, the American Minucini, by the absence of two large brownish setae at the base of the posterior tooth plate on the gastric mill.

**Genus Gelasimus** Latreille, 1817

*Type species:* *Gelasimus (Gelasimus) vocans* (Linnaeus, 1758)

See Shih et al. (2016b) for a recent diagnosis and description.

**Subgenus Gelasimus (Gelasimus)** Latreille, 1817 *status nov.*

*Type species:* *Gelasimus (Gelasimus) vocans* (Linnaeus, 1758)
Species included: Gelasmus (Gelasmus) boësisis (Crane, 1975), Gelasmus (Gelasmus) dampedii (Crane, 1973), Gelasmus (Gelasmus) excissa (Nobili, 1906), Gelasmus (Gelasmus) hepatica (Crane, 1973), Gelasmus (Gelasmus) jozefinae (Shih, Naruse & Ng, 2010), Gelasmus (Gelasmus) vocans (Linnaeus, 1758), Gelasmus (Gelasmus) vomeris (McNeill, 1920)

**Diagnosis:** Medium sized species (carapace breadth 20-20 mm); front narrow; dactyl, pollex of major chela in males flattened, with strong groove on external surface of pollex; generally, 1, 2 large distinct teeth from mid-to-proximal end of pollex, although these can be lost in regenerated chela; presence of pronounced tuberculate ridge on inside of the pollex, and the relatively long fingers and gape in the minor chela.

**Remarks:** The species in this subgenus are readily distinguished from the sister subgenus *Mesuca* by the shape of the major chela, the tuberculate ridge on the inside of the major palm, the strong groove running along the outside of the pollex, and the relatively long fingers and gape in the minor chela.

**Subgenus Gelasmus (Mesuca) Bott, 1973**

**Type species:** Gelasmus (Mesuca) tetrogonon (Herbst, 1790)

**Species included:** Gelasmus (Mesuca) tetrogonon (Herbst, 1790)

**Diagnosis:** Medium sized species (carapace breadth 20-30 mm); front narrow; dactyl, pollex of major chela in males rounded, tapering; long, distinct groove on pollex absent; pronounced tuberculate ridge on inside of major palm absent; no large teeth on pollex; fingers of minor chela short; pleon panoramic mechanism absent.

**Remarks:** The single species in the subgenus, *Gelasmus (Mesuca) tetrogonon*, is easily distinguishable from the species in the sister subgenus *Gelasmus* by the shape of the major chela, the lack of a strong groove on the outer pollex, the tuberculate ridge inside the major palm, and by the length of the fingers on the minor chela.

**Genus Austruca Bott, 1973**

**Type species:** Austruca (Austruca) lactea (De Haan, 1835)

See Shih et al. (2016b) for a recent diagnosis and description.

**Subgenus Austruca (Austruca) Bott, 1973**

**Type species:** Austruca (Austruca) lactea (De Haan, 1835)

**Species included:** Austruca (Austruca) alliniana (Kossmann, 1877), Austruca (Austruca) annulipes (H. Milne-Edwards, 1837), Austruca (Austruca) cryptica (Naderloo, Türkay & Chen, 2010; see Naderloo et al., 2010), Austruca (Austruca) ironica (Pretzmann, 1971), Austruca (Austruca) lactea (De Haan, 1835), Austruca (Austruca) majoergi (Rathbun, 1924), Austruca (Austruca) occidentalis (Naderloo, Schubart & Shih, 2016), Austruca (Austruca) perplexa (H. Milne Edwards, 1852)

**Diagnosis:** Small sized species (carapace breadth 10-20 mm); front broad; vertical row of predistal tubercles on posterior minor merus absent; projecting terminal tube on gonopod absent; pleon panoramic locking mechanism present.

**Remarks:** The subgenus *Austruca* represents the “lactea species complex.” It is generally distinguishable from the other subgenera by the lack of a projecting tube on the distal end of the gonopod; it is also distinguishable from subgenus *Caneuta* by its carapace shape and the lack of a tuberculate row on the minor merus. It is sister to the subgenus *Caneuta*.

**Subgenus Austruca (Caneuta) subgen. nov.**

**Type species:** Austruca (Caneuta) triangularis (A. Milne-Edwards, 1873)

**Species included:** Austruca (Caneuta) variegata (Heller, 1862), Austruca (Caneuta) bengali (Crane, 1973), Austruca (Caneuta) triangularis (A. Milne-Edward, 1873)

**Diagnosis:** Very small to small sized species (carapace breadth 5-20 mm); front broad; orbits strongly slanting; anterolateral margins strongly acute; vertical row of predistal tubercles on posterior minor merus present; projecting terminal tube on gonopod; pleon panoramic locking mechanism present.

**Remarks:** The subgenus *Caneuta* represents the “triangularis species complex.” It can be distinguished from the other subgenera within the genus by the distinct carapace shape (weak to strong, obliquely slanted orbits, with moderate to strong acute anterolateral angles on the corner), as well as the row of tubercles on the minor merus. It can further be distinguished from subgenus *Austruca* by the presence of the long terminal tube on the gonopod. It is sister to the subgenus *Austruca*.

**Nomenclatural statement:** A life science identifier (LSID) number was obtained for the new subgenus: urn:lsid:zoobank.org:pub: 40936747-60A4-4A47-91D4-1F2481D6E80D.

**Subgenus Austruca (Sinduca) subgen. nov.**

**Type species:** Austruca (Sinduca) sindensis (Alcock, 1900)

**Species included:** Austruca (Sinduca) sindensis (Alcock, 1900)

**Diagnosis:** Very small to small sized species (carapace breadth 5-20 mm); front broad; anterolateral margins not strongly acute; projecting terminal tube on gonopod present; pleon panoramic locking mechanism present.

**Remarks:** This monospecific subgenus is distinguishable from the subgenus *Austruca* by the presence of a projecting tube on the distal end of the gonopod, while it differs from *Caneuta in both* carapace shape and the lack of a tuberculate row on the minor merus. Phylogenetically, it is basal to the other two subgenera and appears to be a distant link between those subgenera and other fiddler crab genera in Gelasimini.

**Nomenclatural statement:** A life science identifier (LSID) number was obtained for the new subgenus: urn:lsid:zoobank.org:pub: 40936747-60A4-4A47-91D4-1F2481D6E80D.

**Genus Cranuca Beinlich & von Hagen, 2006**

**Type species:** Cranuca inversa (Hoffmann, 1874)

**Species included:** Cranuca inversa (Hoffmann, 1874)

See Shih et al. (2016b) for a recent diagnosis and description.

**Genus Paraleptuca Bott, 1973**

**Type species:** Paraleptuca chlorophthalmus (H. Milne Edwards, 1837)

**Species included:** Paraleptuca boninensis Shih, Komai & Liu, 2013 (see Shih et al. 2013a), Paraleptuca chlorophthalmus (H. Milne Edwards, 1837), Paraleptuca crassipes (White, 1847), Paraleptuca splendidula (Stimpson, 1858)

See Shih et al. (2016b) for a recent diagnosis and description.
**FRESH LOOK AT FIDDLER CRAB TAXONOMY**

**Genus Tubuca Bott, 1973**

*Type species: Tubuca bellator (White, 1847)*

See Shih et al. (2016b) for a recent diagnosis and description.

**Subgenus Tubuca** (Tubuca) Bott, 1973 status nov.

*Type species: Tubuca (Tubuca) bellator (White, 1847)*

Species included: Tubuca bellator (White, 1847), Tubuca elegans (Jones, 1870), and Tubuca longidigitum (Jones, 1870). This subgenus represents the "acute species complex." It diverges basally from the other subgenera within the genus.

**Genus Xeruca Shih, 2015**

*Type species: Xeruca formosensis (Rathbun, 1921)*

Species included: Xeruca formosensis (Rathbun, 1921). See Shih et al. (2016b) for a recent diagnosis and description.

**Tribe Minucini tribus nov.**

*Type genus: Minuca Bott, 1954*

Diagnosis: Very small to medium sized species (carapace breadth 5–30 mm); front broad; gastric mill with 2 large brownish setae at base of posterior tooth plate; pleonal locking mechanism absent.

Remarks: The tribe Minucini is geographically restricted to the Americas and outlying islands, and contains all three broad-fronted genera from this region. It can be distinguished from its sister tribe, the Indo-West Pacific Gelasimini, by the presence of two large brownish setae at the base of the posterior tooth plate on the gastric mill.

**Genus Minuca Bott, 1954**

*Type species: Minuca morax (Smith, 1870)*

Species included: Minuca argilliola (Crane, 1941), Minuca brevifrons (Stimpson, 1860), Minuca burgessi (Rathbun, 1902), Minuca cuneiformis (Maccagno, 1928), Minuca galapagensis (Rathbun, 1902), Minuca hamlini (Rathbun, 1926), Minuca harradensis (Bott, 1954), Minuca macrocarpa (Smith, 1870), Minuca morax (Smith, 1870), and Minuca osea (Landstorfer & Schubert, 2010). See Shih et al. (2016b) for a recent diagnosis and description.

**Genus Leptuca Bott, 1973**

*Type species: Leptuca stenodactylus (H. Milne Edwards & Lucas, 1843)*

Species included: Leptuca batua (Crane, 1941), Leptuca bubei (Crane, 1941), Leptuca coloradensis (Rathbun, 1893), Leptuca cumulanta (Lockington, 1877), Leptuca cumulans (Crane, 1943), Leptuca dunkleyi (Rathbun, 1935), Leptuca longidactyla (von Hagen, 1968), and Leptuca pumilus (Smith, 1870). See Shih et al. (2016b) for a recent diagnosis and description.
(Crane, 1941), Leptuca saltitans (Crane, 1941), Leptuca speciosa (Ives, 1891), Leptuca spinicarpa (Rathbun, 1900), Leptuca stenodactylus (H. Milne Edwards & Lucas, 1843), Leptuca subcyindrica (Stimpson, 1859), Leptuca tallantica (von Hagen, 1968), Leptuca tenuipes (Crane, 1941), Leptuca terpsichoros (Crane, 1941), Leptuca thyensis (Rathbun, 1900), Leptuca tomentosa (Crane, 1941), Leptuca umbritola (Crane, 1941), Leptuca uruguayensis (Nobili, 1901; see Nobili, 1901a)

See Shih et al. (2016b) for a recent diagnosis and description.

**Genus Petruca Shih, Ng & Christy, 2015**

*Type species:* Petruca panamensis (Stimpson, 1859)

*Species included:* Petruca panamensis (Stimpson, 1859)

See Shih et al. (2016b) for a recent diagnosis and description.

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