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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* (*Cuneatuca*), *Austruca* (*Sinduca*), *Tubuca* (*Tubuca*), *Tubuca* (*Australuca*), and *Tubuca* (*Angustuca*). 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 studies since and has allowed subsequent researchers to use a more piecemeal approach to updating the taxonomy and systematics as necessary (Thurman, 1981, 1982; George & Jones, 1982; Barnwell & Thurman, 1984; von Prahll & Toro, 1985; von Hagen, 1987; von Hagen & Jones, 1989; Levinton *et al.*, 1996; Sturmbauer *et al.*, 1996; Rosenberg, 2001, 2013; Beinlich & von Hagen, 2006; Shih *et al.*, 2009, 2010, 2012, 2013a, 2015, 2016b, 2018, 2019; Spivak & Cuesta, 2009; Landstorfer & Schubart, 2010; Naderloo *et al.*, 2010, 2016; Thurman *et al.*, 2018). Today we recognize 105 extant species (Rosenberg, 2014), with five additional named fossil taxa, a major shift from the 62 extant species (92 taxa with subspecies included) and two fossils recognized by Crane (1975). The

nine subgenera described by Crane (1975) were based on morphological comparison in the absence of quantitative phylogenetic methodology. Advances in molecular phylogenetics resulted in the rearrangement, renaming, and gradual expansion of the recognized subgenera to twelve, until a recent study (Shih *et al.*, 2016b) moved away from the notion of treating fiddler crabs as a single genus and instead has raised eleven of the former subgenera to full genera.

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

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; Beinlich & 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 *vocans* 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 similarly built but smaller data sets, starting with Levinton *et al.* (1996) and Sturmbauer *et al.* (1996), but these earlier authors appear to have written off the result as a taxonomic reconstruction 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 Gelasiminae Miers, 1886 (containing the other nine fiddler crab genera) (Fig. 1). A third subfamily, Ucininae 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 Ucininae 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 require the evolution of a suite of key characters present in all fiddler crabs and absent from close relatives (e.g., extreme sexual dimorphism, extreme male asymmetry, long and thin eyestalks) followed by a nearly complete reversal of these same characters in the ghost crabs (sexual monomorphism, mild asymmetry in both sexes, short and thick eyestalks). While Shih *et al.* (2016b) included a large number of species and samples, their result was based on only three gene fragments (1,936 total sites), two mitochondrial and one nuclear, leading to both a limited number of sites per species and the admixture of two types of genes with known differential inheritance patterns and effective population sizes. Phylogenetic discordance between mitochondrial markers and nuclear markers is a common phenomenon and it is not unusual for phylogenetic studies based on thousands of independent markers

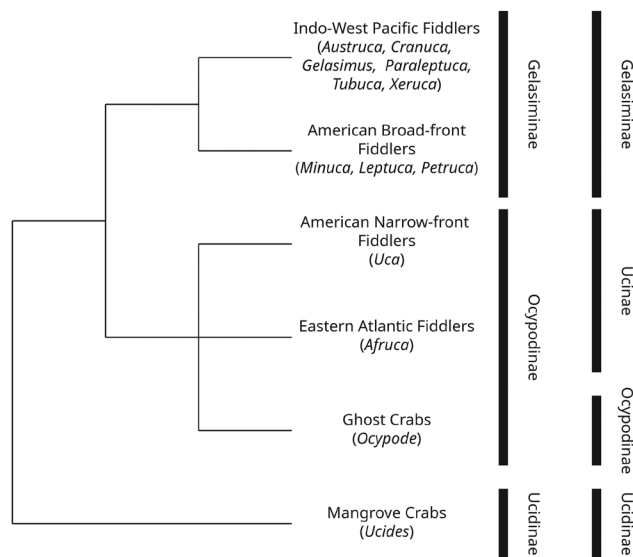


Figure 1. Outline of the phylogeny of fiddler, ghost, and mangrove crabs (after Shih *et al.*, 2016), indicating subfamily designations as given in Shih *et al.* (2016b) and World Register of Marine Species (WoRMS) (5 April 2019).

from NextGen sequencing technologies to produce different results than those found from more limited mitochondrial-focused data sets (e.g., Fisher-Reid & Wiens, 2011; Jacobsen & Omland, 2011; Jockusch *et al.*, 2014; Morgan *et al.*, 2014; Hofmann, 2015; Thielsch *et al.*, 2017; Platt *et al.*, 2018). With all of this in mind, it is not clear whether the paraphyly of fiddler crabs with respect to ghost crabs represents the true evolutionary history of this group or is a gene-sampling artifact that will stand not up to further scrutiny and study when NextGen data becomes available.

A clear benefit of the Shih *et al.* (2016b) result is that it highlights a flaw in our traditional thinking: we tend to focus so much on evolution within groups that we often fail to consider the implication of evolution among groups. For example, fiddler crab researchers have tended to focus on evolution of the large claw in male fiddler crabs with a generally unstated assumption that this large claw evolved from the smaller claw (females, after all, have two small claws). The small claw of males and the two claws of females are at least as divergent, if not more divergent (certainly in size), from the claws of their close relatives (*Ocypode* and *Ucides*, both of whom have moderately large, mildly asymmetric claws in both sexes) than is the large claw of the male. The evolution of the claws of fiddler crabs might have been driven as much, if not more, by reduction of the small claw for more efficient deposit feeding with sexually selected retention of a large claw in males, rather than the other way around.

While the placement of ghost crabs within fiddler crabs required splitting fiddler crabs into multiple genera, these splits could have been justified in the absence of paraphyly, and all of the new fiddler crab genera are more or less identical to the previously recognized subgenera (the subgenus *Australuca* Crane, 1975 had previously been suggested by the same authors to likely be a subset of another subgenus, *Tubuca* Bott, 1973). Furthermore, the remainder of the phylogeny is uncontroversial and can serve as a basis for considering higher-order taxonomic divisions for fiddler crabs. All of the proposed names below are congruent with, if not directly based on, the phylogeny of Shih *et al.* (2016b) and are generally independent of the monophyly/paraphyly question.

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 (*Afruca*) and the American narrow-front species (*Uca*) (equivalent to Ucininae above, combined into a clade with *Ocypode* 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.** (containing *Minuca*, *Leptuca* Bott, 1973 and *Petruca* Shih, Ng & Christy, 2015), and the IWP species should be referred to as the tribe Gelasimini 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 Gelasiminae for just the IWP species and use Minucinae for the American broad-front species, but that division would fail to recognize the clear relationship of those two clades relative to the Ucininae 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, Ucininae would have priority as the subfamily representing all fiddler crabs, but the three named tribes could still be used to represent the three main internal clades without modification (Fig. 2). The subfamily currently called Gelasiminae would instead become the supertribe Gelasimitae **status nov.**, with the supertribe Ucitae **status nov.** serving the role currently occupied by Ucininae.

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. borealis* (Crane, 1975), *G. dampieri* (Crane, 1975), *G. excisa* (Nobili, 1906), *G. hesperia* (Crane, 1975), *G. jocelynae* (Shih, Naruse & Ng, 2010), *G. vocans* (Linnaeus, 1758), and *G. vomeris* (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 consist 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. cryptica* (Naderloo, Türkay & Chen, 2010; see Naderloo *et al.*, 2010), *A. iranica* (Pretzmann, 1971), *A. lactea* (De Haan, 1835), *A. mjoebergi* (Rathbun, 1924), *A. occidentalis* (Naderloo, Schubart & Shih, 2016), and *A. perplexa*

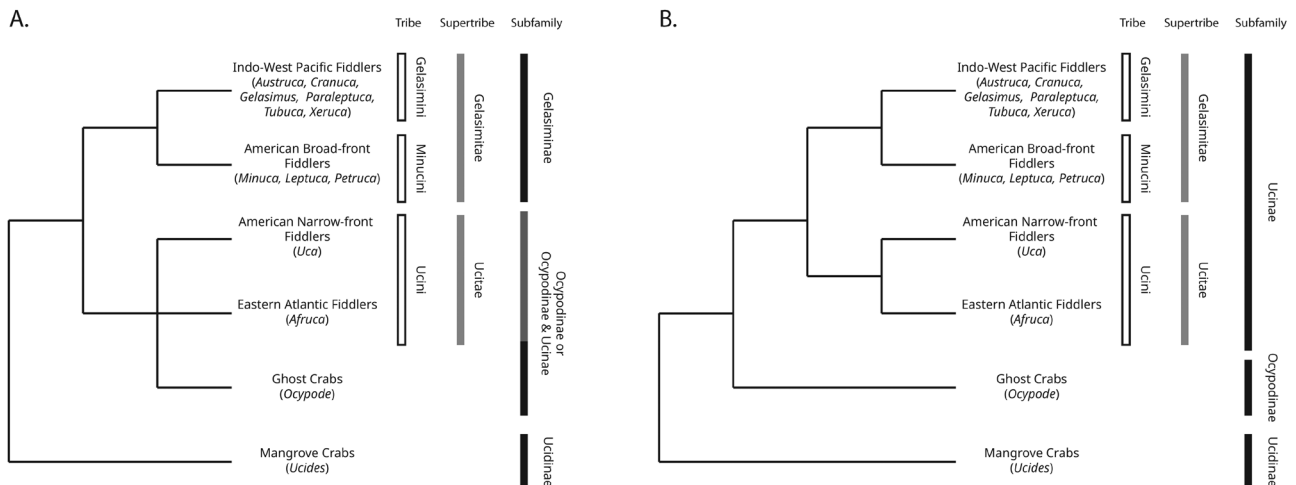


Figure 2. Unlike the subfamilies, proposed tribes and supertribes for fiddler crabs would retain stability whether fiddlers are paraphyletic with respect to ghost crabs or monophyletic.

(H. Milne Edwards, 1852). The other four species in the genus can be divided among two additional new subgenera: *Cuneatuca* **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. sindensis* (Alcock, 1900). The former is derived from the Latin for tapering (describing the sharp pointing 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. alcocki* Shih, Chan & Ng, 2018, *T. arcuata* (De Haan, 1835), *T. capricornis* (Crane, 1975), *T. coarctata* (H. Milne Edwards, 1852), *T. demani* (Ortmann, 1897), *T. dussumieri* (H. Milne Edwards, 1852), *T. flammula* (Crane, 1975), *T. forcipata* (Adams & White, 1848), *T. paradussumieri* (Bott, 1973), *T. typhoni* (Crane, 1975) and *T. urvillei* (H. Milne Edwards, 1852); 2) subgenus *Australuca* Crane, 1975 **status nov.**, consisting of a clade of seven species, *T. bellator* (White, 1847), *T. elegans* (George & Jones, 1982), *T. hisuitmanus* (George & Jones, 1982), *T. longidigitum* (Kingsley, 1880), *T. polita* (Crane, 1975), *T. seismella* (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 *Australuca* 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 conflate 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 *Acanthoplax* 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 resemble pruning shears than the major claws of most other species. The remaining six species are tentatively placed in the subgenus *Uca*: *U. heteropleura* (Smith, 1870), *U. intermedia* von Prahl & Toro, 1985, *U. major* (Herbst, 1782), *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*, *Cranua*, *Xeruca*, and *Petruca*), while the other three (*Leptuca*, *Minuca*, and *Paraleptuca*) currently lack the systematic clarity necessary for further subdivision.

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; Naderloo *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 luisant” 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 pacificensis* Crane, 1975, found in Fiji. This name was later found to be a junior synonym of *Mesuca (Latuca) neocultrimana* Bott, 1973, also described from Fiji (Rosenberg, 2001; Shih *et al.*, 2010). Shih *et al.* (2010) further subdivided 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 thought 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 homonymy was originally recognized by Nobili (1906: 315), 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 pacificensis* 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.

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 has 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), *Tubuca (Tubuca) forcipata* (MSR, unpublished data; H.T. Shih, personal communication), and *Minuca ecuadoriensis* (Barnwell, 1988) 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 known from fossils.

Family Ocypodidae Rafinesque, 1815

Subfamily Ucinæ 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 Prah & 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) marinae*† Dominguez 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 (Eydoux, 1835)

Species included: Afruca miocenica† (Artal, 2008), *Afruca tangeri* (Eydoux, 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: *Gelasimus (Gelasimus) borealis* (Crane, 1975), *Gelasimus (Gelasimus) dampieri* (Crane, 1975), *Gelasimus (Gelasimus) excisa* (Nobili, 1906), *Gelasimus (Gelasimus) hesperiae* (Crane, 1975), *Gelasimus (Gelasimus) jocelynae* (Shih, Naruse & Ng, 2010), *Gelasimus (Gelasimus) vocans* (Linnaeus, 1758), *Gelasimus (Gelasimus) 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 major chela palm; fingers of minor chela long, with gape longer than manus; pleonal locking mechanism absent.

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 *Gelasimus (Mesuca)* Bott, 1973 status nov.

Type species: *Gelasimus (Mesuca) tetragonon* (Herbst, 1790)

Species included: *Gelasimus (Mesuca) tetragonon* (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 chela palm absent; no large teeth on pollex; fingers of minor chela short; pleonal locking mechanism absent.

Remarks: The single species in the subgenus, *Gelasimus (Mesuca) tetragonon*, is easily distinguishable from the species in the sister subgenus *Gelasimus* 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 status nov.

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

Species included: *Austruca (Austruca) albimana* (Kossmann, 1877), *Austruca (Austruca) annulipes* (H. Milne Edwards, 1837), *Austruca (Austruca) cryptica* (Naderloo, Türkay & Chen, 2010; see Naderloo *et al.*, 2010), *Austruca (Austruca) iranica* (Pretzmann, 1971), *Austruca (Austruca) lactea* (De Haan, 1835), *Austruca (Austruca) mjoebergi* (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; pleonal 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 *Cuneatuca* by its carapace

shape and the lack of a tuberculate row on the minor merus. It is sister to the subgenus *Cuneatuca*.

Subgenus *Austruca (Cuneatuca)* subgen. nov.

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

Species included: *Austruca (Cuneatuca) variegata* (Heller, 1862), *Austruca (Cuneatuca) bengali* (Crane, 1975), *Austruca (Cuneatuca) triangularis* (A. Milne-Edwards, 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; pleonal locking mechanism present.

Remarks: The subgenus *Cuneatuca* 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 corners), 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; pleonal 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 *Cuneatuca* 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 splendida* (Stimpson, 1858)

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

Genus *Tubuca* Bott, 1973

Type species: *Tubuca (Tubuca) urvillei* (H. Milne Edwards, 1852)
See [Shih et al. \(2016b\)](#) for a recent diagnosis and description.

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

Type species: *Tubuca (Tubuca) urvillei* (H. Milne Edwards, 1852)

Species included: *Tubuca (Tubuca) alcocki* [Shih, Chan & Ng, 2018](#), *Tubuca (Tubuca) arcuata* ([De Haan, 1835](#)), *Tubuca (Tubuca) capricornis* ([Crane, 1975](#)), *Tubuca (Tubuca) coarctata* (H. Milne Edwards, 1852), *Tubuca (Tubuca) demani* ([Ortmann, 1897](#)), *Tubuca (Tubuca) dussumieri* (H. Milne Edwards, 1852), *Tubuca (Tubuca) flammula* ([Crane, 1975](#)), *Tubuca (Tubuca) forcipata* ([Adams & White, 1848](#)), *Tubuca (Tubuca) paradussumieri* ([Bott, 1973](#)), *Tubuca (Tubuca) typhoni* ([Crane, 1975](#)), *Tubuca (Tubuca) urvillei* (H. Milne Edwards, 1852)

Diagnosis: Small to large sized species (carapace breadth 10–40 mm); front narrow; major cheliped merus without an antero-dorsal crest; groove on exterior of major pollex; 1, 2 grooves on exterior of major dactyl; enlarged tubercles on entire exterior surface of major chela manus; pleonal locking mechanism absent.

Remarks: This subgenus represents one of the two crown clades of the genus and is sister to subgenus *Australuca*.

Subgenus *Tubuca (Australuca)* Crane, 1975 status nov.

Type species: *Tubuca (Australuca) bellator* ([White, 1847](#))

Species included: *Tubuca (Australuca) bellator* ([White, 1847](#)), *Tubuca (Australuca) elegans* ([George & Jones, 1982](#)), *Tubuca (Australuca) hirsutimanus* ([George & Jones, 1982](#)), *Tubuca (Australuca) longidigitum* ([Kingsley, 1880](#)), *Tubuca (Australuca) polita* ([Crane, 1975](#)), *Tubuca (Australuca) seismella* ([Crane, 1975](#)), *Tubuca (Australuca) signata* ([Hess, 1865](#))

Diagnosis: Small to medium sized species (carapace breadth 10–25 mm); front narrow; major cheliped merus with an antero-dorsal crest, but no distally enlarged tooth; long groove on exterior of major pollex absent; large tubercle or single triangular projection along distal half of major pollex; exterior surface of major dactyl, pollex generally smooth, with no large tubercles; large teeth present in gape of minor chela; gonopod tip a produced tube; pleonal locking mechanism absent.

Remarks: *Australuca* was previously considered a subgenus within the single fiddler crab genus *Uca* but was subsumed within the subgenus *Tubuca* when greater phylogenetic resolution was achieved. Within the now-raised-to-genus *Tubuca*, the traditional species within *Australuca* still represent a unique clade.

Subgenus *Tubuca (Angustuca)* subgen. nov.

Type species: *Tubuca (Angustuca) acuta* ([Stimpson, 1858](#))

Species included: *Tubuca (Angustuca) acuta* ([Stimpson, 1858](#)), *Tubuca (Angustuca) rhizophorae* ([Tweedie, 1950](#)), *Tubuca (Angustuca) rosea* ([Tweedie, 1937](#))

Diagnosis: Small to medium sized species (carapace breadth 10–25 mm); front narrow; tubercles absent from orbit floor; anterolateral margins short to absent; anterolateral angles acute and moderately to strongly produced; major cheliped merus without an antero-dorsal crest; groove on exterior of major pollex; 1, 2

long grooves running entire length of major dactyl; enlarged tubercles on exterior surface of major chela manus only near pollex base; pleonal locking mechanism absent.

Remarks: This subgenus represents the “*acuta* species complex.” It diverges basally from the other subgenera within the genus.

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 *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.

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

Genus *Minuca* Bott, 1954

Type species: *Minuca mordax* ([Smith, 1870](#))

Species included: *Minuca argillicola* ([Crane, 1941](#)), *Minuca brevifrons* ([Stimpson, 1860](#)), *Minuca burgersi* ([Holthuis, 1967](#)), *Minuca ecuadoriensis* ([Maccagno, 1928](#)), *Minuca galapagensis* ([Rathbun, 1902](#)), *Minuca hamlini*[†] ([Rathbun, 1926](#)), *Minuca herradurenensis* ([Bott, 1954](#)), *Minuca longisignalis* ([Salmon & Atsides, 1968](#)), *Minuca marguerita* ([Thurman, 1981](#)), *Minuca minax* ([Le Conte, 1855](#)), *Minuca mordax* ([Smith, 1870](#)), *Minuca osa* ([Landstorfer & Schubart, 2010](#)), *Minuca pugnax* ([Smith, 1870](#)), *Minuca rapax* ([Smith, 1870](#)), *Minuca victoriana* ([von Hagen, 1987](#)), *Minuca virens* ([Salmon & Atsides, 1968](#)), *Minuca vocator* ([Herbst, 1804](#)), *Minuca zaca* ([Crane, 1941](#))

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 batuenta* ([Crane, 1941](#)), *Leptuca beebei* ([Crane, 1941](#)), *Leptuca coloradensis* ([Rathbun, 1893](#)), *Leptuca crenulata* ([Lockington, 1877](#)), *Leptuca cumulanta* ([Crane, 1943](#)), *Leptuca deichmanni* ([Rathbun, 1935](#)), *Leptuca dorotheae* ([von Hagen, 1968](#)), *Leptuca festae* ([Nobili, 1901](#); see [Nobili, 1901b](#)), *Leptuca helleri* ([Rathbun, 1902](#)), *Leptuca inaequalis* ([Rathbun, 1935](#)), *Leptuca latimanus* ([Rathbun, 1893](#)), *Leptuca leptodactyla* ([Rathbun, in Rankin, 1898](#)), *Leptuca limicola* ([Crane, 1941](#)), *Leptuca musica* ([Rathbun, 1915](#)), *Leptuca oerstedii* ([Rathbun, 1904](#)), *Leptuca panacea* ([Novak & Salmon, 1974](#)), *Leptuca pugilator* ([Bosc, 1802](#)), *Leptuca pygmaea*

(Crane, 1941), *Leptuca saltitanta* (Crane, 1941), *Leptuca speciosa* (Ives, 1891), *Leptuca spinicarpa* (Rathbun, 1900), *Leptuca stenodactylus* (H. Milne Edwards & Lucas, 1843), *Leptuca subcylindrica* (Stimpson, 1859), *Leptuca tallanica* (von Hagen, 1968), *Leptuca tenuipedis* (Crane, 1941), *Leptuca terpsichores* (Crane, 1941), *Leptuca thayeri* (Rathbun, 1900), *Leptuca tomentosa* (Crane, 1941), *Leptuca umbratila* (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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