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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

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Abstract. The family Ocypodidae is a group of intertidal brachyuran crabs found in tropical to temperate seas worldwide. While the family has historically included many subfamilies, most of these have now been given separate family status within the superfamily Ocypodoidea. The most recent classification recognises only two subfamilies, the ghost crabs: Ocypodinae Rafinesque, 1815; and the fiddler crabs: Ucinae Dana, 1851. The ghost crabs comprise 21 species in two genera, *Ocypode* Weber, 1795, and *Hoplocypode* Sakai & Türkay, 2013. The fiddler crabs are the most species-rich group of this family with 104 species, all belonging to the single genus *Uca* Leach, 1814, with 12 recognised subgenera. The present study supports 13 groups (= genera) belonging to three revised subfamilies. This result is based on molecular evidence from the nuclear 28S rDNA, and the mitochondrial 16S rDNA and cytochrome oxidase subunit I (COI). The family now also includes the monogeneric Ucididae Števčić, 2005, recently recognised as a separate family for *Ucides* Rathbun, 1897, herein relegated to a subfamily of the Ocypodidae. *Uca* (and thus Ucinae) is shown to be paraphyletic, belonging to two widely divergent clades. *Uca* (*Uca*) s. str. from the Americas and *Afruca* Crane, 1975, from the East Atlantic cluster with *Ocypode* and *Hoplocypode*, and thus constitute a revised Ocypodinae. The American broad-fronted group with the Indo-West Pacific subgenera, forming a distinct clade, for which the subfamily name Gelasiminae Miers, 1886, is available. *Australuca* Crane, 1975, and *Hoplocypode* Sakai & Türkay, 2013, are not supported, and are treated as synonyms of *Tubuca* Bott, 1973, and *Ocypode*, respectively. All other subgenera of *Uca* are here recognised as full genera. The three constituent subfamilies of the Ocypodidae are thus as follow: Ocypodinae (*Afruca*; *Ocypode*; *Uca* s. str.); Gelasiminae (*Austruca* Bott, 1973; *Cranuca* Beinlich & von Hagen, 2006; *Gelasimus* Latreille, 1817; *Leptuca* Bott, 1973; *Minuca* Bott, 1954; *Paraleptuca* Bott, 1973; *Petruca* Shih, Ng & Christy, 2015; *Tubuca*; *Xeruca* Shih, 2015); and Ucidinae Števčić, 2005 (*Ucides*).

Key words. fiddler crabs, ghost crabs, mangrove crabs, *Uca*, *Ocypode*, *Ucides*, Ocypodinae, Gelasiminae, Ucidinae, systematics, phylogeny, genera, 28S rDNA, 16S rDNA, COI

INTRODUCTION

The Ocypodidae is a group of intertidal burrowing crabs found in tropical to temperate seas worldwide. They are sometimes categorised as "land crabs" (Hartnoll, 1988), although only a few have completely escaped the need for regular tidal inundation. At present, the Ocypodidae is composed of two subfamilies, the Ocypodinae Rafinesque 1815, for ghost crabs, and the Ucinae Dana, 1851, for fiddler crabs (Ng et al., 2008; Davie et al., 2015).

The ghost crab genus *Ocypode*, after which the family is named, was recently revised by Sakai & Türkay (2013) who recognised 21 species, and established a new genus, *Hoplocypode* Sakai & Türkay, 2013, for *O. occidentalis* Stimpson, 1860, from western America.

Crane (1975) revised the fiddler crabs of the world, recognising 92 taxa (species or subspecies) and nine subgenera, all under a single genus, *Uca* Leach, 1814. The number of species of fiddler crab has been steadily increasing.

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Beinlich & von Hagen (2006) recognised 94 species, with 96 species being listed in Ng et al. (2008) (including *U. australiae* Crane, 1975, and *U. tomentosa* Crane, 1941). Since 2008, seven more species were recognised, viz. *U. boninensis* Shih, Komai & Liu, 2013; *U. cryptica* Naderloo, Türkay & Chen, 2010; *U. iranica* Pretzmann, 1971; *U. jocelynae* Shih, Naruse & Ng, 2010; *U. occidentalis* Naderloo, Schubart & Shih, 2016; *U. osa* Landstorfer & Schubart, 2010; and *U. splendida* (Stimpson, 1858) (Shih et al., 2009, 2010, 2012, 2013a; Landstorfer & Schubart, 2010; Naderloo et al., 2010). Most recently Rosenberg (2014) validated *U. virens* Salmon & Atsaides, 1968, but did not include the questionable *U. australiae*. Thus, 102 species are currently listed on the website "Fiddler Crabs" (http://www.fiddlercrab.info/index.html) (Rosenberg, 2014). Despite several discussions on the possible paraphyly of the genus (Salmon, 1983; Levinton et al., 1996, Beinlich & von Hagen, 2006), workers have continued to use only one genus name for all fiddler crab species. *Uca* species, however, have commonly been broadly split into two categories, those in which the frontal margin is markedly constricted between the eyestalks (narrow-fronted, or NF), and those with a more broadly triangular front (broad-fronted, or BF) (see Crane, 1975; Rosenberg, 2001; Beinlich & von Hagen, 2006; Material and methods in this study).

In the Indo-West Pacific (IWP), there are three narrow-fronted subgenera, *Australuca* Crane, 1975, *Deltuca* Crane, 1975, and *Thalassuca* Crane, 1975; and two broad-fronted ones, *Amphiuca* Crane, 1975, and *Celuca* Crane, 1975. In the Atlantic-East Pacific (AEP) region, only *Uca* (*Uca*) is narrow-fronted, with *Afruca* Crane, 1975, *Celuca* and *Minuca* Bott, 1954, being broad-fronted. Crane's (1975) classification system was comprehensive and used a multi-evidence approach. However, Bott (1973b) had earlier published a short paper that established 10 genera (including two subgenera), and thus his names have nomenclatural priority. Von Hagen (1976), Rosenberg (2001), Beinlich & von Hagen (2006), and Ng et al. (2008) treated all fiddler crabs at the specific level, and continued to follow Crane in recognising a single genus *Uca*, but have replaced her subgeneric names, where necessary, with those by Bott (1973b). Based on larval morphology, Spivak & Cuesta (2009) suggested *U. tangeri* (Eydoux, 1835) should be attributed to the subgenus *Afruca*. The recent revision of the IWP BF subgenera based on molecular evidence (Shih et al., 2013b) supports *Cranuca* Beinlich & von Hagen, 2006, along with the placement of *U. sindensis* (Alcock, 1900) into *Austruca* Bott, 1973. Recently, two additional subgenera, *Xeruca* Shih, 2015, for *U. formosensis* Rathbun, 1921, and *Petruca* Shih, Ng & Christy, 2015, for *U. panamensis* (Stimpson, 1859), have also been established (Shih, 2015; Shih et al., 2015).

There has also been considerable discussion regarding the relationships of another uncertain genus of ocypodid-like mangrove crabs, *Ucides* Rathbun, 1897, with two species, *U. cordatus* (Linnaeus, 1763), and *U. occidentalis* (Ortmann, 1897) (Ng et al., 2008; Davie et al., 2015). *Ucides* was originally placed under the Gecarcinidae (Rathbun, 1918), but later authors referred it to the Ocypodidae or at least the Ocypodoidea. It has been suggested it could be placed in the Heloeciidae H. Milne Edwards, 1852, or as an ocypodid subfamily Ucidinae Števčić, 2005, or even in a separate family, Ucididae (Chace & Hobbs, 1969; Türkay, 1970; Ng et al., 2008). Schubart & Cuesta (2010) showed a close relationship between *Ucides* and *Ocypode* based on 16S rDNA data.

Molecular sequences provide strong evidence to support the phylogeny and systematics of crabs (reviewed by Tsang et al., 2014; Chu et al., 2015). With regard to 16S rDNA studies of *Uca*, Levinton et al. (1996) and Sturmbauer et al. (1996) have shown inconsistent support for the traditional morphological subgeneric groupings, although all support a close relationship with *Ocypode*. There have also been recent molecular studies on both fiddler and ghost crabs (Shih et al., 2009, 2010, 2012, 2013a, b, 2015; Shih, 2015; Wong et al., 2012), but these have been confined to only solving species-group or subgeneric issues. As such, a large-scale multigene study, such as the one reported here, has been lacking to derive a comprehensive overview of ocypodid relationships.

We here use nuclear 28S rDNA, mitochondrial 16S rDNA and cytochrome oxidase subunit I (COI) genetic markers from 92 of the 129 known Ocypodidae species. Based on the results, we propose three subfamilies of the Ocypodidae, a rearrangement of some genera and species, and the recognition of full generic status for the currently recognised subgenera of fiddler crabs (*Uca*).

MATERIAL AND METHODS

Specimens examined representing the majority of species of fiddler and ghost crabs worldwide, and *Ucides*, are included for phylogenetic analysis. *Dotilla*, *Heloecius*, *Macrophthalmus*, *Scopimera*, and *Tmethypocoelis* of the superfamily Ocypodoidea (Ng et al., 2008) are used as outgroups (Appendix 1). The abbreviation G1 is used for the male first gonopods. Measurement is of the carapace width. The front width of the Ocypodidae is relatively narrower compared with other groups of crabs with very wide front, e.g., Grapsoidea and Xanthoidea. In this study, the taxa of the Ocypodidae are defined as narrow-fronted (or NF) and broad-fronted (or BF), with front width about < 1/10 and > 1/5 of the fronto-orbital width (the maximum width between outer orbital angles), respectively (Rathbun, 1918; Chace & Hobbs, 1969; Crane, 1975).

Genomic DNA was isolated from the muscle tissue of legs by using the GeneMark tissue and cell genomic DNA purification kit (Taichung, Taiwan). A region of ~550 basepairs (= bp) of the 5'-end of the 16S gene was selected for amplification with polymerase chain reaction (PCR) using the primers 1471, 1472 (Crandall & Fitzpatrick, 1996), 16Sar and 16Sbr (Palumbi et al., 1991). A portion of the COI gene was amplified with PCR using the primers LCO1490, HCO2198 and COL14 (Folmer et al., 1994; Roman & Palumbi, 2004). The PCR conditions for the above primers were denaturation for 50 s at 94°C, annealing for 70 s at

45–47°C, and extension for 60 s at 72°C (40 cycles), followed by extension for 10 min at 72°C. The primers for 28S were 28L4, 28H4 (Ragionieri et al., 2009), 28L4F, 28H4F (Shih et al., 2013b), as well as the new designed with the annealing temperature 47–50°C in PCR condition. Sequences were obtained by automated sequencing (Applied Biosystems 3730) and aligned with the aid of MUSCLE function of MEGA (v. 5.2.2, Tamura et al., 2011), after verification with the complimentary strand. Sequences of the different sequences have been deposited in the DNA Data Bank of Japan (DDBJ), along with other sequences published in earlier papers of the authors (Appendix 1).

Several 28S sequences were found to be ambiguous so their PCR products were cloned. The products were purified by using the QIAquick Gel Extraction kit (Qiagen) first and were cloned using the pGEM-T Easy Vector System (Promega). Three colonies from each sample were selected, and used for insert verification. Verified colonies were used for additional PCR amplification using the original 28S primers. All products were visualised under ultraviolet light stained with ethidium bromide, with a comigrating 100-bp ladder molecular-weight marker to confirm the correct amplification. Amplification products were cycle-sequenced and the sequences were obtained by automated sequencing (see above). One or two sequences were randomly selected from each sample for the analyses (see Shih et al., 2013b).

For the combined dataset, the best-fitting models for sequence evolution of individual datasets were determined by MrModeltest (v. 2.2, Nylander, 2005), selected by the Akaike information criterion (AIC). The obtained best models for the three individual datasets were all GTR + G + I, and were subsequently used for the partitioned Bayesian inference (BI) and maximum likelihood (ML) analyses. The Bayesian inference analysis was performed with MrBayes (v. 3.2.3, Ronquist et al., 2012). The search was run with 4 chains for 10 million generations and 4 independent runs, with trees sampled every 1000 generations. The convergence of chains was determined by the effective sample size (ESS) (>200 as recommended) in Tracer (v. 1.5, Rambaut & Drummond, 2009) and the first 1200 trees were discarded as the burnin (determined by the average standard deviation of split frequency values below the recommended 0.01; Ronquist et al., 2005). The maximum likelihood analysis was conducted in GARLI (v. 2.0, Zwickl, 2006), with 10 replicate searches (searchreps = 10) and 50 bootstraps (bootstrapreps = 50). The consensus tree from GARLI output was computed using PAUP* program (v. 4.0b10, Swofford, 2003) to assess node supports.

RESULTS AND DISCUSSION

A 589 bp segment of the 16S, 658 bp segment of COI, and 689 bp segment of 28S from 98 species of crabs (including outgroups) were amplified and aligned, with 178 different sequences (Appendix 1). The phylogenetic tree of the combined markers was reconstructed from the BI analysis, with the support values from ML analysis (Figs. 1, 2). The fiddler crabs, ghost crabs and *Ucides* form a large highly

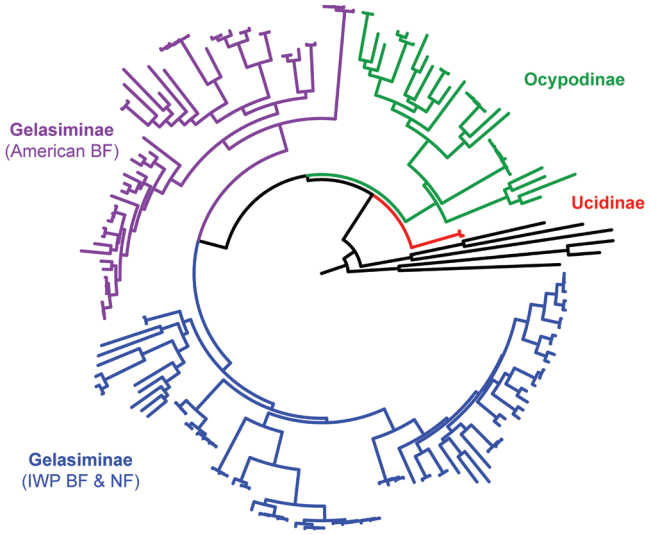

Fig. 1. A Bayesian inference (BI) tree of the family Ocypodidae and outgroups, based on the combined 28S rRNA, 16S rRNA and COI markers, showing the three clades (three subfamilies), indicated in different colours. The subfamily Gelasiminae is composed of two groups, one is for all Indo-West Pacific fiddler crabs, the other for the American broad-fronted fiddler crabs.

supported clade, with three main subclades also having high support values. These three main clades (Figs. 1, 2) are here treated as subfamilies. A simplified tree of the genera and subfamilies is shown in Figure 3. In addition, the distribution of the genera of fiddler crabs are shown in Fig. 4. With regard to the species included within each genus, we follow Ng et al. (2008) and recent studies (see Introduction), with the addition of *U. virens* (see Remarks under *Minuca*) as valid in the updated website (http://www.fiddlercrab.info/index.html; Rosenberg, 2014). Although the identity of *U. australiae* remains uncertain, the name is retained until its status can be ascertained in the future. In total, there are 104 species of fiddler crabs included in this study.

The fiddler crabs clearly include two widely divergent groups: one group (including the AEP *Uca* and *Afruca*) are closely related to *Ocypode* rather than to the other fiddler crabs; and the second group composed of the remaining fiddler crabs (the AEP *Minuca*, *Leptuca* and *Petruca*, as well as all the IWP taxa). Thus, the original genus *Uca* is paraphyletic, and in order to maximise uniformity across the family, and to recognise the monophyly of each group, we treat all the previously accepted subgenera of fiddler crabs as full genera, which are divided between the Ocypodinae and the newly recognised Gelasiminae.

Based on 16S evidence and sampling a limited number of species, Levinton et al. (1996) and Sturmbauer et al. (1996) considered the relationship between ghost crabs and fiddler crabs to be unresolved. They treated *Ocypode* as an outgroup, and suggested three clades for fiddler crabs, viz. the Ancestral American Clade, the Derived American Clade, and the Indo-West Pacific Clade. The main patterns they found agree well with our more comprehensive results based on nuclear and mitochondrial markers, including the latter two clades, as well as the unresolved relationship between *Tubuca* and

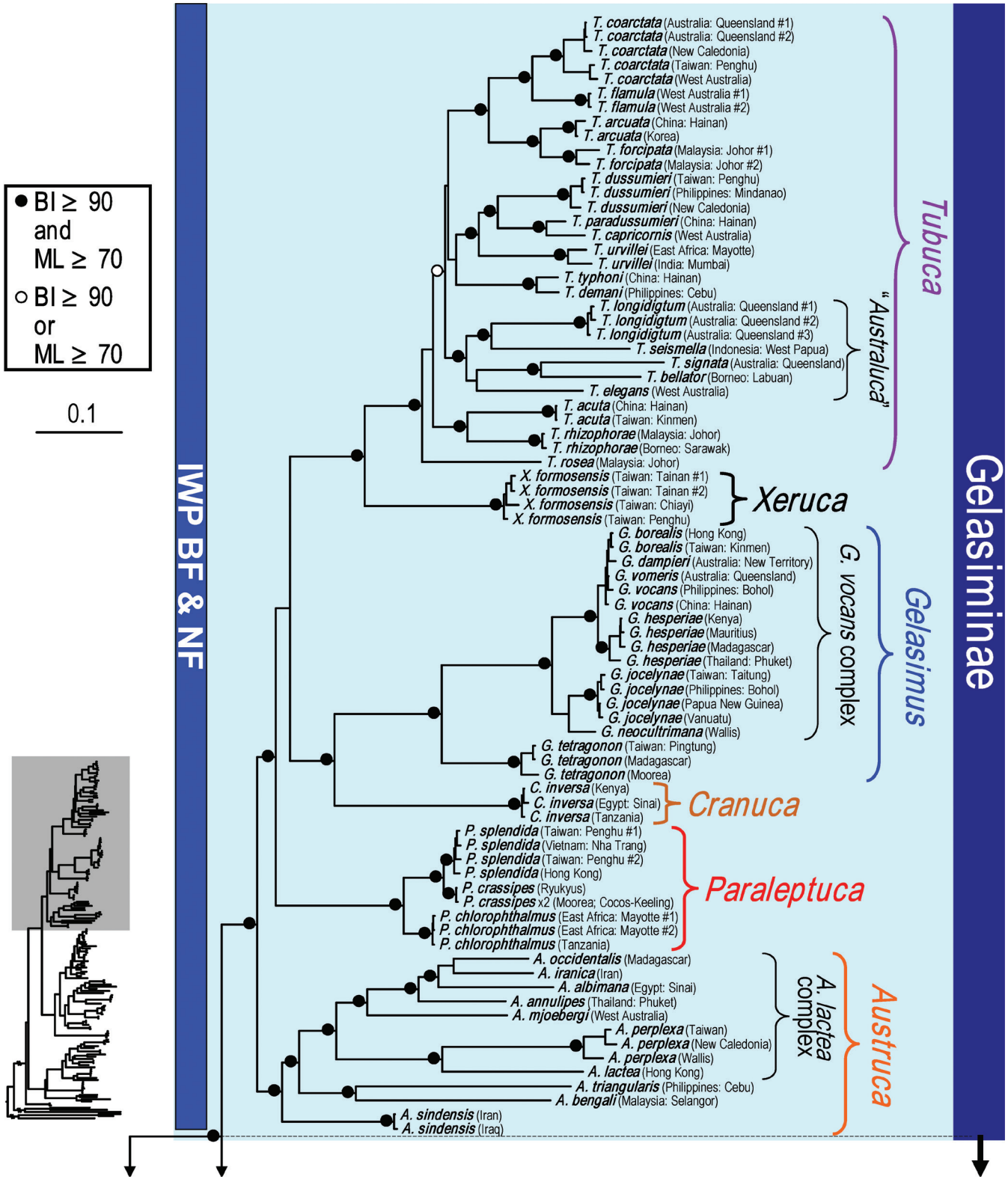

Fig. 2. A Bayesian inference (BI) tree of the family Ocypodidae and outgroups, based on the combined 28S, 16S and COI markers. The solid circle at the node means it is strongly supported by both BI (≥ 90) and ML (≥ 70); and the open circle means only one method is strongly supported. Name of species or genus quoted means it is suggested as a synonym in this study.

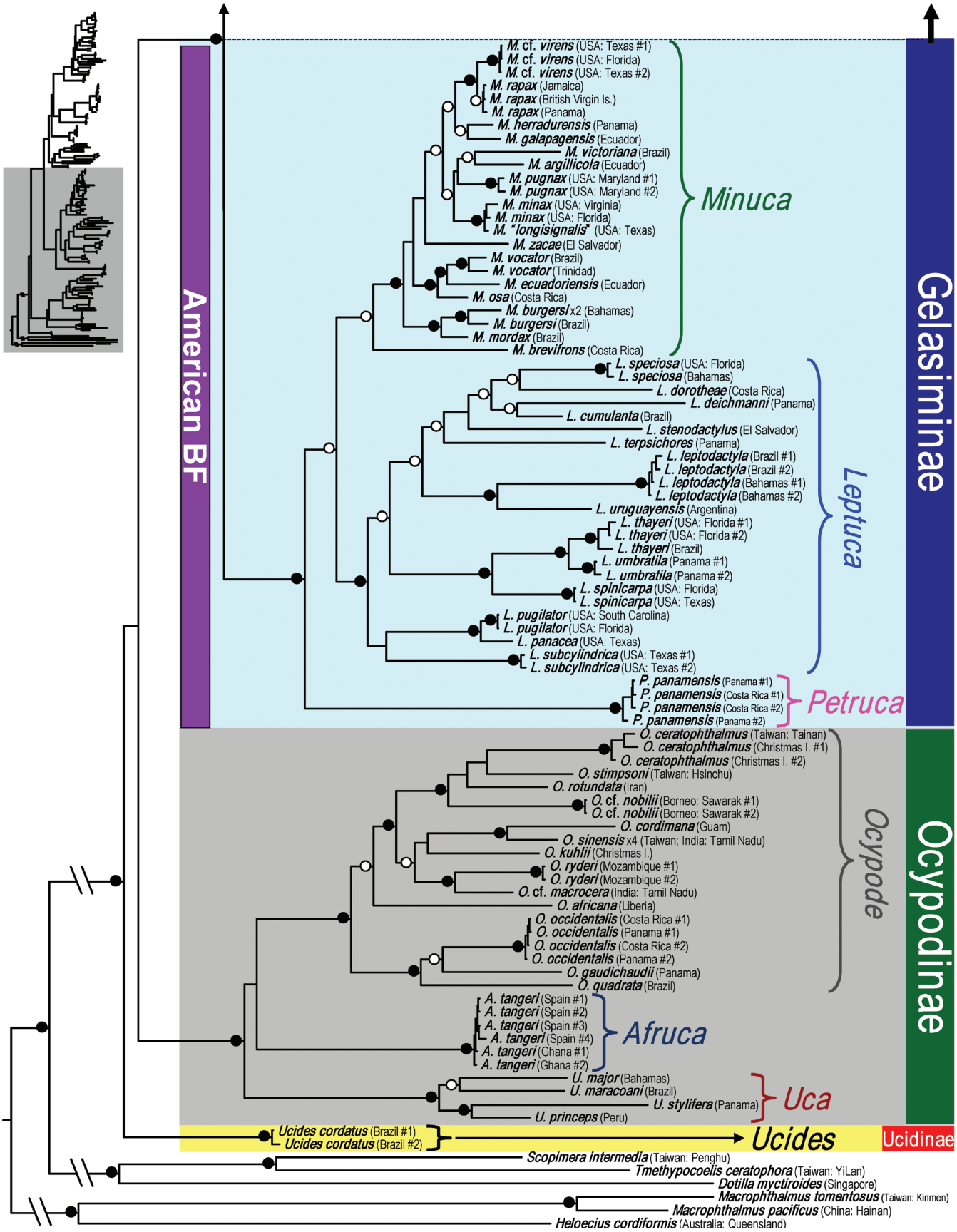

Fig. 2. cont'd above.

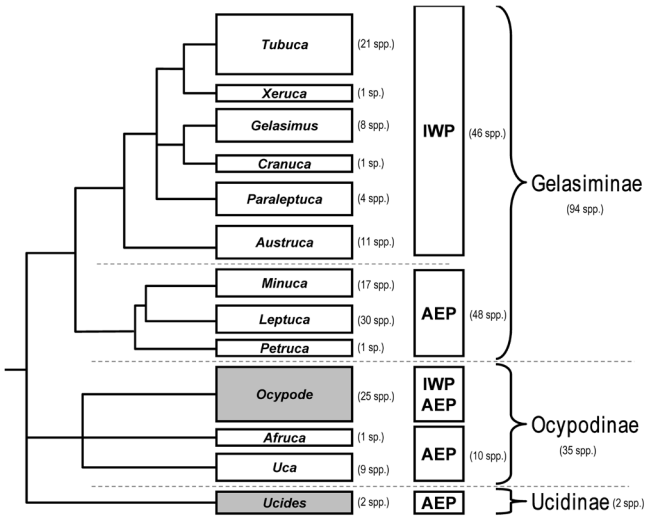

Fig. 3. The simplified phylogenetic tree modified from Figs. 1 & 2, with number of species beside or below the taxa/group. The gray boxes mean the genera are not fiddler crabs.

Australuca. However, using more markers and species, our study confirms the close relationship among *Ocypode*, *Afruca* and *Uca* s. str.; and supports the relationship between the two American BF groups, *Minuca* and *Leptuca*.

The early literature of crab systematics commonly used subgenera for what were believed to be closely related groups. Today, many authors have raised these subgenera to genera, e.g., in the Dorippidae, Potamidae, Potamonautidae, Pseudothelphusidae, Gecarcinuciodae, Sesarmidae and Varunidae (see Ng et al., 2008), Macrophthalmidae (McLay et al., 2010; Davie, 2012), and Portunidae (e.g., Chertoprud et al., 2012; Koch et al., 2015). However, these morphological decisions are not always fully supported by molecular results (e.g., the disparities in the analysis of the Dorippidae by Sin et al., 2009; and the *Helice/Chasmagnathus* complex by Shih & Suzuki, 2008); suggesting that either some genera remain heterogeneous or the morphological characters used may be suspect. In the present study, all recognised genera have good genetic support, and most are highly-supported by BI and ML methods (see below); and in most cases, there is also a morphological basis for their recognition.

The subfamily Ocypodinae as recognised here includes three highly-supported genera, *Ocypode* Weber, 1795, *Uca* Leach, 1814, and *Afruca* Crane, 1975. The genus *Hoplocypode* Sakai & Türkay, 2013, is not supported, as it is nested in a subclade with *O. gaudichaudii* and *O. quadrata*, also from the Americas (see Remarks under *Ocypode*).

The Gelasiminae Miers, 1886, can be subdivided into two groups. An American group is composed of three genera, *Leptuca* Bott, 1973, *Minuca* Bott, 1954, and *Petruca* Shih, Ng & Christy, 2015. The IWP group includes six genera, *Austruca* Bott, 1973, *Cranuca* Beinlich & von Hagen, 2006, *Gelasimus* Latreille, 1817, *Paraleptuca* Bott, 1973, *Tubuca* Bott, 1973, and *Xeruca* Shih, 2015. Most genera are highly-supported by BI and ML, except *Minuca* that has a lower ML support value (Fig. 2). Although species of *Australuca* form

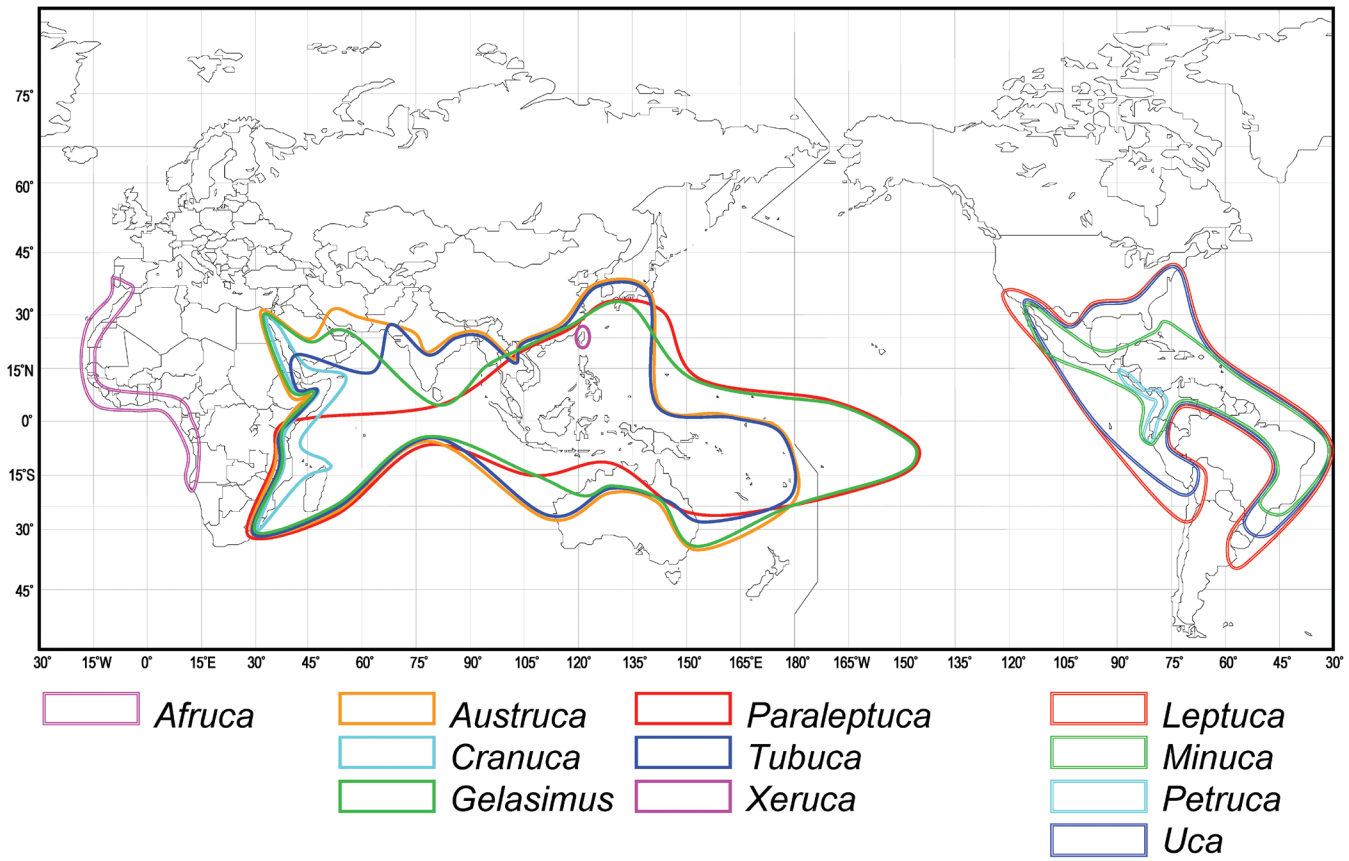

Fig. 4. The distribution of 11 genera of fiddler crabs, mainly based on Crane (1975) and the website (http://www.fiddlercrab.info/index.html; Rosenberg, 2014).

a distinct subclade, to recognise it as a separate genus would make *Tubuca* paraphyletic. As a result, we treat *Australuca* Crane, 1975, as a junior subjective synonym of *Tubuca*.

The recognition of Ucidinae in the Ocypodidae for *Ucides*, is confirmed in this study (Fig. 2) and supports the finding of Schubart & Cuesta (2010) based on 16S. *Ucides* has been recently considered as a separate family Ucididae because the morphology is very different from fiddler and ghost crabs (Ng et al., 2008; Davie et al., 2015). The phylogenetic tree (Fig. 2), however, shows no significant support (less than 50% for both BI and ML methods) for recognising two families. It instead suggests a close relationship with the other two subfamilies. As such, despite its suite of diagnostic morphological features, *Ucides* is placed in a third subfamily, Ucidinae, in the family Ocypodidae.

Members of the genus *Heloecius* (family Heloeciidae) superficially resemble *Uca* (see Beinlich & von Hagen, 2006), and it has also been considered to have some morphological similarities to *Ucides* (e.g., Türkay, 1983). Ng et al. (2008) and Davie et al. (2015), however, considered both Ucidinae Števčić (2005) and the Heloeciinae to be separate families within the Ocypodoidea. Their decision was in part based on studies such as Levinton et al. (1996: fig. 2) that showed no direct relationship between *Heloecius* and the Ocypodidae based on 16S. The 12S and 16S results of Schubart et al. (2006) also revealed that *Heloecius* is not closely related to the Ocypodidae, and this is corroborated by the present results (Fig. 2).

SYSTEMATIC ACCOUNT

Family Ocypodidae Rafinesque, 1815

Ocypodidae Rafinesque, 1815: 96 [as Ocypodia, corrected to Ocypodidae by MacLeay, 1838: 63. Name No. 375 on Official List of Family-group Names in Zoology, see International Commission on Zoological Nomenclature (ICZN, 1964: Opinion 712]. Type genus: *Ocypode* Weber, 1795.

Ucainae Dana, 1851: 289. Type genus: *Uca* Leach, 1814.

Gelasimiden Nauck, 1880: 8, 17, 23, 64, 66 [not Latinised, invalid for nomenclatural purposes].

Gelasimidae Miers, 1886: viii. Type genus: *Gelasimus* Latreille, 1817.

Diagnosis. Carapace deep, subquadrilateral to subovate; dorsal regions indistinct to prominently demarcated; anterolateral margins straight, slightly arched or strongly convex; fronto-orbital distance more than half maximum carapace width; front broad to relatively narrow, deflexed, usually forming lobe between eyestalks; antennules folding obliquely or almost vertically; antennular flagellum small or rudimentary; proepistome broad; third maxillipeds completely or almost completely closing buccal cavern; exopod visible in part or completely, with or without flagellum; chelipeds unequal in adult males, sometimes remarkably so; most species with brush of long setae lining pouch leading into branchial cavity between bases of second and third ambulatory legs; thoracic sternum broad posteriorly; male thoracic sternum narrowed posteriorly, only small part of sternite 8 visible when pleon closed; male gonopore sternal, adjacent to suture between sternites 7 and 8; adult male pleon relatively wide, subrectangular, long, telson reaching or near buccal cavity; somites 4–6 or 5 and 6 partly or completely fused; pleonal locking mechanism usually absent; G1 stout, strongly chitinised, with short pectinate tip fringed with stiff setae which obscuring surface.

Subfamily Ocypodinae Rafinesque, 1815

Ocypodidae Rafinesque, 1815: 96. Type genus: *Ocypode* Weber, 1795.

Ucainae Dana, 1851: 289. Type genus: *Uca* Leach, 1814.

Diagnosis. Carapace deep, subquadrilateral to pentagonal, never cordiform, not swollen; fronto-orbital distance more than 9/10 of maximum carapace width, front narrow to relatively narrow; regions typically indistinct, grooves between regions shallow or indistinct; anterolateral margins straight or slightly arched; orbital floor with distinct tubercle at inner corner adjacent to antennule; eyestalks relatively short to very long, cornea terminal, may have distinct distal ornament (e.g., stylus or long setae); buccal cavern quadrate, not much longer than wide, third maxillipeds completely covering it when closed; ischium and merus of third maxilliped quadrate, fringed with scattered short setae on inner surface; exopod of third maxilliped not concealed by endopod, with or without flagellum; chelipeds unequal in adult males (*Ocypode*), sometimes remarkably so (e.g., *Afruca*, *Uca*), equal or slightly unequal in females, surfaces of male merus, carpus and palm smooth or armed with short spines or tubercles; first to fourth ambulatory legs with scattered long and/or short setae on ventral surface of merus, propodus and dactylus, never dense or obscuring margins; brush of long setae present between bases of coxae of second and third ambulatory legs, leading into branchial cavity; male pleon with all somites free; pleonal locking mechanism absent.

Remarks. The subfamily Ocypodinae is now composed of two BF genera *Ocypode* and *Afruca*, and one NF genus *Uca*. Since the type genus of the subfamily Ucinae Dana, 1851, is *Uca* s. str., this subfamily has to be treated as a junior subjective synonym of Ocypodinae. Our results agree with previous studies (Levinton et al., 1996; Sturmbauer et al., 1996) that the three genera are closely related, although their morphology appears remarkably different, at least superficially. Further studies are necessary to elucidate the key morphological characters of the subfamily.

Ocypode Weber, 1795

(Fig. 5)

Ocypode Weber, 1795: 92. Type species: *Cancer ceratophthalmus* Pallas, 1772, by subsequent designation, see Latreille (1810: 95, 422). Gender feminine.

Ocypode Fabricius, 1798: 312, 347. Type species: *Cancer ceratophthalmus* Pallas, 1772, by subsequent designation, see Latreille (1810). Junior objective homonym of *Ocypode* Weber, 1795. Gender feminine.

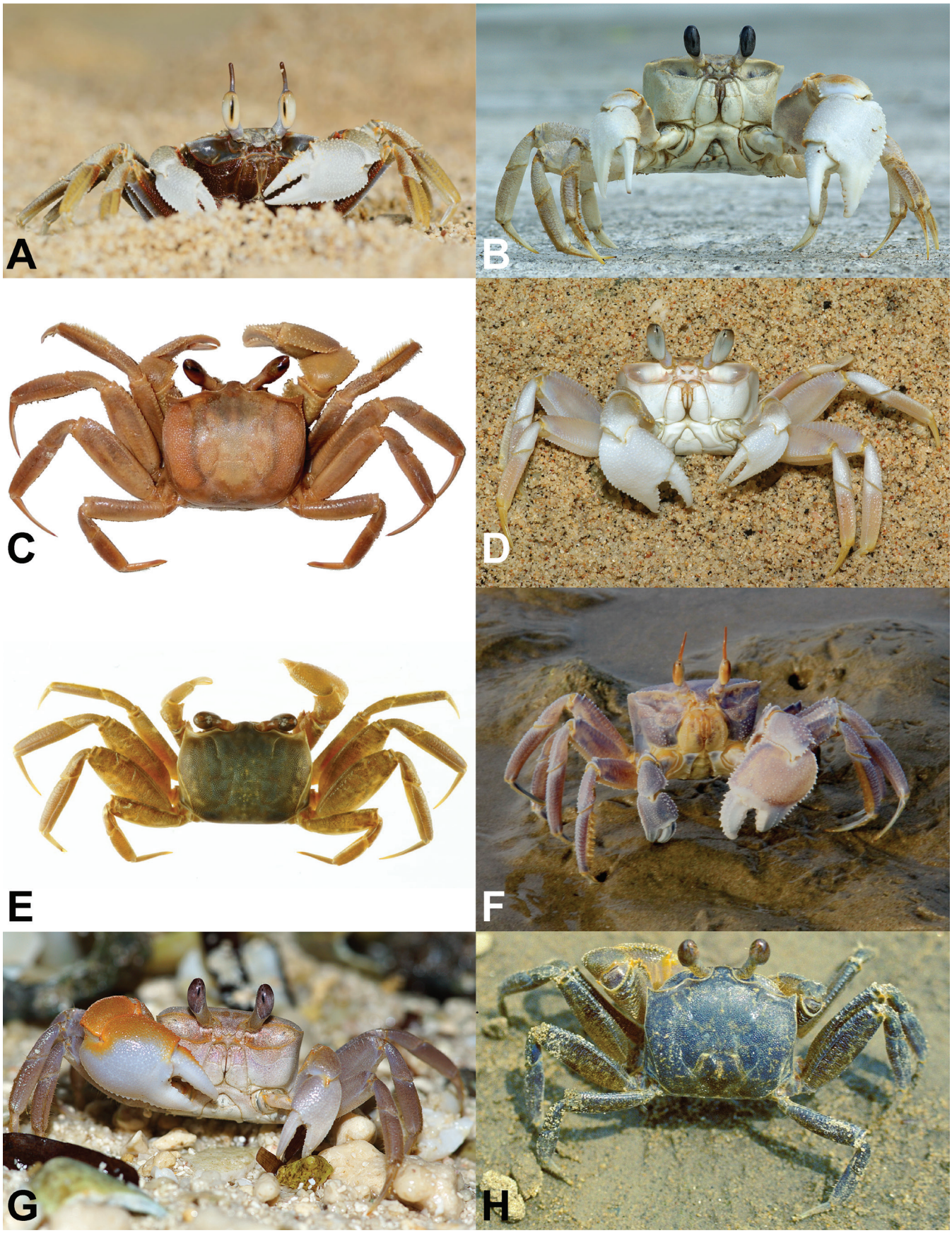

Fig. 5. Photographs of some species of the genus *Ocypode*. A, *O. ceratophthalmus* (Taiwan); B, *O. cordimana* (Dongsha, Taiwan); C, *O. fabricii* (Northern Territory, Australia); D, *O. kuhlii* (Christmas Island); E, *O. occidentalis* (Panama); F, *O. rotundata* (Iran); G. *O. sinensis* (Dongsha, Taiwan); H, *O. stimpsoni* (Taiwan).

Ocypoda Lamarck, 1801: 149 (incorrect subsequent spelling for *Ocypode* Weber, 1795).

Monolepis Say, 1817: 155. Type species: *Monolepis inermis* Say, 1817 (= *Cancer quadratus* Fabricius, 1787) by subsequent designation, see Fowler (1912). Gender feminine.

Ceratophthalma MacLeay, 1838: 64. Type species *Cancer cursor* Linnaeus, 1758, by monotypy.

Parocypoda Neumann, 1878: 26. Type species *Cancer ceratophthalmus* Pallas, 1772, by monotypy. Junior objective synonym of *Ocypode* Weber, 1795. Gender feminine.

Hoplocypode Sakai & Türkay, 2013: 675. Type species *Ocypoda occidentalis* Stimpson, 1860, by original designation. Gender feminine.

Diagnosis. Body deep; carapace subquadrangular, regions poorly defined; front wide, prominently deflexed; eyestalks large, cornea occupying most of ventral surface of stalk, tip cornea sometimes with stylus, horn or prominent setal brush; antenna relatively long; inner antennal septum broad; chelipeds unequal in both sexes, palm of larger chela usually with stridulating ridge of tubercles and/or striae; first to fourth ambulatory legs relatively short, stout, dactylus fluted; pleonal locking mechanism absent; G1 typically simple distally, but may be complex in shape distally, may appear hoof-shaped in mesial view. Atlantic and Indo-Pacific.

Species included:

1. *Ocypode africana* De Man, 1881
   = *Ocypoda hexagonura* Hilgendorf, 1882
   = *Ocypoda edwardsi* Osorio, 1890
2. *Ocypode brevicornis* H. Milne Edwards, 1837
3. *Ocypode ceratophthalmus* (Pallas, 1772)
   = *Cancer arenarius* Toreen, in Osbeck, 1765
   = *Cancer caninus* Herbst, 1782
   = *Ocipode urvillei* Guérin, 1829
   = *Ocypoda brevicornis* var. *longicornuta* Dana, 1852
   = *Ocypoda macleayana* Hess, 1865
   = *Cancer francisci* Curtiss, 1938
4. *Ocypode convexa* Quoy & Gaimard, 1824
5. *Ocypode cordimana* Latreille, 1818
   = *Cancer roberti* Curtiss, 1938
6. *Ocypode cursor* (Linnaeus, 1758)
   = *Cancer eques* Aubert de la Chesnaye des Bois, 1759
   = *Ocypoda ippeus* Olivier, 1804
7. *Ocypode fabricii* H. Milne Edwards, 1837
8. *Ocypode gaudichaudii* H. Milne Edwards & Lucas, 1843
9. *Ocypode jousseaumei* (Nobili, 1905)
10. *Ocypode kuhlii* De Haan, 1835
11. *Ocypode macrocera* H. Milne Edwards, 1852
    = *Ocypode portonovoensis* Prem Kumar & Tiwari, 1964
12. *Ocypode madagascariensis* Crosnier, 1965
13. *Ocypode mortoni* George, 1982
14. *Ocypode nobilii* De Man, 1902
15. *Ocypode occidentalis* Stimpson, 1860
16. *Ocypode pallidula* Hombron & Jacquinot, 1846
    = *Ocypoda laevis* Dana, 1852
17. *Ocypode pauliani* Crosnier, 1965
18. *Ocypode platytarsis* H. Milne Edwards, 1852
19. *Ocypode pygoides* Ortmann, 1894
20. *Ocypode quadrata* (Fabricius, 1787)
    = *Cancer arenarius* Catesby, 1771 (not available name)
    = ?*Ocypode rhombea* Fabricius, 1798
    = *Ocypode albicans* Bosc, 1801
    = *Monolepis inermis* Say, 1817
21. *Ocypode rotundata* Miers, 1882
    = *Ocypode rotundata* var. *arabica* Nobili, 1906
22. *Ocypode ryderi* Kingsley, 1880
23. *Ocypode saratan* (Forskål, 1775)
    = *Ocypode aegyptica* Gerstaecker, 1856
24. *Ocypode sinensis* Dai, Song & Yang, 1985
25. *Ocypode stimpsoni* Ortmann, 1897

Two species are nomina dubia: *Ocypode laevis* Fabricius, 1798; and *Ocypode minuta* Fabricius, 1798 (see Ng et al., 2008).

Remarks. The ghost crabs have been revised in detail by Sakai & Türkay (2013) with the recognition of 21 valid species, although Ng et al. (2008) listed 26 species. *Hoplocypode* Sakai & Türkay, 2013, was recently established for *O. occidentalis* (central east Pacific coast of the Americas) based on the morphology of G1 (Sakai & Türkay, 2013); but this taxon is not supported in our study (Fig. 2). Interestingly, our tree does support two subclades of ghost crabs: *O. gaudichaudii*, *O. occidentalis*, and *O. quadrata* belong to a highly-supported American subclade; while all remaining species form the other, although with a lower ML support value. The three members of the American subclade share similar first gonopodal characters and may prove to be a distinct genus. However, even if they need to be placed in their own genus, *Hoplocypode* Sakai & Türkay, 2013, will still be a junior subjective synonym of *Monolepis* Say, 1817, whose type species is *Monolepis inermis* Say, 1817 (= *Cancer quadratus* Fabricius, 1787). Sakai & Türkay (2013) synonymised a number of species, notably *O. sinensis* Dai, Song & Yang, 1985, with *O. cordimana* Latreille, 1818. However, Huang et al. (1998) already showed they differ in a number of adult morphological characters (although juveniles are very close and hard to separate) and there are also genetic differences (Fig. 1; Wong et al., 2012: fig. 9). Further evidence showing morphological and molecular differences between these two species is being prepared (Shih et al., in prep.). Further studies with more species of *Ocypode* than included herein will be necessary to clarify the relationships within this genus.

Afruca Crane, 1975, status nov.

(Fig. 6A, B)

Uca (*Afruca*) Crane, 1975: 116. Type species: *Gelasimus tangeri* Eydoux, 1835, by original designation. Gender feminine.

Diagnosis. Large-sized (carapace width about 35 mm in adults); dorsal surface carapace mostly covered with prominent tubercles, without posterolateral striae; front broad; cornea round; eyestalks slender; orbital floor with a spinous tubercle near inner corner; spoon-tipped setae of second maxilliped with proximal spine opposing these

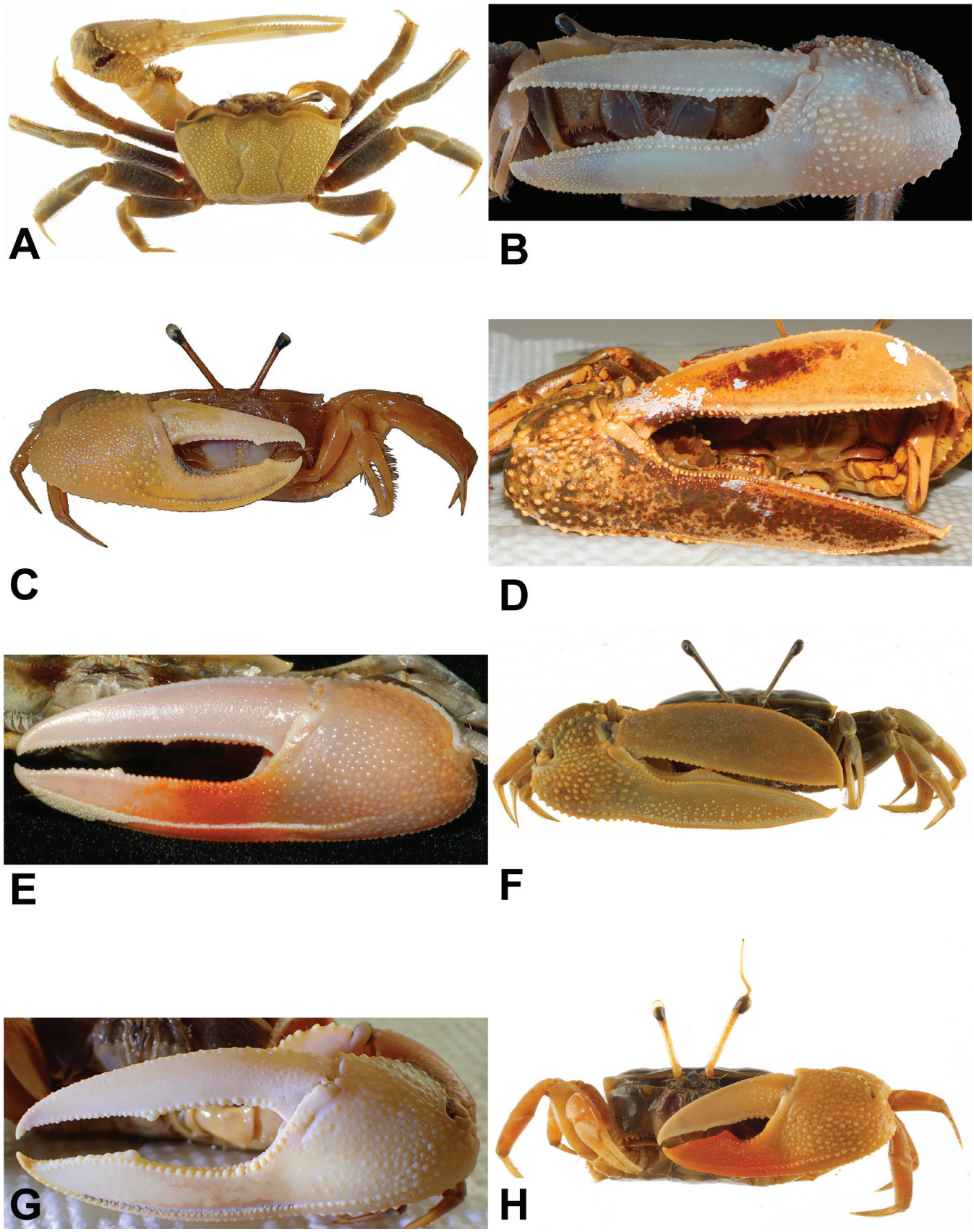

Fig. 6. Photographs of some species of the genera *Afruca* and *Uca* s. str. A, B, *A. tangeri* (Spain); C, *U. heteropleura* (Panama); D, *U. insignis* (El Salvador); E, *U. major* (Bahamas); F, *U. maracoani* (Brazil); G, *U. princeps* (Peru); H, *U. stylifera* (Panama).

setae; adult male major cheliped extremely large; individuals right- or left-handed, with deep fingers, pollex with ventral carina, outer surface of major manus with large tubercles; both chelipeds small in female; pleonal locking mechanism absent. Confined to East Atlantic coasts.

Species included:

Afruca tangeri (Eydoux, 1835).
= *Gelasimus perlatus* Herklots, 1851
= *Gelasimus cimatodus* Rochebrune, 1883
= *Uca tangeri* var. *platydactylus* Monod, 1927 (pre-occupied name)
= +*Uca tangeri* var. *matandensis* Monod, 1928

Remarks. Crane (1975) established the subgenus *Afruca* for the BF *Uca tangeri*, from the eastern Atlantic Ocean (Fig. 4), but later several authors treated this species and the American NF taxa under the subgenus *Uca* (Levinton et al., 1996; Sturmbauer et al., 1996; Rosenberg, 2001; Beinlich & von Hagen, 2006; Ng et al., 2008). Spivak & Cuesta (2009) suggested *Afruca* is valid based on larval data and should be considered as a distinct genus. The validity of the genus *Afruca* is supported in this study (Fig. 2), with a close relationship to *Uca* and *Ocypode*.

Uca Leach, 1814

(Fig. 6C–H)

Uca Leach, 1814: 430. Type species: *Uca una* Leach, 1814 (= *Cancer vocans major* Herbst, 1782) by monotypy. Gender feminine.

Heteruca Bott, 1973b: 323. Type species: *Gelasimus heteropleurus* Smith, 1870, by original designation. Gender feminine.

Acanthoplax H. Milne Edwards, 1852: 151. Type species: *Acanthoplax insignis* H. Milne Edwards, 1852, by monotypy.

Eurycheles Rathbun, 1914: 126. Type species: *Uca monilifera* Rathbun, 1914, by monotypy. Gender masculine.

Diagnosis. Medium- to large-sized species (carapace width about 25–40 mm in adults); dorsal carapace surface without posterolateral striae; front relatively narrow; cornea round; eyestalks slender; eye on major side sometimes with distal style; orbital floor with spinous tubercle near inner corner; spoon-tipped setae of second maxilliped with proximal spine opposing spoon; adult male major cheliped extremely large; right- or left-handed, with deep finger (straight cutting margins <1/2 length of fingers, or with conspicuously deep dactylus and pollex), pollex with ventral carina, outer surface of major manus with large tubercles; both chelipeds small in female; pleonal locking mechanism absent. Confined to Atlantic and East Pacific coasts of Americas.

Species included:

1. *Uca heteropleura* (Smith, 1870)
2. *Uca insignis* (H. Milne Edwards, 1852)
   = *Gelasimus* (*Acanthoplax*) *excellens* Gerstaecker, 1856
   = *Gelasimus armatus* Smith, 1870
3. *Uca intermedia* von Prahl & Toro, 1985
4. *Uca major* (Herbst, 1782)
   = *Ocypoda heterochelos* Lamarck, 1801
   = *Cancer uka* Shaw & Nodder, 1803
   = *Uca una* Leach, 1814
   = *Gelasimus platydactylus* H. Milne Edwards, 1837
   = *Gelasimus grangeri* Desbonne, in Desbonne & Schram, 1867
5. *Uca maracoani* (Latreille, 1803)
6. *Uca monilifera* Rathbun, 1914
7. *Uca ornata* (Smith, 1870)
   = *Uca pizarri* von Hagen, 1968
8. *Uca princeps* (Smith, 1870)
9. *Uca stylifera* (H. Milne Edwards, 1852)
   = *Gelasimus heterophthalmus* Smith, 1870

Remarks. The description of the genus *Uca* by Seba (1758) was based on a picture of the type species, "*Cancer uka una*, *Brasiliensibus*", which later authors considered to be *Cancer vocans major* Herbst, 1782. However, Bott (1973a) realised that the species in the picture was not the American *Uca major*, but instead the East Atlantic "*U. major*" (= *U. tangeri*). To avoid nomenclatural problems, the International Commission on Zoological Nomenclature (ICZN) officially ruled that the holotype of *Gelasimus platydactylus* would henceforth also be the neotype of *Cancer vocans major* (Holthuis, 1979; ICZN, 1983). This maintained the name *Uca major* for the American species and *Afruca tangeri* for the East Atlantic species (see Rosenberg, 2001 for details).

Uca s. str. now includes nine NF species from both sides of the Americas (Fig. 4). The major cheliped of several species has a conspicuously deep dactylus and pollex, e.g., *U. insignis* (Fig. 6C), *U. maracoani* (Fig. 6D), *U. monilifera* (Crane, 1975: pl. 18E–H), and *U. ornata* (Crane, 1975: pl. 21E–H), and the waving displays have been consequently modified as a result of the heavier chelae (Crane, 1975).

Subfamily Gelasiminae Miers, 1886

Gelasimiden Nauck, 1880: 8, 17, 23, 64, 66 [not Latinised, invalid for nomenclatural purposes].

Gelasimidae Miers, 1886: viii. Type genus: *Gelasimus* Latreille, 1817.

Diagnosis. Carapace distinctly transverse, trapezoidal, widest between exorbital angles; fronto-orbital distance more than 9/10 of maximum carapace width, front wide to relatively narrow; regions typically indistinct, grooves between regions shallow or indistinct; anterolateral margins slightly arched; orbital floor without or with vestigial tubercle at inner corner adjacent to antennule; eyestalks slender, very long, cornea terminal without any distal ornament; buccal cavern quadrate, not much longer than wide, third maxillipeds completely covering it when closed; ischium and merus of third maxilliped quadrate, fringed with scattered short setae on inner surface; exopod of third maxilliped not concealed by endopod, with flagellum; chelipeds strongly unequal in adult males, both chelipeds small in females, surfaces of male merus, carpus and palm smooth or armed with short spines or low tubercles; first to fourth ambulatory legs with scattered long and/or short setae on ventral surface of merus, propodus and dactylus, never obscuring margins; brush of long setae present between bases of coxae of second and third

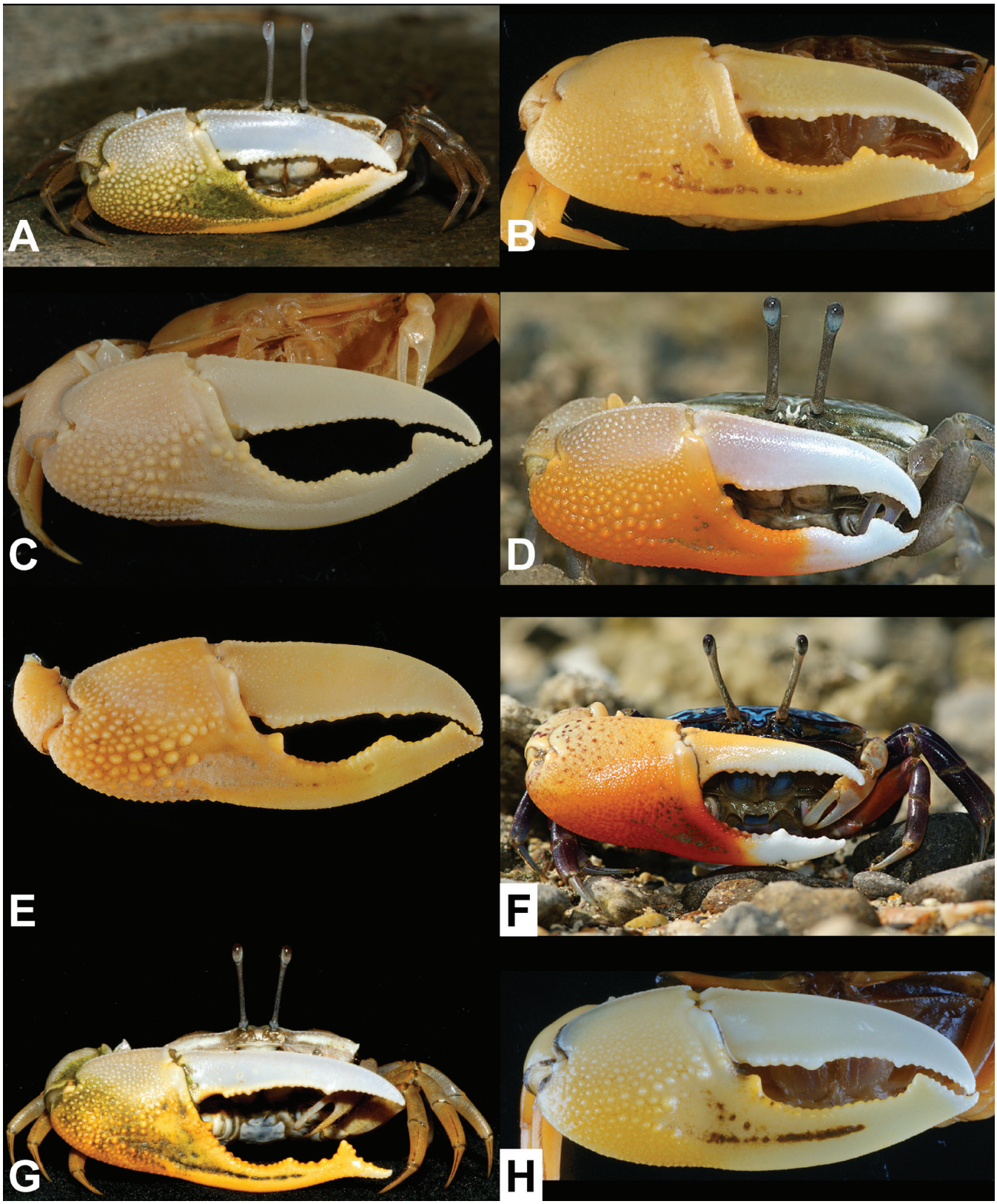

Fig. 7. Photographs of some species of the genus *Gelasimus*. A, *G. borealis* (Taiwan); B, *G. dampieri* (Northern Territory, Australia); C, *G. hesperiae* (Zanzibar, holotype); D, *G. jocelynae* (Penghu, Taiwan); E, *G. neocultrimana* (Fiji); F, *G. tetragonon* (Penghu, Taiwan); G, *G. vocans* (Labuan, Malaysia); H, *G. vomeris* (Queensland, Australia).

ambulatory legs, leading into branchial cavity; male pleon with all somites free or somites 4–6 partly or completely fused; pleonal locking mechanism sometimes present.

Remarks. This subfamily contains all the fiddler crabs not otherwise transferred to the revised Ocypodinae. Miers (1886: viii) introduced the family Gelasimidae Miers, 1886, but this has been long considered to be a junior synonym of Ucinae Dana, 1851. However, because of the current diagnoses of the genera and present reappraisal, Gelasiminae can now be used; since *Uca* s. str. is here transferred to the Ocypodinae. As a result, Gelasiminae is now the largest ocypodid subfamily, with nine genera and 94 species, belonging to two groups: 1) the American BF genera *Leptuca*, *Minuca* and *Petruca*; and 2) the Indo-West Pacific NF genera *Gelasimus*, *Tubuca* and *Xeruca*, and the BF genera *Austruca*, *Cranuca* and *Paraleptuca* (Figs. 1–3).

In Shih et al. (2013b), *Leptuca* and *Minuca* were found to form an unresolved clade, but this was to be most likely the result of analysing too few species. However, Shih et al. (2015) and the results of the present study, show both genera have high and medium support, respectively; especially with the removal of the newly recognised *Petruca*, and generic reassignment of some other species (see below). *Australuca*, on the other hand, is nested within *Tubuca* and must therefore be regarded as a junior subjective synonym of that genus (see Remarks under *Tubuca*).

A number of species are regarded as nomina dubia by Ng et al. (2008): *Gelasimus huttoni* Filhol, 1886; *Gelasimus leptostyla* Nutting, 1919; *Goneplax nitida* Desmarest, 1817 (= *Gelasima nitida* Desmarest, 1822); *Gelasimus minor* Owen, 1839; *Gelasimus rectilatus* Lockington, 1877; and *Gelasimus rubripes* Hombron & Jacquinot, 1846.

Gelasimus Latreille, 1817
(Fig. 7)

Gelasimus Latreille, 1817: 517. Type species: *Cancer vocans* Linnaeus, 1758 by subsequent designation, see H. Milne Edwards (1841: pl. 18, fig. 1). Gender masculine.

Latuca Bott, 1973b: 317. Type species: *Mesuca* (*Latuca*) *neocultrimana* Bott, 1973 by original designation. Gender feminine.

Mesuca Bott, 1973b: 316. Type species: *Cancer tetragonon* Herbst, 1790 by original designation. Gender feminine.

Thalassuca Crane, 1975: 75. Type species: *Cancer tetragonon* Herbst, 1790 by original designation. Gender feminine.

Diagnosis. Medium- to large-sized (carapace width about 20–30 mm in adults); dorsal carapace surface without posterolateral striae; front narrow; cornea round; eyestalks slender; adult male chelipeds very large, always right-handed, pollex without ventral carina, outer surface of major manus with moderate to large tubercles; male pleonites free; pleonal locking mechanism absent; setae present on lateral margins of posterior stem region of urocardiac ossicles in gastric mill. Indo-West Pacific.

Species included:

1. *Gelasimus borealis* (Crane, 1975)
2. *Gelasimus dampieri* (Crane, 1975)
3. *Gelasimus hesperiae* (Crane, 1975) (nomen protectum)
   = *Gelasimus tetragonon* var. *spinicarpa* Kossmann, 1877 (nomen oblitum)
4. *Gelasimus jocelynae* (Shih, Naruse & Ng, 2010)
5. *Gelasimus neocultrimanus* (Bott, 1973)
   = *Uca* (*Thalassuca*) *vocans pacificensis* Crane, 1975
6. *Gelasimus tetragonon* (Herbst, 1790)
   = *Gelasimus affinis* Guérin, 1829
   = *Gelasimus duperreyi* Guérin, 1829
   = *Gelasimus variatus* Hess, 1865
7. *Gelasimus vocans* (Linnaeus, 1758)
   = *Gelasimus marionis* Desmarest, 1823
   = *Gelasimus nitidus* Dana, 1851
   = *Gelasimus cultrimanus* White, 1847
   = *Uca marionis* forma *excisa* Nobili, 1906
8. *Gelasimus vomeris* (McNeill, 1920)

Remarks. *Gelasimus* is widely-distributed in the Indo-West Pacific (Fig. 4). Bott (1973b) established *Mesuca* as a genus including two subgenera, *Mesuca* (*Mesuca*) for *Uca tetragonon* and four other species now reassigned elsewhere, and *Mesuca* (*Latuca*) for *U. neocultrimana* and three other species also here reassigned to other genera. The current morphological and genetic data suggests this is one monophyletic group. If future studies indicate that *Gelasimus* is polyphyletic, then *Mesuca* and *Latuca* would be available names for use as possible subgenera or genera.

Interestingly, Shih et al. (2010) found that the 16S and COI markers do not show differences between the species within the complex of *U. borealis*, *U. dampieri*, *U. vocans* and *U. vomeris*, despite good morphological characters to separate them. However, some species can be successfully separated genetically using the nuclear internal transcribed spacers (ITS-1) (Shih unpublished; Chu et al., 2015), which suggests that speciation has been very recent.

While *Gelasimus* is the only genus with right-handed cheliped for most males, the remaining species are right- or left-handed with nearly the same ratio (Barnwell, 1982; Yamaguchi, 1994). Juvenile males possess two large chelipeds, and the asymmetry will be attained by losing of either one cheliped that regenerates into a small cheliped (Morgan, 1923; Yamaguchi & Henmi, 2001). However, the mechanism of losing the left cheliped by juvenile *Gelasimus* species is still unknown.

Austruca Bott, 1973, status nov.
(Fig. 8)

Austruca Bott, 1973b: 322. Type species: *Gelasimus annulipes* H. Milne Edwards, 1837 by original designation.

Diagnosis. Small- to medium-sized species (carapace width about 15 mm in adults); dorsal carapace surface smooth, with or without posterolateral striae; front broad; cornea round; eyestalks slender; adult male cheliped very large,

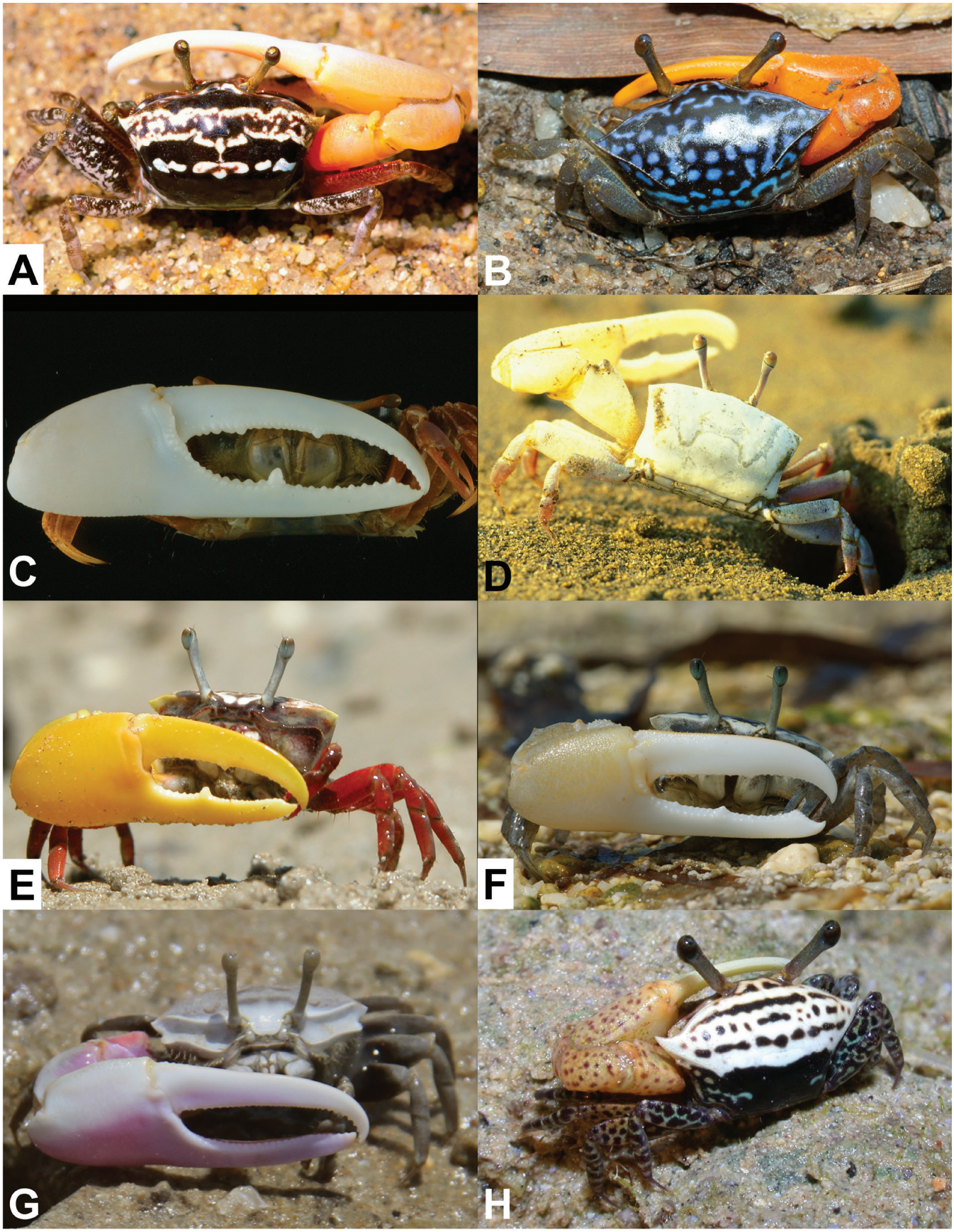

Fig. 8. Photographs of some species of the genus *Austruca*. A, *A. annulipes* (Tioman, Malaysia); B, *A. bengali* (Selangor, Malaysia); C, *A. iranica* (Iran); D, *A. lactea* (Taiwan); E, *A. mjoebergi* (New Territory, Australia); F, *A. perplexa* (Dongsha, Taiwan); G, *A. sindensis* (Iran); H, *A. triangularis* (Cebu, Philippines). E, courtesy of P. Backwell.

right- or left-handed, pollex sometimes with ventral carina, outer surface of major manus smooth, without depression near base of pollex, carpal cavity with distal extension; male pleonites free; with pleonal clasping apparatus; gastric mill without large brownish setae at base of posterior tooth plate. Indo-West Pacific.

Species included:
1. *Austruca albimana* (Kossmann, 1877)
2. *Austruca annulipes* (H. Milne Edwards, 1837)
   = *Gelasimus porcellanus* White, 1847
   = *Uca consobrinus* Verwey, 1930
3. *Austruca bengali* (Crane, 1975)
4. *Austruca cryptica* (Naderloo, Türkay & Chen, 2010)
5. *Austruca iranica* (Pretzmann, 1971)
6. *Austruca lactea* (De Haan, 1835)
   = *Gelasimus forceps* H. Milne Edwards, 1837
7. *Austruca occidentalis* (Naderloo, Schubart & Shih, 2016)
8. *Austruca mjoebergi* (Rathbun, 1924)
9. *Austruca perplexa* (H. Milne Edwards, 1852)
   = *Uca annulipes* var. *orientalis* Nobili, 1901
10. *Austruca sindensis* (Alcock, 1900)
11. *Austruca triangularis* (A. Milne-Edwards, 1873)

Remarks. Most species of *Austruca* agree well with Crane's (1975) definition of the IWP *Celuca*, with the exception of *U. sindensis* (cf. Shih et al., 2013b; Fig. 2) which was previously placed under *Paraleptuca* (= *Amphiuca* Crane 1975). One main character of *Paraleptuca* is the outer major manus with a small round depression near pollex base which does not appear in *Austruca*, including *A. sindensis*. *Austruca* is widely-distributed in the IWP (Fig. 4), with four species added since Crane (1975), viz., *A. albimana*, *A. cryptica*, *A. iranica* and *A. occidentalis* (Shih et al., 2009; Naderloo et al., 2010, 2016). The genus contains three species-complexes: 1) the *U. lactea* complex with seven species, including an unnamed species from East Africa, twice as many as listed in Crane (1975); 2) *U. triangularis* and *U. bengali* as revealed in this study; 3) *U. sindensis* (Fig. 2).

Cranuca Beinlich & von Hagen, 2006, status nov.
(Fig. 9A)

Cranuca Beinlich & von Hagen, 2006: 25. Type species *Gelasimus inversa* Hoffmann, 1874, by original designation. Gender feminine.

Diagnosis. Medium-sized species (carapace width about 20 mm in adults); dorsal carapace surface without posterolateral striae; front broad; cornea round; eyestalks slender; adult male cheliped very large, right- or left-handed, pollex without ventral carina, major dactylus with large subdistal tooth, outer surface of major manus with moderate-sized tubercles; male pleonites free; without pleonal clasping apparatus; gastric mill without large brownish setae at base of posterior tooth plate. Indo-West Pacific.

Species included:
Cranuca inversa (Hoffmann, 1874).

Remarks. *Cranuca* is monotypic, containing only a single species, the BF *C. inversa*, which occurs only in East Africa (Fig. 4). This species was placed under *Amphiuca* (= *Paraleptuca*) as a subspecies (of *U. inversa*) together with *U. sindensis* by Crane (1975). However, some unique morphological characters led Beinlich & von Hagen (2006) to established *Cranuca* for this species. This decision was later supported by molecular evidence that showed a close relationship with the NF *Gelasimus* species (Shih et al., 2013b; Fig. 2).

Leptuca Bott, 1973, status nov.
(Fig. 9B–F)

Leptuca Bott, 1973b: 324. Type species: *Gelasimus stenodactylus* H. Milne Edwards & Lucas, 1843, by original designation. Gender feminine.

Celuca Crane, 1975: 211. Type species: *Uca deichmani* Rathbun, 1935, by original designation. Gender feminine.

Planuca Bott, 1973b: 324. Type species: *Uca thayeri* Rathbun, 1900, by original designation. Gender feminine.

Boboruca Crane, 1975: 109. Type species: *Uca thayeri* Rathbun, 1900, by original designation. Gender feminine.

Diagnosis. Small- to large-sized species (carapace width about 5–25 mm in adults); anterolateral margins short; 0–2 posterolateral striae on dorsal carapace surface; front broad; cornea round; eyestalks slender; adult male major cheliped very large, right- or left-handed, pollex sometimes with ventral carina, outer surface of major manus smooth; male pleonites free or somites 4–6 partly or fully fused; pleonal locking mechanism absent; gastric mill with 2 large brownish setae at base of posterior tooth plate. Confined to the Atlantic and East Pacific coasts of the Americas.

Species included:
1. *Leptuca batuenta* (Crane, 1941)
2. *Leptuca beebei* (Crane, 1941)
3. *Leptuca coloradensis* (Rathbun, 1893)
4. *Leptuca crenulata* (Lockington, 1877)
   = *Gelasimus gracilis* Rathbun, 1893
5. *Leptuca cumulanta* (Crane, 1943)
6. *Leptuca deichmanni* (Rathbun, 1935)
7. *Leptuca dorotheae* (von Hagen, 1968)
8. *Leptuca festae* (Nobili, 1902)
   = *Uca guayaquilensis* Rathbun, 1935
   = *Uca orthomana* Bott, 1954
   = *Uca leptochela* Bott, 1954
   = *Uca leptochela eibli* Bott, 1958
9. *Leptuca helleri* (Rathbun, 1902)
10. *Leptuca inaequalis* (Rathbun, 1935)
11. *Leptuca latimanus* (Rathbun, 1893)
12. *Leptuca leptodactyla* (Rathbun, in Rankin, 1898)*
13. *Leptuca limicola* (Crane, 1941)
14. *Leptuca musica* (Rathbun, 1914)
15. *Leptuca oerstedi* (Rathbun, 1904)
16. *Leptuca panacea* (Novak & Salmon, 1974)
17. *Leptuca pugilator* (Bosc, 1802)
   = *Ocypode citharoedicus* Say, 1817 (unavailable name)
18. *Leptuca pygmaea* (Crane, 1941)

19. *Leptuca saltitanta* (Crane, 1941)
20. *Leptuca speciosa* (Ives, 1891)
21. *Leptuca spinicarpa* (Rathbun, 1900)
22. *Leptuca stenodactylus* (H. Milne Edwards & Lucas, 1843)
    = *Gelasimus gibbosus* Smith, 1870
23. *Leptuca subcylindrica* (Stimpson, 1859)
24. *Leptuca tallanica* (von Hagen, 1968)
25. *Leptuca tenuipedis* (Crane, 1941)
26. *Leptuca terpsichores* (Crane, 1941)
27. *Leptuca thayeri* (Rathbun, 1900)
28. *Leptuca tomentosa* (Crane, 1941)
    = *Uca mertensi* Bott, 1954
29. *Leptuca umbratila* (Crane, 1941)
    = *Uca thayeri zilchi* Bott, 1954
30. *Leptuca uruguayensis* (Nobili, 1901)
    = *Uca olympioi* Oliveira, 1939

* This name has been sometimes spelt as '*leptodactylus*' following the original unpublished manuscript name of Guérin (see Ng et al., 2008). Rathbun's original spelling, however, was "*leptodactyla*", and this should be followed (see Chace & Hobbs, 1969: 212; Crane, 1975: 306; ICZN, 1999: Article 31.2.2).

Remarks. The results of the present genetic analyses show two distinct clades for the American BF genera *Leptuca* and *Minuca*, thus supporting their validity. These two genera (including *U. thayeri* and *U. umbratila*, see below) can, for the most part, be separated morphologically with the characters stated in the diagnosis. However, the placement of some species has proven problematic (see examples in Beinlich & von Hagen, 2006). The species constitution of *Leptuca* has been partially discussed by Shih et al. (2015), and noteworthy is the transfer from *Minuca* to *Leptuca* of *L. subcylindrica*, *L. thayeri* and *L. umbratila*; the close relationships between *L. panacea* and *L. pugilator*, and between *L. thayeri*, *L. umbratila* and *L. spinicarpa*; as well as the establishment of *Petruca* for *Gelasimus panamensis* (see Remarks under *Petruca*).

Several authors have tried to separate *Leptuca* and *Minuca* by characters such as the shape of the anterolateral margins and number of posterolateral striae on the carapace, the degree of fusion of pleonites 4–6, the presence of a ventral carina on the major pollex, and the shapes of the G1 (Crane, 1975; Rosenberg, 2001; Beinlich & von Hagen, 2006; Bezerra, 2012). Despite this, there are still no consistently useful characters to reliably define the genera. Similarly, earlier 16S genetic analyses were unable to resolve their relationships (Levinton et al., 1996; Sturmbauer et al., 1996). *Minuca* has been considered a smaller "homogeneous" group, compared to the more speciose "heterogeneous" *Leptuca* (Barnwell & Thurman, 1984; Beinlich & von Hagen, 2006; Ng et al., 2008).

There are presently 30 species within *Leptuca* which makes it the most diverse genus within the family. *Leptuca* species are more widely distributed in the Americas than those of *Minuca* and *Uca* (Fig. 4). Because fewer than half (14) species of *Leptuca* were analysed for this study, it is vital that more species are examined and sequenced in the future to confirm their generic position, and to further clarify their relationships within the genus. This is an aspect which will need further study.

***Minuca* Bott, 1954, status nov.**

(Figs. 9G, H, 10A, B)

Minuca Bott, 1954: 155, 160. Type species: *Gelasimus mordax* Smith, 1870, by original designation. Gender feminine.

Diagnosis. Small- to medium-sized species (carapace width about 10–30 mm in adults); anterolateral margins long, curving into dorsolaterals; 2 posterolateral striae on dorsal carapace surface; front broad; cornea round; eyestalks slender; adult male major cheliped very large, right- or left-handed, pollex without ventral carina, outer surface of major manus smooth or with small to moderate-sized tubercles; male pleonites free; pleonal locking mechanism absent; gastric mill with 2 large brownish setae at base of posterior tooth plate. Confined to the Atlantic and East Pacific coasts of the Americas.

Species included:

1. *Minuca argillicola* (Crane, 1941)
2. *Minuca brevifrons* (Stimpson, 1860)
3. *Minuca burgersi* (Holthuis, 1967)
   = *Uca panema* Coelho, 1972
4. *Minuca ecuadoriensis* (Maccagno, 1928)
   = *Uca schmitti* Crane, 1943
5. *Minuca galapagensis* (Rathbun, 1902)
   = *Gelasimus macrodactylus* H. Milne Edwards & Lucas, 1843 (suppressed by ICZN)
6. *Minuca herradurensis* (Bott, 1954)
7. *Minuca longisignalis* (Salmon & Atsaides, 1968)
8. *Minuca marguerita* (Thurman, 1981)
9. *Minuca minax* (LeConte, 1855)
10. *Minuca mordax* (Smith, 1870)
11. *Minuca osa* (Landstorfer & Schubart, 2010)
12. *Minuca pugnax* (Smith, 1870)
    = *Ocypoda pusilla* Rafinesque, 1817 (named suppressed for priority)
13. *Minuca rapax* (Smith, 1870)
    = ?*Gelasimus palustris* H. Milne Edwards, 1852
    = ?*Uca pugnax* var. *brasiliensis* de Oliveira, 1939
14. *Minuca virens* (Salmon & Atsaides, 1968)
15. *Minuca victoriana* (von Hagen, 1987)
16. *Minuca vocator* (Herbst, 1804)
    = *Uca salsisitus* Oliveira, 1939
    = *Uca murifecenta* Crane, 1943
    = *Uca lanigera* von Hagen, 1968
17. *Minuca zacae* (Crane, 1941)
    = *Uca macrodactyla glabromana* Bott, 1954

Remarks. The present genetic analysis supports the reassignment by earlier authors of a number of species that were previously placed in *Minuca*, viz., *Leptuca pygmaea* and *L. subcylindrica* (see Beinlich & von Hagen, 2006), *Petruca panamensis*, *L. thayeri* and *L. umbratila* (see Shih

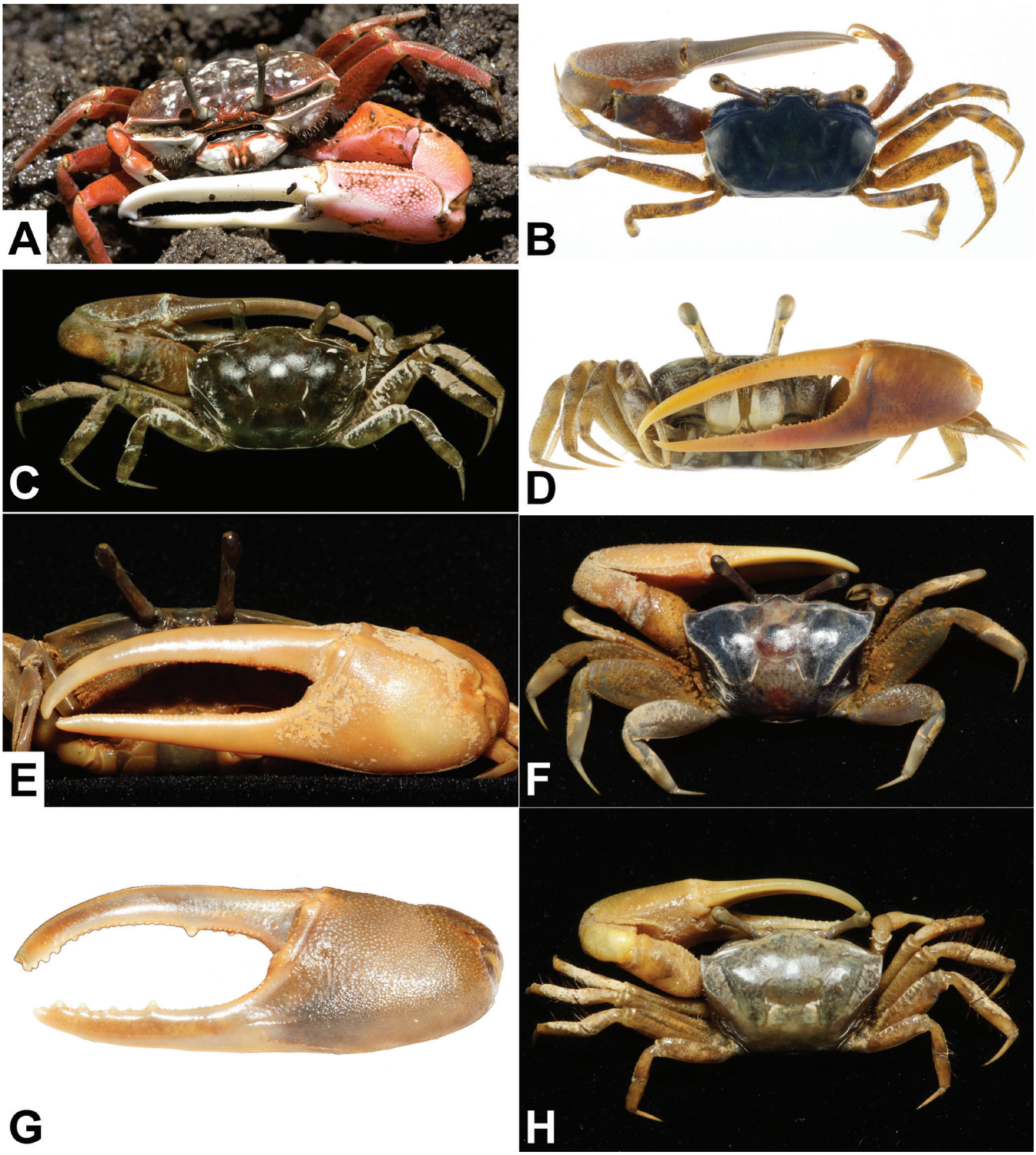

Fig. 9. Photographs of some species of the genera *Cranuca*, *Leptuca* and *Minuca*. A, *C. inversa* (East Africa); B, *L. deichmanni* (Panama); C, *L. speciosa* (Bahamas); D, *L. terpsichores* (Panama); E, *L. thayeri* (Brazil); F, *L. umbratila* (Panama); G, *M. brevifrons* (Costa Rica); H, *M. burgersi* (Bahamas). A, courtesy of S. Cannicci.

et al., 2015; also see present Remarks under *Petruca* and *Leptuca*). Similarly, the transfer of *Minuca argillicola* from *Leptuca* by Beinlich & von Hagen (2006) is also supported (Fig. 2).

Compared with *Leptuca*, we have molecular data for all the *Minuca* species except *M. marguerita*. Some species of *Minuca* have been discussed in earlier studies, e.g., the transisthmian species-pairs of *M. vocator* / *M. ecuadoriensis*, and *M. herradurensis*/*M. galapagensis* (Landstorfer & Schubart, 2010); the early split of *M. brevifrons* from other species (Shih et al., 2015); the close relationships between *M. burgersi* and *M. mordax* (Shih et al., 2015) and between *M. osa*, *M. vocator* and *M. ecuadoriensis* (Landstorfer & Schubart, 2010); and the taxonomic uncertainty regarding *M. virens* and *M. longisignalis* (the former may be valid, while the latter is likely to be a junior synonym of *M. minax*). Shih et al. (2015) used *U.* cf. *virens* and "*U. longisignalis*" to refer to these taxa, and this terminology is retained in Figure 2 and Appendix 1. This matter will need further attention and is currently being studied by one of the authors (CDS). Overall, *Minuca* has a more limited distribution in the Americas than *Uca* and *Leptuca* (Fig. 4).

Paraleptuca Bott, 1973, status nov.

(Fig. 10C, D)

Paraleptuca Bott, 1973b: 322. Type species: *Gelasimus chlorophthalmus* H. Milne Edwards, 1837, by original designation. Gender feminine.

Amphiuca Crane, 1975: 96. Type species: *Gelasimus chlorophthalmus* H. Milne Edwards, 1837, by original designation. Gender feminine.

Diagnosis. Medium-sized species (carapace width about 20 mm in adults); dorsal carapace with posterolateral striae; front broad; cornea round; eyestalks slender; adult male chelipeds extremely large, right- or left-handed, pollex without ventral carina, outer surface of major manus smooth, with small round depression near base of pollex, carpal cavity not continued distally; male pleonites free; with pleonal clasping apparatus; gastric mill without large brownish setae at base of posterior tooth plate. Indo-west Pacific.

Species included:

1. *Paraleptuca crassipes* (White, 1847)
   = *Gelasimus gaimardi* H. Milne Edwards, 1852
   = *Gelasimus pulchellus* Stimpson, 1858
   = *Gelasimus latreillei* H. Milne Edwards, 1852
   = *Uca novaeguineae* Rathbun, 1913
2. *Paraleptuca boninensis* (Shih, Komai & Liu, 2013)
3. *Paraleptuca chlorophthalmus* (H. Milne Edwards, 1837)
   = *Uca amazonensis* Doflein, 1899
4. *Paraleptuca splendida* (Stimpson, 1858)

Remarks. In Crane's (1975) system, *Amphiuca* (= *Paraleptuca*) contained four taxa, viz., *Uca chlorophthalmus*, *U. crassipes*, *U. inversa* and *U. sindensis*. In contrast, Beinlich & von Hagen (2006) established *Cranuca* for *U. inversa*, and believed that the members of the *U. lactea* and *U. triangularis* species complexes should be included within their revised concept of *Paraleptuca*. However, this has not been supported genetically (Shih et al., 2013b; Fig. 2). *Uca sindensis* has since been transferred to *Austruca* (Shih et al., 2013b; Fig. 2); while *P. boninensis* and *P. splendida* have now been added to *Paraleptuca* (Shih et al., 2012, 2013a).

The revised concept of *Paraleptuca* here shows considerable variation in morphology and coloration among the four species (Crane, 1975; Shih et al., 2012, 2013a), perhaps due in part to their unusual distributions (Fig. 4). *Paraleptuca chlorophthalmus* occurs only in East Africa; *P. crassipes* is widely distributed across the IWP; *P. splendida* is restricted to East Asia and Vietnam; and P. *boninensis* is endemic to the Ogasawara Islands (= Bonin Island), Japan. The latter species is morphologically closest to *P. splendida*, but genetically (16S and COI), it is nearly identical to *P. crassipes*. Only the sequences from the mitochondrial control region (= D-loop) can separate the species satisfactorily (Shih et al., 2013a). This is a strong indication that it is a young species that evolved very recently.

Petruca Shih, Ng & Christy, 2015, status nov.

(Fig. 10F)

Petruca Shih, Ng & Christy, 2015: 476. Type species: *Gelasimus panamensis* Stimpson, 1859, by original designation. Gender feminine.

Diagnosis. Medium-sized species (carapace width about 15 mm in adults); carapace widest between tips of anterolateral angles; dorsal carapace surface almost flat, smooth, with posterolateral striae; front broad; cornea round; eyestalks slender; orbital floor with spinous tubercle near inner corner; adult male major cheliped very large, right- or left-handed, pollex without ventral carina, major chela smooth in inner or outer surfaces, with posterior extension of manus; tips of minor fingers of both sexes with brush of long setae; male pleonites free; pleonal locking mechanism absent; gastric mill with 2 large brownish setae at base of posterior tooth plate. Confined to the East Pacific coasts of the Americas.

Species included:

Petruca panamensis (Stimpson, 1859).

Remarks. *Gelasimus panamensis* Stimpson, 1859, has been placed either in *Minuca* or *Leptuca*, but Shih et al. (2015) established a new subgenus for it based on a number of unusual characters, e.g., the relatively flat dorsal carapace surface, the posterior extension of the major manus, the smooth inner and outer surfaces of the major chela, the brush of long stiff setae on the finger tips of the minor cheliped, the armature at the inner corner of the orbital floor, and the characteristic urocardiac ossicles of the gastric mill. In addition, its ecology and behavior are peculiar for fiddler crabs, e.g. lives on cobble beaches rather than sandy-muddy substrates, has no deep or permanent burrows, and swallow food particles directly (see Shih et al., 2015). The distribution is limited to the Pacific side of Central America and northern South America (Fig. 4).

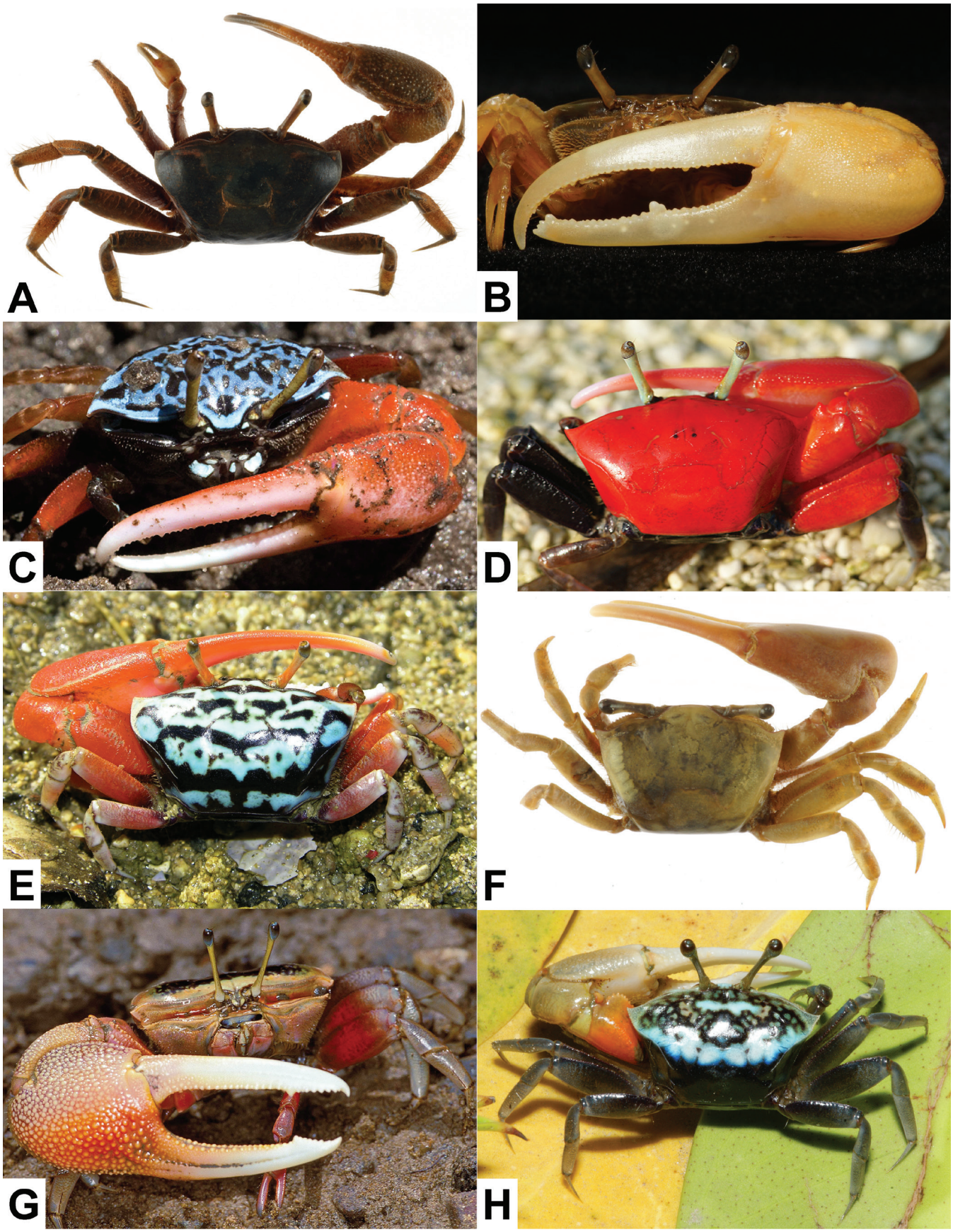

Fig. 10. Photographs of some species of the genera *Minuca*, *Paraleptuca*, *Petruca* and *Tubuca*. A, *M. herradurensis* (Panama); B, *M. rapax* (Brazil); C, *Pa. chlorophthalmus* (East Africa); D, *Pa. crassipes* (Donghsa, Taiwan); E, *Pa. splendida* (Penghu, Taiwan); F, *Pe. panamensis* (Costa Rica); G, *T. arcuata* (Hainan, China); H, *T. bellator* (Labuan, Malaysia). C, courtesy of S. Cannicci.

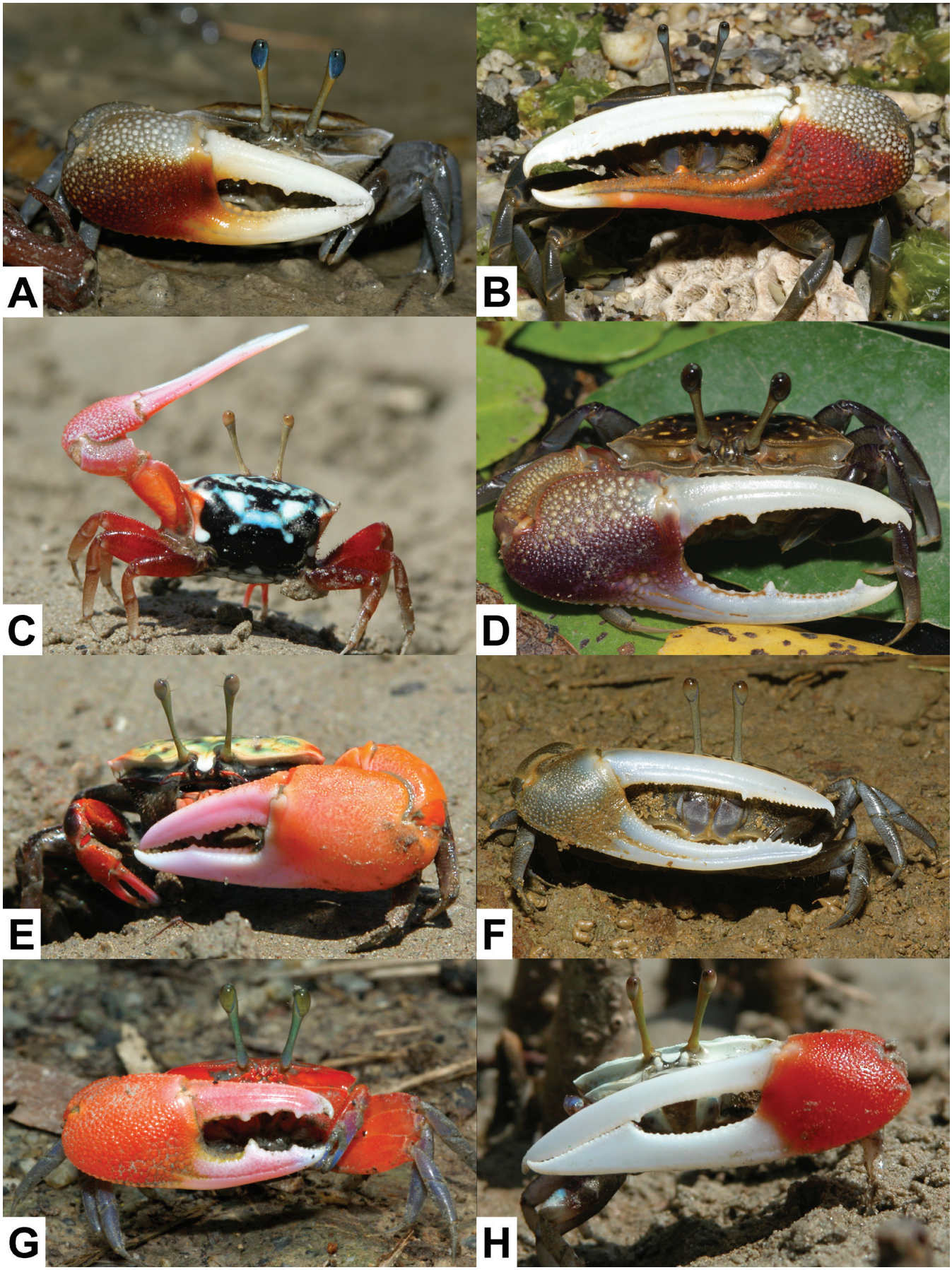

Fig. 11. Photographs of some species of the genus *Tubuca*. A, *T. coarctata* (Taiwan); B, *T. dussumieri* (Penghu, Taiwan); C, *T. elegans* (New Territory, Australia); D, *T. forcipata* (Sarawak, Malaysia); E, *T. polita* (Northern Territory, Australia); F, *T. rhizophorae* (Johor, Malaysia); G, *T. rosea* (Selangor, Malaysia); H, *T. signata* (New Territory, Australia). C, E, H, courtesy of P. Backwell.

Tubuca Bott, 1973, status nov.
(Figs. 10G, H, 11A–H, 12A)

Tubuca Bott, 1973b: 322. Type species: *Gelasimus urvillei* H. Milne Edwards, 1852, by original designation. Gender feminine.
Australuca Crane, 1975: 62. Type species: *Gelasimus bellator* Adams & White, 1849, by original designation. Gender feminine.
Deltuca Crane, 1975: 21. Type species: *Gelasimus forcipatus* Adams & White, 1849, by original designation. Gender feminine.

Diagnosis. Medium- to large-sized species (carapace width about 15–35 mm in adults); dorsal carapace surface always with posterolateral striae in female, absent in males; front narrow; cornea round; eyestalks slender; adult male major cheliped very large, right- or left-handed, pollex sometimes with ventral carina, outer surface of major manus with small to large tubercles, carpus with antero-dorsal area flattened to facilitate chela flexion, setae on merus of minor cheliped short, stiff; male pleonites free; pleonal locking mechanism absent; no setae on lateral margins of posterior stem region of urocardiac ossicles in gastric. Indo-west Pacific.

Species included:
1. *Tubuca acuta* (Stimpson, 1858)
2. *Tubuca australiae* (Crane, 1975)
3. *Tubuca arcuata* (De Haan, 1835)
   = *Uca brevipes* H. Milne Edwards, 1852
4. *Tubuca bellator* (White, 1847)
5. *Tubuca capricornis* (Crane, 1975)
   = *Uca pavo* George & Jones, 1982
6. *Tubuca coarctata* (H. Milne Edwards, 1852)
   = *Uca rathbunae* Pearse, 1912
   = *Uca ischnodactylus* Nemec, 1939
   = ?*Uca mearnsi* Rathbun, 1913
   = ?*Gelasimus thomsoni* Kirk, 1881
7. *Tubuca demani* (Ortmann, 1897)
   = *Uca zamboangana* Rathbun, 1913
8. *Tubuca dussumieri* (H. Milne Edwards, 1852) (nomen protectum)
   = *Gelasimus caerulens* Adams, in Belcher, 1848 (nomen oblitum)
   = *Gelasimus dubius* Stimpson, 1858
9. *Tubuca elegans* (George & Jones, 1982)
10. *Tubuca flammula* (Crane, 1975)
11. *Tubuca forcipata* (Adams & White, 1849)
   = *Uca rubripes* Estampador, 1937
   = *Uca manii* Rathbun, 1909
11. *Tubuca hirsutimanus* (George & Jones, 1982)
12. *Tubuca longidigitum* (Kingsley, 1880)
13. *Tubuca paradussumieri* (Bott, 1973)
   = *Uca* (*Deltuca*) *dussumieri spinata* Crane, 1975
14. *Tubuca polita* (Crane, 1975)
15. *Tubuca rhizophorae* (Tweedie, 1950)
16. *Tubuca rosea* (Tweedie, 1937)
17. *Tubuca seismella* (Crane, 1975)
18. *Tubuca signata* (Hess, 1865)
19. *Tubuca typhoni* (Crane, 1975)
20. *Tubuca urvillei* (H. Milne Edwards, 1852)

Remarks. The molecular analyses (Fig. 2) reveal one major clade containing all the *Tubuca* and *Australuca* species. Although the *Australuca* species do form a distinct subclade, their inclusion causes *Tubuca*, as presently conceived, to become paraphyletic. Thus, in order to maintain *Australuca* as a separate genus, we would have to further split *Tubuca* and this seems unjustified at this time. We therefore treat *Australuca* Crane, 1975, as a junior synonym of *Tubuca* Bott, 1973, as the latter has nomenclatural priority. This revised concept of *Tubuca* makes it the most speciose genus in the IWP, with 21 species. Although the genus is widely-distributed in the IWP, it does not extend as far as the eastern margin of Polynesia, where only *Paraleptuca* and *Gelasimus* species occur (Poupin & Juncker, 2010; Fig. 4).

Xeruca Shih, 2015, status nov.
(Fig. 12B)

Xeruca Shih, 2015: 154. Type species: *Uca formosensis* Rathbun, 1921, by original designation. Gender feminine.

Diagnosis. Large-sized species (carapace width about 30 mm in adults); dorsal carapace surface without posterolateral striae; front narrow; cornea round; eyestalks slender; adult male major cheliped very large; right- or left-handed, deep fingers (with straight cutting margins >1/2 length of fingers), pollex without ventral carina, outer surface of major manus with moderate-szied to large tubercles, carpus with antero-dorsal area flattened to facilitate chela flexion, setae on merus of minor cheliped long, thin; male pleonites free; pleonal locking mechanism absent; no setae on lateral margins of posterior stem region of urocardiac ossicles in gastric mill. Taiwan endemic.

Species included:
Xeruca formosensis (Rathbun, 1921).

Remarks. Although Rathbun described this large endemic Taiwanese species in Rathbun (1921), it was not well known until the work of Shih et al. (1999). Crane (1975) placed it with *U. tetragonon* and the *U. vocans* species-complex, in *Thalassuca* (= *Gelasimus*), although she had examined only a few specimens. Shih et al. (1999) suggested that it was closely related to *Tubuca*, but cautioned that more study was needed to confirm its status. Shih (2015) recently established a separate taxon *Xeruca* for this species based on morphological (see Rosenberg, 2001) and molecular evidence. The present work (Fig. 2) and Shih (2015) show *Xeruca* to be basal to the main *Tubuca* clade which confirms earlier relationship speculation (Crane, 1975; Shih et al., 1999; Rosenberg, 2001). The monotypic *Xeruca* is confined to Taiwan Island and the adjacent Penghu Islands, and thus has the smallest distribution of any genus in the Ocypodidae (Fig. 4).

Subfamily Ucidinae Števčić, 2005

Diagnosis. Carapace subovate, cordiform, very thick, swollen; regions distinct, grooves deep; fronto-orbital distance 1/2–2/3 of maximum carapace width, front broad; anterolateral margins strongly convex; orbital floor with

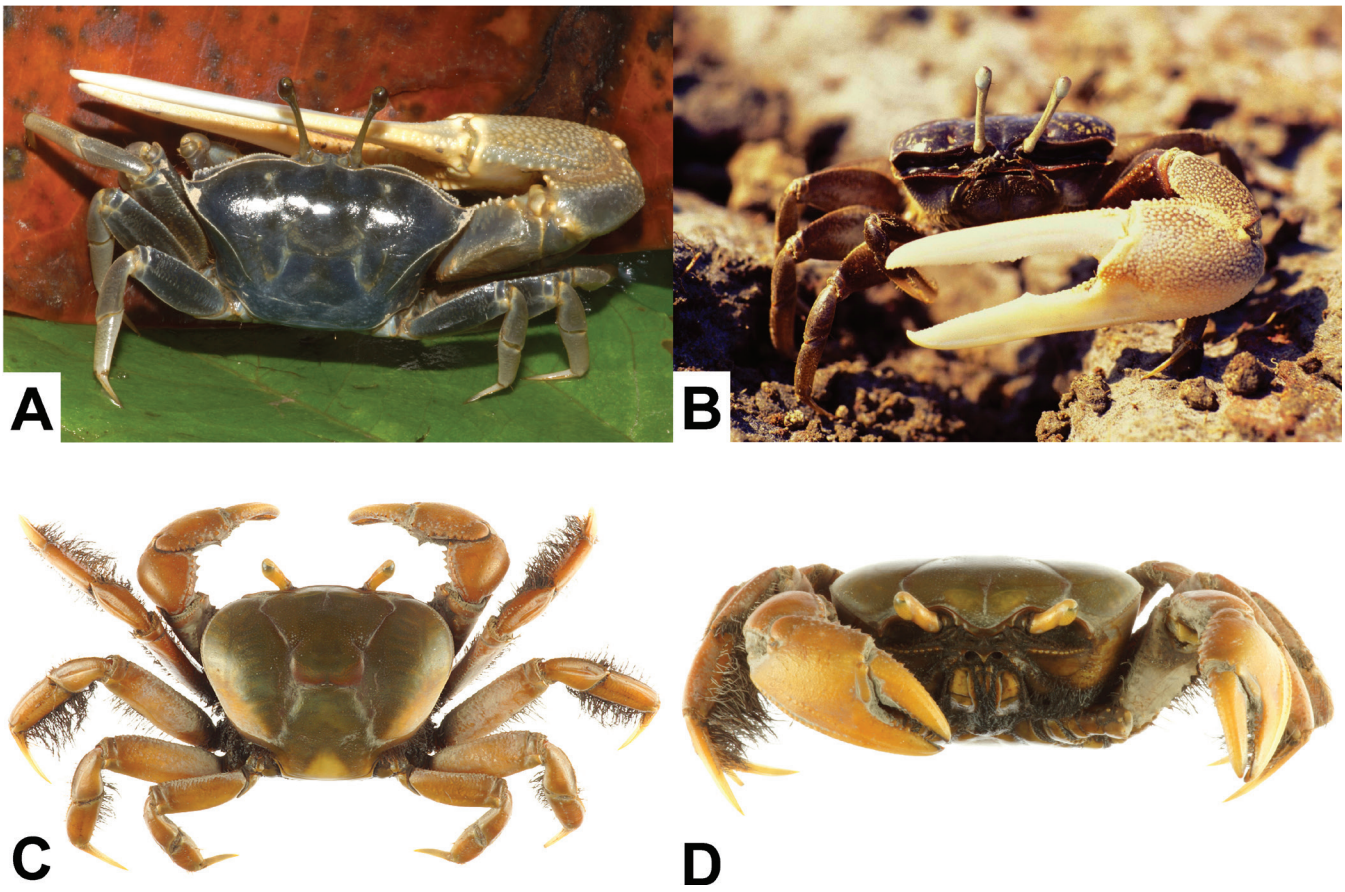

Fig. 12. Photographs of some species of the genera *Tubuca*, *Xeruca* and *Ucides*. A, *T. urvillei* (Ranong, Thailand); B, *X. formosensis* (Taiwan); C, D, *U. cordatus* (Brazil).

tubercle at inner corner adjacent to antennule; eyestalks relatively short, cornea terminal without any distal ornament; buccal cavern elongated anteriorly, appearing longer than broad, third maxillipeds not completely covering it when closed; ischium and merus of third maxilliped elongate, fringed with long setae on inner surface; exopod of third maxilliped mostly concealed by endopod, with flagellum; chelipeds prominently unequal in adult males, less so in females, surfaces of male merus, carpus and palm armed with strong spines; first to fourth ambulatory legs with dense, long setae on ventral surface of merus, propodus and dactylus which obscure margins; no distinct brush of setae between bases of coxae of second and third ambulatory legs; male pleon with somites 5 and 6 fused; pleonal locking mechanism usually absent.

Ucides Rathbun, 1897
(Fig. 12C, D)

Uca Latreille, 1819: 96. Type species *Cancer uca* Linnaeus, 1767; junior homonym of *Uca* Leach, 1814. Gender feminine.
Ucea Guérin-Méneville, 1844: 8, pl. 5(3) (incorrect spelling).
Ucides Rathbun, 1897: 154. Type species *Cancer cordatus* Linnaeus, 1763, by original designation. Gender masculine.
Oedipleura Ortmann, 1897: 334 (replacement name for *Uca* Latreille, 1819).

Diagnosis. See Diagnosis for subfamily. Confined to the Atlantic and East Pacific coasts of the Americas.

Species included:
1. *Ucides cordatus* (Linnaeus, 1763)
   = *Cancer uca* Linnaeus, 1767
   = *Ocypode fossor* Latreille, 1803
   = *Uca pilosipes* Gill, 1859
2. *Ucides occidentalis* (Ortmann, 1897)
   = *Uca laevis* H. Milne Edwards, 1837 (pre-occupied name)

Remarks. The morphology of *Ucides* is superficially similar to that of the gecarcinids, but Chace & Hobbs (1969) provided a suite of characters (especially relating to the maxillipeds and ambulatory legs) that show *Ucides* to be closer to ocypodids. Schubart & Cuesta (2010), using 16S, found that *Ucides cordatus* and *Ocypode quadrata* formed a separate clade, and concluded that both genera are closely related. The present study, nevertheless, supports the recognition of a separate subfamily Ucidinae, typically placed basally within the Ocypodidae (Figs. 1–3).

Key to the subfamilies and genera of Ocypodidae

1. Fronto-orbital distance 1/2–2/3 of maximum carapace width, front relatively broad; no brush of long setae between bases of second and third ambulatory legs leading to branchial cavity. ..... *Ucides* (Ucidinae)
– Fronto-orbital distance > 9/10 of maximum carapace width, front relatively narrow; prominent brush of long setae between bases of second and third ambulatory legs leading to branchial cavity. 2

2. Orbital floor with tubercle at inner corner adjacent to antennule. Males of some species with distal end of cornea of eyestalks possessing ornament (horn, stylus or setal brush). Gastric mill with 1 protrusion or 2 pairs of transverse ridges of median teeth on posterior tooth plate, gaps shallow, prominently separated from central ridge. ..... 3 (Ocypodinae)
– Orbital floor without tubercle at inner corner adjacent to antennule (vestigial in *Petruca*). Males never with ornament at distal end of cornea of eyestalks. Gastric mill with 2 or more pairs of transverse ridges of median teeth on posterior tooth plate, gaps deep, reaching or near central ridge. ....5 (Gelasiminae)

3. Eyestalks short, cornea large, ovate. Chelipeds unequal in both sexes but major one never prominently enlarged. .....*Ocypode*
– Eyestalks slender, cornea round. Male with major cheliped prominently enlarged; minor male and female chelipeds small.....4

4. Front narrow, carapace not covered with tubercles. ..... *Uca*
– Front wide, carapace covered with prominent tubercles. ....*Afruca*

5. Front narrow. 6
– Front wide. 8

6. Carpus of major cheliped with anterodorsal area not flattened; >90% ratio of males with right major chela. Floor of orbit without any elevations. Gastric mill with setal structure on lateral margins of stem region of urocardiac ossicles..... .....*Gelasimus*
– Carpus of major cheliped with anterodorsal area flattened; ratio of males with right or left major chela ca. 50%. Floor of orbit often with tubercles, ridge or mound. Gastric mill without setal structure on stem region of urocardiac ossicles. 7

7. Major cheliped with forceps-shaped fingers or with straight cutting margins <1/2 length of fingers. Minor cheliped merus with short, stiff setae.....*Tubuca*
– Major cheliped with deep fingers, with straight cutting margins >1/2 length of fingers. Minor cheliped merus with long, thin setae. .....*Xeruca*

8. Dorsal edge of orbit distinctly broad. Gastric mill with 2 large brownish setae at base of posterior tooth plate.....9
– Dorsal edge of orbit narrow. Gastric mill without large brownish setae at base of posterior tooth plate.....11

9. Manus of major cheliped with posterior extension. Tips of minor fingers with brush of long setae. Orbital floor with small spinous tubercle near inner corner.....*Petruca*
– Manus of major cheliped without posterior extension. Tips of minor fingers without brush of long setae. Orbital floor without spinous tubercle near inner corner.....10

10. Anterolateral margin short; carapace with 0–2 posterolateral striae. All pleonites free, or somites 4–6 partly or completely fused. Major pollex without ventral carina. .....*Leptuca*
– Anterolateral margin long, curving into dorsolateral surface; carapace with 2 posterolateral striae. All pleonites free. Major pollex may possess ventral carina. .....*Minuca*

11. Dactylus of major cheliped with large subdistal tooth; major manus with some tubercles on outer surface. Without pleonal clasping apparatus. .....*Cranuca*
– Dactylus of major cheliped without large subdistal tooth; major manus with outer surface smooth. With pleonal clasping apparatus.....12

12. Outer manus of major cheliped with small round depression near base of pollex; carpal cavity not continued distally. ....*Paraleptuca*
– Outer manus of major cheliped without small round depression near base of pollex; carpal cavity with distal extension..... .....*Austruca*

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Appendix 1. Specimens examined and the different sequences of 16S rDNA, COI and 28S rDNA for the species of fiddler crabs, ghost crabs (genus *Ocypode*), mangrove crabs (genus *Ucides*) and outgroups used in this study. ASIZ, Institute of Zoology, Academia Sinica, Taipei, Taiwan; NMNS, National Museum of Natural Science, Taichung, Taiwan; MZUF, Museo Zoologico dell'Università di Firenze, Italy; NCHUZOOL, the Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan; NTOU, Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University, Keelung, Taiwan; QM, Queensland Museum, Brisbane, Australia; SMF, Senckenberg Museum, Frankfurt am Main, Germany; TAU, Steinhardt National Collections of Natural History, Tel Aviv University, Israel; TMCD, National Taiwan Museum, Taipei, Taiwan; UCR, Museo Zoológico de la Universidad de Costa Rica, San José; USNM, U.S. National Museum for Natural History, Smithsonian Institution, Washington D.C., USA; ZRC, Zoological Reference Collection of the Lee Kong Chian Natural History Museum (formerly Raffles Museum of Biodiversity Research), National University of Singapore, Singapore. *, see Remarks under *Minuca*.

Genus	Species	Locality	Catalogue No.	DDBJ Access. No. of 16S	DDBJ Access. No. of COI	DDBJ Access. No. of 28S
Afruca	*Af. tangeri*	(#1, #2) Spain: Puerto de Santa María, Cádiz	NCHUZOOL 13585	AB813666	AB813682	AB813711, LC150456
		(#3, #4) Spain: Puerto de Santa María, Cádiz	NCHUZOOL 14911	AB813666	LC150399	LC150457, LC150458
		(#1, #2) Ghana: Elmina	NCHUZOOL 13654	LC053362	LC053380	LC053399, LC150459
Austruca	*Au. albimana*	Egypt: Nabq, Sinai	NCHUZOOL 13242	AB471893	AB471906	AB813689
	Au. annulipes	Thailand: Phuket	NCHUZOOL 13258	AB471894	AB491161	AB813686
	Au. occidentalis	southern Madagascar	ZRC THH04-30	AB813648	AB813669	AB813687
	Au. bengali	Malaysia: Selangor	NCHUZOOL 13575	AB813651	AB813672	AB813695
	Au. iranica	Iran: Gavbandi	NCHUZOOL 13245	AB471896	AB471908	AB813688
	Au. lactea	Hong Kong	NCHUZOOL 13250	AB471898	AB471912	AB813693
	Au. mjoebergi	Australia: Bedford I., West Australia	QM W20253	AB471900	AB471914	AB813690
	Au. perplexa	Taiwan: Dulanwan, Taitung	NTOU	AB471901	AB471915	AB813691
		New Caledonia: Ouano Bay	NCHUZOOL 13573	AB813649	AB813670	AB813692
		Wallis and Futuna:Pointe Utu	NCHUZOOL 14912	LC150339	LC150400	LC150460
	Au. sindensis	Iran: Qeshm	NCHUZOOL 13576	AB813652	AB813673	AB813696
		Iraq: Khur Al-Zubair	ZRC 2010.0103	LC015059	LC015060	LC150461
	Au. triangularis	Philippines: Cebu	NCHUZOOL 13574	AB813650	AB813671	AB813694

Genus	Species	Locality	Catalogue No.	DDBJ Access. No. of 16S	DDBJ Access. No. of COI	DDBJ Access. No. of 28S
Cranuca	*C. inversa*	Kenya: Gazi	MZUF 1024	AB813658	AB813674	AB813703
		Egypt: Sinai	TAU SLR 1475	AB813658	LC087973	LC088004
		Tanzania: Dar es Salaam	NCHUZOOL 13255	AB471904	AB471917	AB813703
Gelasimus	*G. borealis*	Hong Kong	NCHUZOOL 13207	LC053359	LC053376	LC053394
		Taiwan: Kinmen	TMCD CHCD853	AB535403	AB535428	LC150462
	G. dampieri	Australia: Darwin, New Territory	QM W19180	AB535399	AB535430	LC150463
	G. hesperiae	Thailand: Phuket	ZRC 2000.1056	AB535398	AB535422	LC150464
		Kenya: Mida Creek	NCHUZOOL 13172	LC150340	LC150401	LC150465
		Madagascar	ZRC THH04-30	LC150341	LC150402	LC150465
		Mauritius	ZRC THH04-30	LC150342	LC150403	LC150466
	G. jocelynae	Taiwan: Dulanwan, Taitung	NTOU	AB535392	AB535411	LC054955
		Philippines: Panglao	ZRC 2009.0925 [M9]	AB535392	AB535414	LC150467
		Papua New Guinea	QM W26812	AB535394	AB535417	LC150468
		Vanuatu: Santo	ZRC 2009.0930 [VM53]	AB535396	AB535418	LC150468
	G. neocultrimana	Wallis I.: Pointe Utu	NCHUZOOL 13303	AB535397	AB535420	LC150469
	G. tetragonon	Taiwan: Kenting, Pingtung	TMCD CHCD 526	AB535405	AB535431	LC053395
		Madagascar: Sarodrano	ZRC THH04-17	AB535405	LC053377	LC053396
		Moorea I.	MNHN	LC150343	LC150404	LC150470
	G. vocans	Philippines: Bohol	NCHUZOOL 13667	AB535399	AB813683	AB813712
		China: Hainan	NCHUZOOL 13182	AB535399	AB535424	LC150471
	G. vomeris	Australia: Boggy Creek, Queensland	QM W23884	AB535399	AB491163	LC150472
Leptuca	*L. cumulanta*	Brazil: Rio de Janeiro	NCHUZOOL 13949	LC087932	LC087960	LC087988
	L. deichmanni	Panama: Culebra I.	NCHUZOOL 13583	AB813660	AB813676	AB813705
	L. dorotheae	Costa Rica: Tempisque R.	ZRC	LC087933	LC087961	LC087989

Genus	Species	Locality	Catalogue No.	DDBJ Access. No. of 16S	DDBJ Access. No. of COI	DDBJ Access. No. of 28S
	L. leptodactyla	(#1) Bahamas: Pigeon Creek, San Salvador	ZRC	LC087934	LC087962	LC087990
		(#2) Bahamas: Pigeon Creek	ZRC	LC087934	LC087962	LC087991
		(#1) Brazil: Sao Paulo	NCHUZOOL 14914	LC150344	LC150405	LC150473
		(#2) Brazil: Enseada do Mucuripe	NCHUZOOL 14915	LC150345	LC150406	LC150474
	L. panacea	Texas, USA: South Padre I., Cameron	NCHUZOOL 13950	LC087935	LC087963	LC087992
	L. pugilator	South Carolina, USA: Georgetown	NCHUZOOL 13586	AB813662	AB813678	AB813707
		Florida, USA: Seahorse Key	ASIZ	AB813662	AB813678	LC087993
	L. speciosa	Florida, USA: Alligator Point	NCHUZOOL 13951	LC087936	LC087964	LC087994
		Bahamas: N.of Pigeon Creek, San Salvador	ZRC	LC087936	LC087965	LC087995
	L. spinicarpa	Florida, USA: Money Bayou, Gulf County	NCHUZOOL 13947	LC087937	LC087966	LC087996
		Texas, USA: Boliver I.	ZRC 2009.0295	LC087937	LC087967	LC087997
	L. stenodactylus	El Salvador	SMF 2357	LC150748	LC150749	LC150750
	L. subcylindrica	(#1) Texas, USA: Kingsville	NCHUZOOL 13952	LC087938	LC087968	LC087998
		(#2) Texas, USA: Kingsville	NCHUZOOL 13952	LC087938	LC087968	LC087999
	L. terpsichores	Panama: Culebra I.	NCHUZOOL 13582	AB813661	AB813677	AB813706
	L. thayeri	(#1, #2) Florida, USA: Hutchinson I., Fort Pierce	NCHUZOOL 13953	LC087939	LC087969	LC088000, LC150475
		Brazil: Anchieta, Espírito Santo	NCHUZOOL 13954	LC087940	LC087970	LC088001
	L. umbratila	(#1) Panama: Diablo Heights mangroves	NCHUZOOL 13579	AB813663	AB813679	AB813708
		(#2) Panama: Diablo Heights mangroves	NCHUZOOL 13579	LC087941	LC087971	LC088002

Genus	Species	Locality	Catalogue No.	DDBJ Access. No. of 16S	DDBJ Access. No. of COI	DDBJ Access. No. of 28S
	L. uruguayensis	Argentina: Samborombón	NCHUZOOL 13577	AB813659	AB813675	AB813704
Minuca	*M. argillicola*	Ecuador: Puerto Morro	SMF 34737	LC150346	FN430701	FN430713
	M. brevifrons	Costa Rica: Playa San Juanillo	ZRC 2012.0126	LC087919	LC087949	LC087976
	M. burgersi	Bahamas: Salt Pan San Salvador	ZRC	LC087920	LC087950	LC087977
		Brazil	NCHUZOOL 13956	LC150347	LC150407	LC150476
	M. ecuadoriensis	Ecuador: Puerto Morro	SMF 34740	LC150348	FN430704	FN430716
	M. galapagensis	Ecuador: Puerto Morro	SMF 34741	LC150349	FN430705	FN430717
	M. herradurensis	Panama: Diablo Heights mangroves	NCHUZOOL 13580	AB813664	AB813680	AB813709
	M. minax	Virginia, USA: Chesapeake Bay	NCHUZOOL 13939	LC087921	LC087951	LC087978
	M. minax	Florida, USA	NCHUZOOL 13957	LC150350	LC150408	LC150477
	"*M. longisignalis*"*	Texas, USA: Ingleside Cove, Corpus Christi	NCHUZOOL 13938	LC087922	LC087952	LC087979
	M. mordax	Brazil: São Paulo	NCHUZOOL 13940	LC087923	LC087953	LC087980
	M. osa	Costa Rica: Golfo Dulce	UCR 2620-01	LC150351	FN430711	FN430722
	M. pugnax	(#1) Maryland, USA: Assateague I.	NCHUZOOL 13941	LC087924	LC087954	LC087981
		(#2) Maryland, USA: Assateague I.	NCHUZOOL 13941	LC087925	LC087955	LC087982
	M. rapax	Jamaica: Trelawny	NCHUZOOL 13942	LC087926	LC087956	LC087983
		British Virgin: Paraquita Bay	NCHUZOOL 13943	LC087927	LC087956	LC087984
		Panama: Bocas del Toro	NCHUZOOL 13944	LC087928	LC087957	LC087984
	M. victoriana	Brazil: Bahia	NCHUZOOL 13945	LC087929	LC087958	LC087985
	M. cf. *virens* (identified as *M. rapax*)*	(#1) Texas, USA: Ingleside Cove, Corpus Christi Bay	NCHOZUUL 13584	AB813665	AB813681	AB813710

Genus	Species	Locality	Catalogue No.	DDBJ Access. No. of 16S	DDBJ Access. No. of COI	DDBJ Access. No. of 28S
		(#2) Texas, USA: Ingleside Cove, Corpus Christi Bay	NCHOZUUL 13584	LC087930	AB813681	LC087986
		Florida, USA: Money Bayou, Gulf County	NCHUZOOL 13946	AB813665	AB813681	LC087984
	M. vocator	Brazil: Ceara	NCHUZOOL 13948	LC087931	LC087959	LC087987
		Trinidad	SMF 34745	LC150352	FN430709	FN430720
	M. zacae	El Salvador	SMF 2104a	LC150353	FN430710	FN430721
Ocypode	*O. africana*	Liberia	SMF 9823	LC150354	LC150409	LC150478
	O. ceratophthalmus	Taiwan: Tainan	NCHUZOOL 14916	LC150355	LC150410	LC150479
		(#1) Christmas I.	ZRC 2010 0008	LC150356	LC150411	LC150480
		(#2) Christmas I.	ZRC 2010 0007	LC150357	LC150412	LC150481
	O. cordimana	Guam	NCHUZOOL 14917	LC150358	LC150413	LC150482
	O. gaudichaudii	Panama: Culebra	ZRC	LC150359	LC150414	LC150483
	O. kuhlii	Christmas I.	ZRC	LC150360	LC150415	LC150484
	O. cf. *macrocera*	India: Tamil Nadi	ZRC	LC150361	LC150416	LC150485
	O. cf. *nobilii*	(#1) Malaysia: Kuching	NCHUZOOL 14918	LC150362	LC150417	LC150486
		(#2) Malaysia: Kuching	NCHUZOOL 14919	LC150363	LC150418	LC150487
	O. occidentalis	(#1) Costa Rica	ZRC	LC150364	LC150419	LC150488
		(#2) Costa Rica	ZRC 2012.0125	LC150365	LC150420	LC150488
		(#1) Panama: Culebra	ZRC	LC150366	LC150421	LC150488
		(#2) Panama: Playa Venado	ZRC	LC150367	LC150422	LC150488
	O. quadrata	Brazil	NCHUZOOL 14920	LC150368	LC150423	LC150489
	O. rotundata	Iran	SMF 40586	LC150369	LC150424	LC150490
	O. ryderii	(#1) Mozambique: Inharrime	ZRC	LC150370	LC150425	LC150491
		(#2) Mozambique: Inharrime	ZRC	LC150371	LC150426	LC150491
	O. sinensis	Taiwan: Pingtung	NCHUZOOL 14806	LC150372	LC150427	LC150492
	O. stimpsoni	Taiwan: Hsinchu	NCHUZOOL 14921	LC150373	LC150428	LC150493

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Paraleptuca	*Pa. crassipes*	Ryukyus, Japan: Okinawa	NCHUZOOL 13467	AB813656	AB734656	AB813700
		Moorea, Polynesia: Haapiti	NCHUZOOL 13478	AB813656	AB734656	AB813701
	Pa. splendida	Hong Konng: Tai Tam	NCHUZOOL 13368	AB813655	AB734648	AB813699
		(#1, #2) Taiwan: Cingluo, Penghu	NCHUZOOL 13457	AB813653	AB734641	AB813697, LC150494
		Vietnam: Nha Trang	NCHUZOOL 13448	AB813654	AB734654	AB813698
	Pa. chlorophthalmus	(#1) Mayotte: mangrove de Malamani	MNHN-IU-2011-5599	AB813657	JX050999 (MDECA791-12)	AB813702
		(#2) Mayotte: mangrove de Malamani	MNHN-IU-2011-5600	AB813657	JX050997 (MDECA793-12)	AB813702
		Tanzania: Dar es Salaam	NCHUZOOL 13561	AB813657	LC087972	LC088003
Petruca	*Pe. panamensis*	(#1) Panama: Culebra I.	USNM 1294205 (neotype)	LC087917	LC087943	LC087975
		(#2) Panama: Culebra I.	NCHOZOOL 13581	LC087918	LC087944	LC087975
		(#1) Costa Rica: San Juanillo rocky shore, Ostional	NCHUZOOL 14753	LC087918	LC087945	LC087975
		(#2) Costa Rica: Playa San Juanillo	ZRC 2012.0126	LC087918	LC087948	LC087975
Tubuca	*T. acuta*	China: Hainan	NCHUZOOL 13351	LC150374	LC150429	LC150495
		Taiwan: Kinmen	NCHUZOOL 13650	LC053352	LC053369	LC053387
	T. arcuata	China: Dongzhai, Hainan	NCHUZOOL 13363	AB813667	AB813684	AB813713
		Korea: Incheon	NCHUZOOL 13651	LC053353	LC053370	LC053388
	T. capricornis	Australia: Bedford I.	QM W. 20267	LC150375	LC150430	LC150496
	T. coarctata	Taiwan: Penghu	NCHUZOOL 13231	LC053354	LC053371	LC053389
		Australia: Turtle Bay	QM W. 21032	LC150376	LC150431	LC150497
		(#1) Australia: Queensland	QM W19920	LC150377	LC150432	LC150498

Genus	Species	Locality	Catalogue No.	DDBJ Access. No. of 16S	DDBJ Access. No. of COI	DDBJ Access. No. of 28S
		(#2) Australia: Queensland	QM W19245	LC150377	LC150433	LC150498
		New Caledonia	QM W29055	LC150377	LC150434	LC150499
	T. demani	Philippines: Cebu	NCHUZOOL 13372	LC150378	LC150435	LC150500
	T. dussumieri	Taiwan: Penghu	NCHUZOOL 14717	LC150379	LC150436	LC150501
		Philippines: Mindanao	NCHUZOOL 14922	LC150380	LC150437	LC150502
		New Caledonia	QM W29054	LC150381	LC150438	LC150503
	T. flamula	(#1) Australia: Kimberly coast, West Australia	QM W20214	LC150382	LC150439	LC150504
		(#2) Australia: Dampiei, West Australia	ZRC Aus 010800/13	LC150383	LC150440	LC150505
	T. forcipata	(#1) Malaysia: Johor	NTOU	LC150384	LC150441	LC150506
		(#2) Malaysia: Johor	NTOU	LC053355	LC053372	LC053390
	T. paradussumieri	China: Hainan	NCHUZOOL 13381	LC053356	LC053373	LC053391
	T. rhizophorae	Malaysia: Mersing	NCHUZOOL 14923	LC150385	LC150442	LC150507
		Malaysia: Madang	NCHUZOOL 14924	LC150386	LC150443	LC150508
	T. rosea	Malaysia: Johor	NTOU	LC053357	LC053374	LC053392
	T. typhoni	China: Hainan	NCHUZOOL 13371	LC150387	LC150444	LC150509
	T. urvillei	Mayotte: Poroani	ZRC 1999.1107	LC053358	LC053375	LC053393
		India: Mumbai	NCHUZOOL 14925	LC150388	LC150445	LC150510
("*Australuca*")	*T. bellator*	Borneo: Labuan, Malaysia	NCHUZOOL 13649	LC053348	LC053365	LC053383
	T. elegans	Australia: Lacrosse I., West Australia	QM W21038	LC053349	LC053366	LC053384
	T. longidigitum	(#1) Australia: Redland Bay, Brisbane, Queensland	NCHUZOOL 13656	LC150389	LC150446	LC150511
		(#2) Australia: Hervey Bay, Queensland	QM W19274	LC053350	LC053367	LC053385
		(#3) Australia: Boggy Creek, Myrtletown, Queensland	QM W23884	LC150390	LC150447	LC150512

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	T. seismella	Indonesia: Irian Jaya	ZRC 2000.2059	AB813668	AB813685	AB813714
	T. signata	Australia: Hucks Landing, Queensland	QM W19211	LC053351	LC053368	LC053386
Uca	*U. major*	Bahamas: Pigeon Creek	ZRC	LC053360	LC053378	LC053397
	U. maracoani	Brazil: Itapissuma, Pernambuco	NCHUZOOL 13955	LC087942	LC087974	LC088005
	U. princeps	Peru	SMF 13164	LC150391	LC150448	LC150513
	U. stylifera	Panama: Rodman	NCHUZOOL 13578	LC053361	LC053379	LC053398
Xeruca	*X. formosensis*	Taiwan: estuary of Bajhang R., Chiayi	NCHUZOOL 13742	LC053346	LC053363	LC053381
		Taiwan: Cinglo, Penghu	NCHUZOOL 13770	LC053347	LC053364	LC053382
		(#1, #2) Taiwan: Cigu, Tainan	NCHUZOOL 13691	LC150392	LC150449	LC150514, LC150515
Ucides	*Ucides cordatus*	(#1) Brazil: Estuario do Rio Camaragibe	NCHUZOOL 14926	LC150393	LC150450	LC150516
		(#2) Brazil: Estuario do Rio Camaragibe	NCHUZOOL 14926	LC150394	LC150451	LC150517
outgroups	*Dotilla myctiroides*	Singapore	NCHUZOOL 14927	LC150395	LC150452	LC150518
	Heloecius cordiformis	Australia: Fitzroy R., Queensland	QM W20824	LC097114	LC097138	LC150523
	Macrophthalmus pacificus	China: Hainan	NCHUZOOL 14929	LC150397	LC150454	LC150521
	M. tomentosus	Taiwan: Kinmen	NCHUZOOL 14930	LC150398	LC150455	LC150522
	Scopimera intermedia	Taiwan: Penghu	NCHUZOOL 13225	LC097113	AB515326	LC150519
	Tmethypocoelis ceratophora	Taiwan: Yilan	NCHUZOOL 14928	LC150396	LC150453	LC150520