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# THE SYSTEMATICS AND TAXONOMY OF FIDDLER CRABS: A PHYLOGENY OF THE GENUS *UCA*

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## ABSTRACT

Although fiddler crabs (genus *Uca*) have been among the most widely studied organisms with respect to sexual selection, agonistic behavior, asymmetry, and visual and acoustic signaling, the phylogenetic relationships within the genus have remained largely a mystery. After reviewing the systematic history of the genus and its species, including a discussion of the systematic conflicts between two alternative proposals of subgeneric division, a phylogenetic analysis was performed for 88 species on a data matrix of 236 discrete morphological characters. These results were compared to a previously published molecular analysis of 16S ribosomal DNA for 28 species. To a large extent, the uncertainty in the proper taxonomic names for the subgenera can be resolved with these results. The biogeographic history of the genus is discussed, although these results do not provide enough support to allow complete resolution of the deep divergences between Indo-West Pacific and American clades. There is strong morphological evidence to support the monophyly of the broad-front taxa; molecular evidence suggests biogeographic subdivisions.

Fiddler crabs (Ocypodidae, *Uca*) are a well-known group of small, intertidal brachyuran crabs, characterized by strong sexual dimorphism and male asymmetry. Male fiddler crabs exhibit one of the most extreme levels of body asymmetry of any bilateral organism, having a large major claw (which contains a third to half of the animal's body mass) and a small minor claw; females have a pair of small claws that resemble the male's minor claw. The major claw is used for only two functions: display and combat; the minor claw is used for feeding. The waving display of male fiddler crabs serves a function in both male-male aggression and male-female species recognition and mate choice. The genus is cosmopolitan, primarily concentrated in the tropics, although the crabs range from as far north as Massachusetts to as far south as South Africa.

Fiddler crabs have been the subject of a wide variety of studies, including sexual selection (Christy, 1983, 1987; Backwell *et al.*, 1999), reproductive isolation (Salmon *et al.*, 1978, 1979; Salmon and Kettler, 1987), visual and acoustic display (Salmon, 1965; Salmon and Atsaides, 1968a; Hyatt, 1977; von Hagen, 1983, 1984), combat (Crane, 1967; Hyatt and Salmon, 1978, 1979; Jennions and Backwell, 1996), foraging (Miller, 1961; Weissburg, 1992, 1993; Wolfrath, 1992), asymmetry (Huxley and Callow, 1933; Yamaguchi, 1973; Takeda and Murai, 1993), allometry (Veitch, 1978; von Hagen, 1987a), regeneration (Weis, 1977; Trinkaus-Randall, 1982; Hopkins *et al.*, 1999), claw mechanics (Levinton and Judge, 1993; Levinton *et al.*, 1995), morphometrics (Rosenberg, 1997), circadian rhythms (Brown and Webb, 1949; Brown and Stephens, 1951; Brown *et al.*, 1954; Palmer, 1964, 1988, 1989, 1991; Barnwell, 1966, 1968), color change histology (Coohill *et al.*, 1970; Fingerman and Fingerman, 1977; Hanumante and Fingerman, 1981), osmoregulation, heat tolerance (Vernberg and Tashian, 1959; Vernberg and Vernberg, 1968; Vernberg and O'Hara, 1972), visual neurology (Land and Layne, 1995a, b; Zeil and Al-Mutairi, 1996; Zeil and Zanker, 1997; Layne, 1998), toxicity, environmental monitoring, and pollution (Devi, 1987; Weis and Kim, 1988; Ismail *et al.*, 1991). Despite these and hundreds of other studies, there has been very little comparative work on the genus. Most studies have concentrated on just one or two species. This is due, in large part, to the lack of a good phylogeny with which to ground comparative studies in a phylogenetic framework (Harvey and Pagel, 1991).

The purpose of this work is to create a coherent phylogeny for the genus *Uca* and use it to clear up systematic uncertainties in the delineation of subgenera. This phylogeny should also prove useful in providing a framework for comparative studies in the future. Before presenting the current work, I will briefly describe the history of systematic study of fiddler crabs at a variety of taxonomic levels, concentrating particularly on the past 30 years.

## HISTORY

The taxonomic history of the genus *Uca* is somewhat complicated, and much of the confusion and disagreement over the proposed generic, subgeneric, and specific taxonomy of the genus is due to these historical complications.

### Genus *Uca* Leach, 1814

*Type Species.—Cancer vocans major* Herbst, 1782.

The earliest description of the type species of *Uca* is from a picture by Seba (1758), which he called *Cancer uka una, Brasiliensibus.* A number of authors subsequently used this same picture as a basis for naming the species (Manning and Holthuis, 1981). *Cancer vocans major* Herbst, 1782; *Ocypode heterochelos* Lamarck, 1801; *Cancer uka* Shaw and Nodder, 1802; and *Uca una* Leach, 1814, are all objective synonyms, because they are all based on the picture and description from Seba (1758). Because of this, the type species of the genus *Uca* is *Cancer vocans major.* The earliest description of this species based on actual specimens and not on Seba's drawing was *Gelasimus platydactylus* Milne-Edwards, 1837.

For about 60 years, the genus was known as *Gelasimus*, until Rathbun (1897) showed that the abandonment of the older name *Uca* did not conform to zoological naming conventions. The type species of *Uca* was known as both *Uca heterochelos* and *U. platydactylus,* until Rathbun (1918) suggested the adoption of *U. heterochelos* as the valid name. Almost 50 years later, Holthuis (1962) pointed out that *U. heterochelos* was an objective junior synonym of *U. major,* and the type species has been referred to as *U. major* ever since.

However, Bott (1973a) discovered that there has been a universal misinterpretation of the type species; the species pictured by Seba is not the American species commonly referred to as *U. major,* but rather the West African/Portuguese species called *U. tangeri* (Eydoux, 1835). Correcting this error would have caused a somewhat painful change of names (Holthuis, 1979; Manning and Holthuis, 1981). The type species would still be called *U. major,* but would refer to the West African/European species rather than the American one; the American species, which has been called *U. major* since 1962, would be called *U. platydactylus,* a name not used since 1918.

To deal with this dilemma, the International Commission on Zoological Nomenclature officially designated the holotype of *Gelasimus platydactylus* as a neotype of *Cancer vocans major* (Holthuis, 1979; ICZN, 1983). The result of this decision is that we retain the names *U. major* for the American species and *U. tangeri* for the West African/European species. It also means that although *U. tangeri* is technically the species upon which the genus is named, *U. major* (*Cancer vocans major*) is still the official type species of the genus *Uca.*

### The Subgenera of *Uca*

Historically, naturalists recognized informal subdivisions within the genus *Uca* (e.g., Milne-Edwards, 1852; Smith, 1870; Kingsley, 1880); the first official splitting of the genus was not until Bott (1954), who recognized two subgenera: the *Minuca,* or broad-front species, and the *Uca,* or narrow-front species. The front is the part of the carapace between the eyestalks (Fig. 1). Relative front width and eyestalk length are necessarily inversely proportional in *Uca,* because the eyestalks are constrained to fit within the orbital cavity of the carapace; the longer the eyestalks, the narrower the front must be.

In the mid-1970s the subdivisions became much more complicated. In 1975, Jocelyn Crane's long awaited monograph on fiddler crabs was finally published. Most of the book consists of detailed descriptions of each species and subspecies (she recognized 62 species and 92 taxa). Based on her hypotheses about the evolutionary history of fiddler crabs, she split the genus into nine subgenera (Table 1). Four of the subgenera (*Deltuca, Uca, Thalassuca,* and *Australuca*) contained narrow-front species; the other five (*Minuca, Celuca, Boboruca, Amphiuca,* and *Afruca*) contained the broad-front species.

Unfortunately, while Crane's book was in

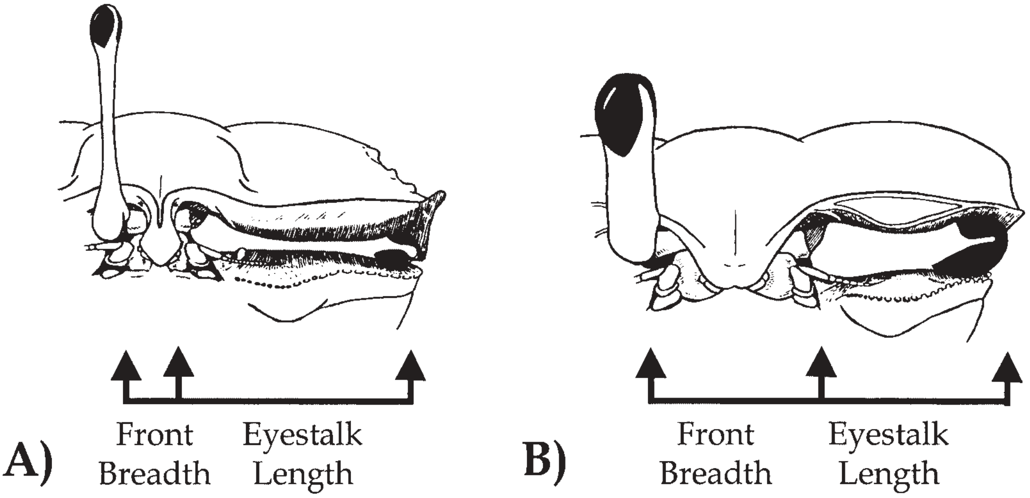

Fig. 1. Examples of narrow-front and broad-front morphologies. A) *U. ornata;* B) *U. terpsichores.* Figure modified from Crane (1975).

press, Bott (1973b) published his own division of the genus. In a short (11 pages) paper, Bott split the genus *Uca* into two informal geographic groups (America and Africa/Indo-West Pacific) with 10 separate genera and one genus split into two subgenera (Table 2). Bott only recognized 52 taxa (half as many as Crane); many of the names he used turned out to be junior synonyms according to Crane's treatment. Bott's descriptions are poor, inadequate, and often appear to be based on questionable hypotheses.

To make matters worse, Bott's and Crane's subdivisions are largely incompatible. Only about half of their taxa can easily be equated (von Hagen, 1976; Manning and Holthuis, 1981). Some of these differences and incompatibilities are due to Bott's (1973a) discovery about the misnaming of the type species (see above). By the rules of nomenclature, Bott's names have priority over those of Crane. According to von Hagen (1976), Crane's subgenera *Thalassuca*, *Amphiuca*, and *Boboruca* should be called (after Bott) *Mesuca*, *Paraleptuca*, and *Planuca*, respectively. In addition, if we accept Crane's subdivisions as correct, her *Deltuca* and *Celuca* should be called *Tubuca* and *Leptuca*. According to Manning and Holthuis (1981), Crane's *Thalassuca* should not be replaced by *Mesuca* as suggested by von Hagen (1976), but rather by *Gelasimus*. In this case, the group Bott referred to as *Gelasimus* would take the name *Acanthoplax*. Unfortunately, all of this does little to help resolve the proper names of the other (sub)genera.

These issues are best resolved with a greater understanding of the evolutionary relationships within the genus. Neither Crane's nor Bott's subdivision of the genus is based on numeric systematic methodology. Crane's descriptions are very complete and are based on her hypotheses regarding the biogeographic history of the genus. Bott's descriptions are poor, but have priority. In recent years, most scientists have actively ignored both potential subdivisions. Whenever there has been a reference to a subgenus, however, it has almost always been Crane's nomenclature (e.g., Nakasone, 1982; von Prahl, 1982; Hogarth, 1986).

## The Species of *Uca*

For an overview of all *Uca* species, the best reference is Crane (1975); any earlier major work would be overridden by Crane's descriptions. For the most part, the taxa recognized by Crane are still accepted today. A number of new species have been described since the publication of her monograph, one of her new species has been discovered to be invalid, and two of her new species were previously described by Bott (1973b); as with the subgenera, his names have priority and take precedence. These changes are summarized in Table 3.

Table 1. Subdivisions of the genus *Uca* according to Crane (1975). An asterisk indicates the type species.

| Subgenus | Author | Species | Subspecies |
|---|---|---|---|
| *Deltuca* | Crane, 1975 | *forcipata** (Adams and White, 1848) | |
| | | *rosea* (Tweedie, 1937) | |
| | | *dussumieri* | *dussumieri* (Milne-Edwards, 1852) |
| | | | *capricornis* Crane, 1975 |
| | | | *spinata* Crane, 1975 |
| | | *demani* | *demani* Ortmann, 1897 |
| | | | *typhoni* Crane, 1975 |
| | | | *australiae* Crane, 1975 |
| | | *arcuata* (de Haan, 1835) | |
| | | *coarctata* | *coarctata* (Milne-Edwards, 1852) |
| | | | *flammula* Crane, 1975 |
| | | *urvillei* (Milne-Edwards, 1852) | |
| | | *acuta* | *acuta* (Stimpson, 1858) |
| | | | *rhizophorae* Tweedie, 1950 |
| *Australuca* | Crane, 1975 | *bellator** | *bellator* (Adams and White, 1848) |
| | | | *signata* (Hess, 1865) |
| | | | *minima* Crane, 1975 |
| | | | *longidigita* (Kingsley, 1880) |
| | | *seismella* Crane, 1975 | |
| | | *polita* Crane, 1975 | |
| *Thalassuca* | Crane, 1975 | *tetragonon** (Herbst, 1790) | |
| | | *formosensis* Rathbun, 1921 | |
| | | *vocans* | *vocans* (Linnaeus, 1758) |
| | | | *borealis* Crane, 1975 |
| | | | *herperiae* Crane, 1975 |
| | | | *pacificensis* Crane, 1975 |
| | | | *dampieri* Crane, 1975 |
| | | | *vomeris* McNeill, 1920 |
| *Amphiuca* | Crane, 1975 | *chlorophthalmus** | *chlorophthalmus* (Milne-Edwards, 1852) |
| | | | *crassipes* (Adams and White, 1848) |
| | | *inversa* | *inversa* (Hoffmann, 1874) |
| | | | *sindensis* (Alcock, 1900) |
| *Boboruca* | Crane, 1975 | *thayeri** | *thayeri* Rathbun, 1900b |
| | | | *umbratila* Crane, 1941 |
| *Afruca* | Crane, 1975 | *tangeri** (Eydoux, 1835) | |
| *Uca* | Leach (*sensu* Bott, 1954) | *maracoani** | *maracoani* (Latreille, 1802–1803) |
| | | | *insignis* (Milne-Edwards, 1852) |
| | | *heteropleura* (Smith, 1870) | |
| | | *major* (Herbst, 1782) | |
| | | *stylifera* (Milne-Edwards, 1852) | |
| | | *princeps* | *princeps* (Smith, 1870) |
| | | | *monilifera* Rathbun, 1914 |
| | | *ornata* (Smith, 1870) | |
| *Minuca* | Bott, 1954 | *mordax** (Smith, 1870) | |
| | | *pygmaea* Crane, 1941 | |
| | | *vocator* | *vocator* (Herbst, 1804) |
| | | | *ecuadoriensis* Maccagno, 1928 |
| | | *burgersi* Holthuis, 1967 | |
| | | *panamensis* (Stimpson, 1859) | |
| | | *minax* (LeConte, 1855) | |
| | | *brevifrons* (Stimpson, 1860) | |
| | | *galapagensis* | *galapagensis* Rathbun, 1902 |
| | | | *herradurensis* Bott, 1954 |
| | | *rapax* | *rapax* (Smith, 1870) |
| | | | *longisignalis* Salmon and Atsaides, 1968b |
| | | *pugnax* | *pugnax* (Smith, 1870) |
| | | | *virens* Salmon and Atsaides, 1968b |
| | | *zacae* Crane, 1941 | |
| | | *subcylindrica* (Stimpson, 1859) | |

Table 1. Continued.

| Subgenus | Author | Species | Subspecies |
|---|---|---|---|
| *Celuca* | Crane, 1975 | *deichmanni** Rathbun, 1935 | |
| | | *argillicola* Crane, 1941 | |
| | | *pugilator* (Bosc, 1802) | |
| | | *uruguayensis* Nobili, 1901a | |
| | | *crenulata* | *crenulata* (Lockington, 1877) |
| | | | *coloradensis* (Rathbun, 1893) |
| | | *speciosa* | *speciosa* (Ives, 1891) |
| | | | *spinicarpa* Rathbun, 1900a |
| | | *cumulanta* Crane, 1943 | |
| | | *batuenta* Crane, 1941 | |
| | | *saltitanta* Crane, 1941 | |
| | | *oerstedi* Rathbun, 1904 | |
| | | *inaequalis* Rathbun, 1935 | |
| | | *tenuipedis* Crane, 1941 | |
| | | *tomentosa* Crane, 1941 | |
| | | *tallanica* von Hagen, 1968 | |
| | | *festae* Nobili, 1901c | |
| | | *helleri* Rathbun, 1902 | |
| | | *leptochela* Bott, 1954 | |
| | | *dorotheae* von Hagen, 1968 | |
| | | *beebei* Crane, 1941 | |
| | | *stenodactylus* (Milne-Edwards and Lucas, 1843) | |
| | | *triangularis* | *triangularis* (Milne-Edwards, 1873) |
| | | | *bengali* Crane, 1975 |
| | | *lactea* | *lactea* (de Haan, 1835) |
| | | | *annulipes* (Milne-Edwards, 1837) |
| | | | *perplexa* (Milne-Edwards, 1837) |
| | | | *mjobergi* Rathbun, 1924 |
| | | *leptodactyla* Rathbun, 1898 | |
| | | *limicola* Crane, 1941 | |
| | | *musica* | *musica* Rathbun, 1914 |
| | | | *terpsichores* Crane, 1941 |
| | | *latimanus* (Rathbun, 1893) | |

Crane (1975) tended to lump related taxa into subspecies rather than treat them as distinct species. A number of studies since that time have raised virtually all of her subspecies to specific status (e.g., Salmon *et al.*, 1979; Thurman, 1979, 1982; Barnwell, 1980; Green, 1980; Barnwell and Thurman, 1984; Collins *et al.*, 1984; Salmon and Kettler, 1987; von Hagen and Jones, 1989). It has become common practice with many authors to ignore all of the subspecific designations and treat each as a separate species (e.g., George and Jones, 1982; von Hagen and Jones, 1989; Jones and Morton, 1995), and I shall follow this practice.

## The Phylogeny of *Uca*

The genus *Uca* belongs to the family Ocypodidae, subfamily Ocypodinae. Ghost crabs (genus *Ocypode*) have long been considered the sister-group to fiddler crabs (e.g., Milne-Edwards, 1852; Crane, 1975; Manning and Holthuis, 1981), these currently being the only two genera in the subfamily; this relationship has been confirmed by recent molecular work (Levinton *et al.*, 1996; Sturmbauer *et al.*, 1996; Kitaura *et al.*, 1998).

Crane (1975) proposed the first phylogeny of *Uca*. In her monograph, she includes dendrograms depicting her hypotheses as to the phylogenetic history of the genus. These hypotheses are not based on any numeric phylogenetic methodology, but rather simply her expertise on the genus and the geographic distribution of the species. She based her major divisions primarily on front width, the form of the gills on the third maxilliped, and the morphological structures of the gonopods and orbits. Crane believed that the fiddler crabs showed an evolutionary progression from low intertidal to high intertidal (reflecting evolution away from the purportedly marine ancestor) and from simple mating behaviors to complex mating behaviors. These beliefs,

Table 2. Divisions of the genus *Uca* according to Bott (1973b). An asterisk indicates the type species; names in brackets indicate the correct species name as revised by Crane (1975) (the exceptions being *U. neocultrimana* and *U. paradussumieri,* see below).

| Genus | Subgenus | Author | Species |
|---|---|---|---|
| African/Indo-West Pacific Genera: | | | |
| *Uca* | | Leach, 1814 | *tangeri** |
| | | | *marionis* (Desmarest, 1825) [*vocans*] |
| *Mesuca* | *Mesuca* | Bott, 1973b | *tetragonon** |
| | | | *forcipatus* |
| | | | *coarctata* |
| | | | *brevipes* (Milne-Edwards, 1852) [*arcuata*] |
| | | | *rhizophorae* |
| | *Latuca* | Bott, 1973b | *neocultrimana** Bott, 1973b [*pacificensis*] |
| | | | *paradussumieri* Bott, 1973b [*spinata*] |
| | | | *rosea* |
| | | | *dussumieri* |
| *Tubuca* | | Bott, 1973b | *urvillei** |
| | | | *forceps* (Milne-Edwards, 1937) [*lactea*] |
| *Austruca* | | Bott, 1973b | *annulipes** |
| | | | *lactea* |
| | | | *inversa* |
| | | | *orientalis* Nobili, 1901b [*perplexa*] |
| | | | *sindensis* |
| *Paraleptuca* | | Bott, 1973b | *chlorophthalmus** |
| | | | *gaimardi* (Milne-Edwards, 1852) [*crassipes*] |
| American Genera: | | | |
| *Minuca* | | Bott, 1954 | *mordax** |
| | | | *burgersi* |
| | | | *lanigera* von Hagen, 1968 [*ecuadoriensis*] |
| | | | *panamensis* |
| | | | *herradurensis* |
| | | | *rapax* |
| | | | *brevifrons* |
| | | | *murifecenta* Crane, 1943 [*vocator*] |
| *Planuca* | | Bott, 1973b | *thayeri** |
| | | | *zilchi* Bott, 1954 [*umbratila*] |
| | | | *deichmanni* |
| | | | *galapagensis* |
| | | | *macrodactyla* (Milne-Edwards and Lucas, 1843) [*galapagensis*] |
| | | | *uruguayensis* |
| | | | *pugilator* |
| *Leptuca* | | Bott, 1973b | *stenodactylus** |
| | | | *leptochela* |
| | | | *leptodactyla* |
| | | | *festae* |
| | | | *coloradensis* |
| | | | *beebei* |
| | | | *oerstedti* |
| | | | *inaequalis* |
| | | | *saltitanta* |
| | | | *terpsichores* |
| | | | *mertensi* Bott, 1954 [*tomentosa*] |
| *Gelasimus* | | Latreille, 1817 | *maracoani** |
| | | | *platydactylus* (Milne-Edwards, 1837) [*major*] |
| | | | *stylifera* |
| | | | *insignis* |
| | | | *princeps* |
| *Heteruca* | | Bott, 1973b | *heteropleurus** |

coupled with the biogeography of fiddler crabs led her to propose the following scenario for fiddler crab evolution. Fiddler crabs arose in the Indo-West Pacific as primitive narrow-front species; these early crabs split into multiple narrow- and one broad-front lineages. One narrow-front lineage migrated to the New World and gave rise to the Ameri-

Table 3. Changes to the species-level taxonomy of the genus *Uca* since Crane (1975).

| New species† | Reference |
|---|---|
| *Uca panacea* | Novak and Salmon (1974) |
| *Uca marguerita* | Thurman (1981) |
| *Uca elegans* | George and Jones (1982) |
| *Uca hirsutimanus* | George and Jones (1982) |
| *Uca intermedia* | von Prahl and Toro (1985) |
| *Uca victoriana* | von Hagen (1987b) |

| Junior synonym | Correct name | Reference(s) |
|---|---|---|
| *Uca minima* | *Uca signata* | George and Jones (1982) |
| *Uca spinata* | *Uca paradussumieri* | Dai and Yang (1991); Jones and Morton (1995) |
| *Uca pacificensis* | *Uca neocultrimana* | This study |

| Incorrect spelling | Correct spelling | Reference |
|---|---|---|
| *Uca longidigita* | *Uca longidigitum* | von Hagen and Jones (1989) |
| *Uca mjobergi* | *Uca mjoebergi* | von Hagen and Jones (1989) |

†The newly described species *Uca pavo* George and Jones, 1982, is a junior synonym of *Uca capricornis* (see von Hagen and Jones, 1989).

can (and West African) broad- and narrow-front species. Later, one of the American broad-front taxa (*Celuca*) migrated back to the Indo-West Pacific, to explain the distribution as seen today.

Salmon and Zucker (1988) suggested that a widespread fiddler crab fauna, containing both broad- and narrow-front species, was subdivided into the Indo-West Pacific group and the American group in conjunction with the closing of the Tethys seaway in the late Oligocene. They believed the similarity in certain broad- and narrow-front species in the Indo-West Pacific to those in the Americas, was due to parallel evolution and not shared phylogenetic history. This would imply that the subgenus *Celuca* was polyphyletic, because Crane included both American and Indo-West Pacific species in this taxon. They disagreed with Crane's behavioral hypotheses of "primitive" and "advanced" behaviors, and showed that some so-called "primitive" species show remarkable overlap in behavior with "advanced" species.

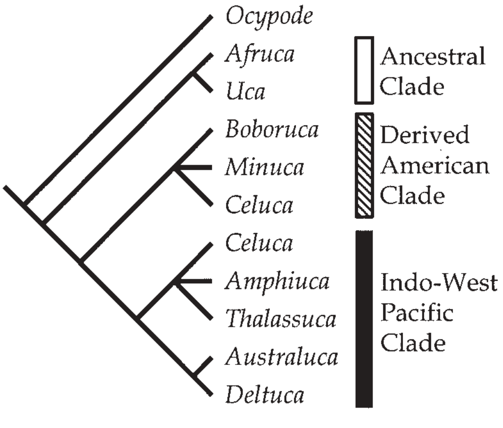

Fig. 2. Phylogenetic relationships of Crane's (1975) subgenera, according to Sturmbauer *et al.* (1996) and Levinton *et al.* (1996).

Very little molecular phylogenetic work has been conducted on *Uca* (Albrecht and von Hagen, 1981; Suzawa *et al.*, 1993; Levinton *et al.*, 1996; Sturmbauer *et al.*, 1996). Albrecht and von Hagen (1981) studied the phylogenetic relationships of ten American species (representing five subgenera, *sensu* Crane) using a combination of electrophoretic and morphological characters. They found the same relationships among the subgenera as proposed by Crane with the single exception of *Boboruca*. Crane had proposed this to be a primitive clade with an uncertain place on the fiddler crab tree; Albrecht and von Hagen found *Boboruca* to be a more advanced clade nested within the subgenus *Minuca*.

Suzawa *et al.* (1993) studied the phylogenetic relationships of seven Malaysian species of fiddler crab (representing three subgenera, *sensu* Crane) using 10 enzyme and protein markers. They found the same relationships among the species as proposed by Crane, with the exception of the relationship of three closely related species (*U. acuta, U. forcipata,* and *U. rosea*) within Crane's *Deltuca*. Neither Albrecht and von Hagen nor Suzawa *et al.* (1993) examined the relationships between the American and Indo-West Pacific species, instead restricting themselves to either one or the other group.

Sturmbauer *et al.* (1996) and Levinton *et al.* (1996) represent the most comprehensive molecular phylogenetic work on fiddler crabs to date. Their phylogeny is based on 16S ribosomal DNA sequences for 28 species, including all nine subgenera (*sensu* Crane). They also included one species from each of four other genera within the Ocypodidae, a gecarcinid species, and a grapsid species as outgroups. Their work revealed three interesting results (Fig. 2). First, it confirmed that *Ocypode* is the sister group to *Uca,* while the other ocypodids are quite distant from both genera. Second, it found that the Indo-West Pacific species form a monophyletic clade. Third, it split the American species into two clades: a basal clade consisting of the single West African species and the narrow-front American species (the subgenera *Uca* and *Afruca, sensu* Crane), and a crown clade consisting of the broad-front American species (the subgenera *Minuca, Boboruca,* and most of *Celuca, sensu* Crane). Crane's subgenus *Celuca* is apparently polyphyletic, with the Indo-West Pacific species being in a separate clade from the American species; even within the American group, the *Celuca* may not be monophyletic. Although these three major clades (basal American, crown American, and Indo-West Pacific) were well supported, the specific relationships of species and subgenera within these clades remained unresolved.

The goal of this research is to construct a phylogeny encompassing the entire genus, based on morphological characters, which resolves questions about subgeneric and specific relationships within the genus, and allows one to clarify systematic uncertainties with regard to subgeneric specifications.

## MATERIALS AND METHODS

An initial morphological character list was generated by combing through numerous species descriptions, comparisons, and identification keys (Rathbun, 1933; von Hagen, 1968, 1980; Novak and Salmon, 1974; Crane, 1975; Altevogt and Davis, 1979; Guinot, 1979; Thurman, 1979, 1981, 1982; Barnwell, 1982; George and Jones, 1982; Jones and George, 1982; von Prahl, 1982; Barnwell and Thurman, 1984; Collins *et al.*, 1984; Hendrickx, 1984; von Prahl and Toro, 1985; Abele and Kim, 1986; Bairagi and Misra, 1988; von Hagen and Jones, 1989; Dai and Yang, 1991; Jones and Morton, 1995; Shih *et al.*, 1999). Numerous additional characters were added upon direct examination of specimens.

Table 4. Species of *Uca* not included in the phylogenetic analysis. Subgenera refer to Crane (1975).

| Species | Subgenus *sensu* Crane/comments |
|---|---|
| *Uca helleri* | *Celuca* |
| *Uca leptochela* | *Celuca* |
| *Uca musica* | Sister species of *U. terpsichores* (see Crane, 1975) |
| *Uca acuta* | Sister species of *U. rhizophorae* (see Crane, 1975) |
| *Uca longisignalis* | *Minuca,* possibly related to *U. minax* (see Thurman, 1982) |
| *Uca pygmaea* | *Minuca* |
| *Uca monolifera* | Sister species of *U. princeps* (see Crane, 1975) |
| *Uca australiae* | Known from only 1 specimen; probably not a valid species (Crane, 1975; George and Jones, 1982) |
| *Uca victoriana* | *Minuca* |

Every morphological character that could be identified was included in the data matrix. A single character (handedness) represents a population-level characteristic, rather than the characteristic of an individual. Most fiddler crab species have populations with equal numbers of right- and left-handed individuals (handedness refers to the side with the major claw in males). A few Indo-West Pacific species are predominantly (greater than 95%) right-handed (Green and Schochet, 1972; Yamaguchi, 1977; Altevogt and Davis, 1979; Barnwell, 1982; Jones and George, 1982; Shih *et al.,* 1999). Handedness has been proposed as a potential phylogenetic character (Jones and George, 1982) and was therefore included in this analysis. Although they have been used to identify phylogenetic relationships in the past (e.g., Crane, 1975), no behavioral characters were used in this analysis.

Specimens examined were obtained through personal collections and from museum collections (Appendix I). Of the 97 recognized fiddler crab species, 88 were included in the analysis; the remaining nine were unavailable for examination and are listed in Table 4. The missing species are spread across the genus with regards to their taxonomic position, and their exclusion should not change the overall conclusions.

Although *Ocypode* is clearly the sister genus to *Uca,* using the *Ocypode* to root the *Uca* tree is problematic. The overwhelming dominant feature of *Uca* is the extreme sexual dimorphism and asymmetry of the chelipeds; roughly one-third of the characters are specific to either the major or minor cheliped. While the chelipeds of *Ocypode* are asymmetric, they in no way can be considered a major and minor (the chelipeds of *Ocypode* much more resemble the classic crusher/cutter claw dichotomy seen in many other Decapods, e.g., lobsters), and it is impossible to reasonably assign states for any of those characters in the genus *Ocypode.* The problem is related to the extreme divergence the genera took with regard to feeding behavior: while *Uca* species are specialist deposit feeders, the *Ocypode* are classic predators.

Attempts to use *Ocypode* as an outgroup in these analyses led to a fairly strange rooting of the cladogram, although the ingroup relationships were largely unaffected

Table 5. Suites of characters that were inapplicable for some taxa. Characters not listed had a weight of 1.

| Morphological feature | Character numbers | Weight |
|---|---|---|
| Minor chela gape serration | 22 | 0.750 |
| Ventral supramarginal groove of major manus | 46, 47 | 0.500 |
| Oblique tuberculate ridge of major palm | 54–57 | 0.250 |
| Trench on major palm at pollex base | 62 | 0.750 |
| Outer median groove of major pollex | 86, 87 | 0.500 |
| Outer subdorsal groove of major dactyl | 90 | 0.750 |
| Setae on margins of ambulatories | 149–164 | 0.500 |
| Posterolateral striae of carapace | 211, 212 | 0.500 |
| Gonopod thumb | 224 | 0.750 |
| Gonopod flanges | 226, 227 | 0.500 |

(results not shown). The analysis always placed *Ocypode* next to *Uca minax;* the similarities appear to be primarily due to both species having broad-fronts and similar setae patterns on the ambulatory legs (although it should be pointed out that the setae on the legs of *Ocypode* and those on *Uca* are really not at all similar). Rooting at this point turns the tree upside down with respect to any previous study (Crane, 1975; Levinton *et al.,* 1996; Sturmbauer *et al.,* 1996) and is almost impossible to explain under any reasonable biogeographic scenario. Any other genus, even within the family Ocypodidae, would suffer from similar problems and would be even more divergent from *Uca* (Levintion *et al.,* 1996). Because of this problem, the results of the Levinton *et al.* (1996) and Sturmbauer *et al.* (1996) studies were followed; the subgenera *Uca* and *Afruca sensu* Crane were used to root the tree. Both molecular (Levinton *et al.,* 1996; Sturmbauer *et al.,* 1996) and morphological (Crane, 1975) evidence strongly supports the close relationship of these species.

A matrix with 236 discrete morphological characters was subjected to maximum parsimony analysis with PAUP* 4.0b3a (Swofford, 1999); these characters are listed in Appendix II (the data matrix is given in Appendix III). All characters were unordered, and multistate characters were treated as polymorphisms. Because of the large size of the matrix, a heuristic search algorithm with TBR branch swapping was used; 1,000 searches were performed, with the order of the taxa in the matrix randomized each time to ensure that the search was not being trapped in a local tree-length minimum (Maddison, 1991). Nonparametric bootstrap percentages were calculated for nodes on all trees; each of the 100 bootstrap replicates consisted of 100 separate heuristic searches with the taxa order randomized for each replicate.

A critical issue in phylogenetic analysis, and one that bears heavily on this data set, is how to treat inapplicable characters (Platnick *et al.,* 1991; Maddison, 1993; Pleijel, 1995; Hawkins *et al.,* 1997). These are different from missing data in so far as inapplicable characters refer to a set of characters that do not exist for certain taxa; missing data refers to characters that are unknown. For example, in the present data set, there are a set of characters concerned with the size, shape, and structure of the oblique tuberculate ridge on the palm of the major cheliped (characters 54–57, Appendix II). However, there are 11 species that do not have this ridge at all. Consequently, all of the characters that refer to aspects of the ridge have no meaning for those taxa. Traditionally, these characters would have been treated as unknowns, but this is not logically tenable, can add a large degree of uncertainty to the data matrix, and has been shown to lead to unexpected and undesirable results (Maddison, 1993). An alternative approach is to add an additional state to each character that indicates the lack or inapplicability of the character. The problem with this approach is that as the number of characteristics of the missing feature increases, additional weight is being given to the absence of this feature because it is repeated for multiple characters. The problem is particularly acute when it is recognized that such a large weight is being given to the absence of something. This problem is not restricted to morphological analyses but is equivalent to the coding of a gap in molecular data. It has been suggested that new algorithms and phylogenetic programs need to be designed to account for the conceptualization of missing characters (Maddison, 1993; Hawkins *et al.,* 1997).

Unfortunately, there is currently no definitive solution to the problem. The approach I have taken is as follows: an additional character state "N" was created for each character that was missing from some taxa. Characters that contained this alternate character state were downweighted based on the number of characters that referred to the missing feature. All of the characters with adjusted weights are listed in Table 5.

To compare the results of these analyses with those of Levinton *et al.* (1996) and Sturmbauer *et al.* (1996), alternative branching arrangements were entered as constraint trees and analyzed separately. Two constraint configurations were tested. In the first, the Indo-West Pacific taxa were constrained to form one clade and the American taxa to form a second clade (Fig. 3a). In the second the Indo-West Pacific taxa were constrained to form one clade, the crown American taxa, *sensu* Levinton *et al.* (1996) and Sturmbauer *et al.* (1996), were constrained to form a second clade, and the basal taxa were constrained as a third clade (Fig. 3b). A Wilcoxon signed-rank test (Templeton, 1983; Larson, 1994; Sokal and Rohlf, 1995) was used to test whether the character state distribution was significantly different for the topologies obtained from the constrained and unconstrained analyses. Although formally a one-tailed test under these circumstances, a conservative approach was taken and this test was evaluated with a two-tailed probability (Felsenstein, 1985; Larson, 1994).

## RESULTS

Two hundred four of the 236 characters were parsimony informative. The heuristic search found 12 MPTs of length 1,517 (consistency index (CI) = 0.161, retention index

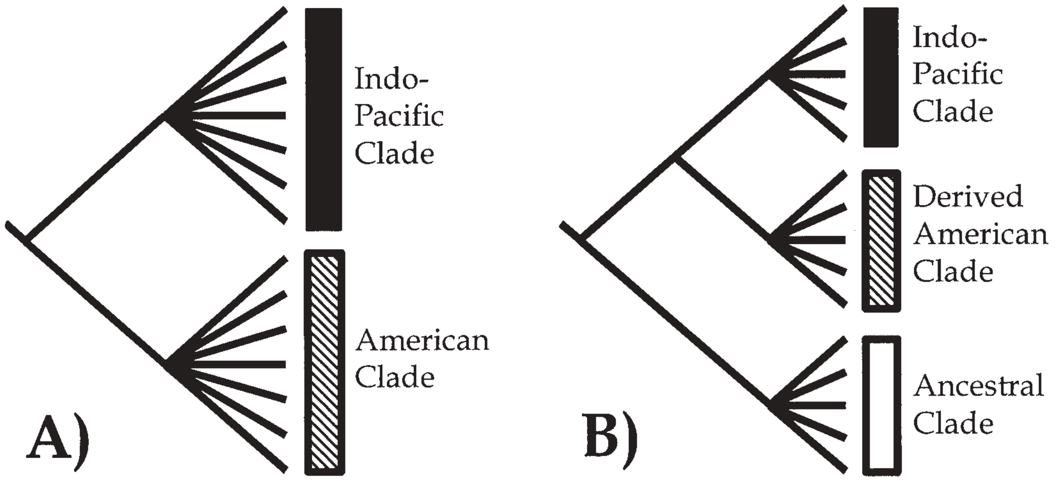

Fig. 3. Conceptualization of constraint trees used to compare these analyses to other hypotheses. A) Indo-West Pacific vs. American dichotomy; B) Indo-West Pacific vs. crown American dichotomy, with basal American outgroup.

(RI) = 0.660) (Fig. 4). Referring to the subgenera *sensu* Crane (1975), the *Uca, Deltuca, Australuca,* and *Amphiuca* are all monophyletic. The *Thalassuca* are nearly so, with only *U. formosensis* falling outside of the clade (see Discussion). The single-species subgenus *Afruca* (*U. tangeri*) groups with the *Uca,* and the two-species subgenus *Boboruca* falls within the midst of the *Minuca.* The broad-front taxa are monophyletic, with the Indo-West Pacific species and one strange American species, *U. argillicola,* basal to an American clade. The *Minuca* are paraphyletic, with the *Boboruca* and a pair of *Celuca* (*U. panacea* and *U. pugilator*) falling in their midst, and *U. panamensis* falling outside. The *Celuca* are polyphyletic.

The general geographic pattern has the narrow-front Indo-West Pacific clades branching one after another along the derived branch (treating *Uca* and *Afruca* as basal). However, while each of these clades has bootstrap support for their monophyly, their basal relationships to each other are only weakly supported (except for the sister status of the *Deltuca* and *Australuca*).

Although very few characters do not show some homoplasy, a number help define specific clades. The *Uca* and *Afruca* clade is supported by the basal process on the spoon-tipped setae of the second maxilliped, the lack of setae on the ventral margins of the ambulatory meri, and the absence of a lower margin on the eyebrow (the area along the dorsal margin of the orbits often bounded by raised edges). The *Uca* have a narrow-front, while the one species of the *Afruca* (*Uca tangeri*) has a broad front. The *Thalassuca* (excluding *U. formosensis*) are supported by the large gill on the third maxilliped, the predominance of right handed males in their populations, and a distal tooth on the anterodorsal margin of the major merus.

The *Deltuca* and *Australuca* clade is supported by a narrow front, the presence of a median groove on the dactyl, small suborbital crenulations that are fused or missing along the length of the margin, and a vertical lateral margin that does not reach the dorsal surface of the carapace. The separation between the two subgenera is as follows: the *Deltuca* are supported by the presence of a trench at the base of the palm, the outer tubercle row on the major pollex starts below the dactyl base, and a crest at the outer corner of the suborbital margin. The *Australuca* have a crest on the anterodorsal margin of the major merus.

There are eighteen character changes at the base of the clade containing *Minuca, Celuca, Boboruca*, and *Amphiuca.* This clade is supported by the broad front, small turbercles on the outside of the lower major manus, the absence (in most species) of an outer median groove along the major pollex, tuberculate striae on the ambulatory meri, an inclined eyebrow, posterolateral striae on the carapace of most species, and a specialized pleonal

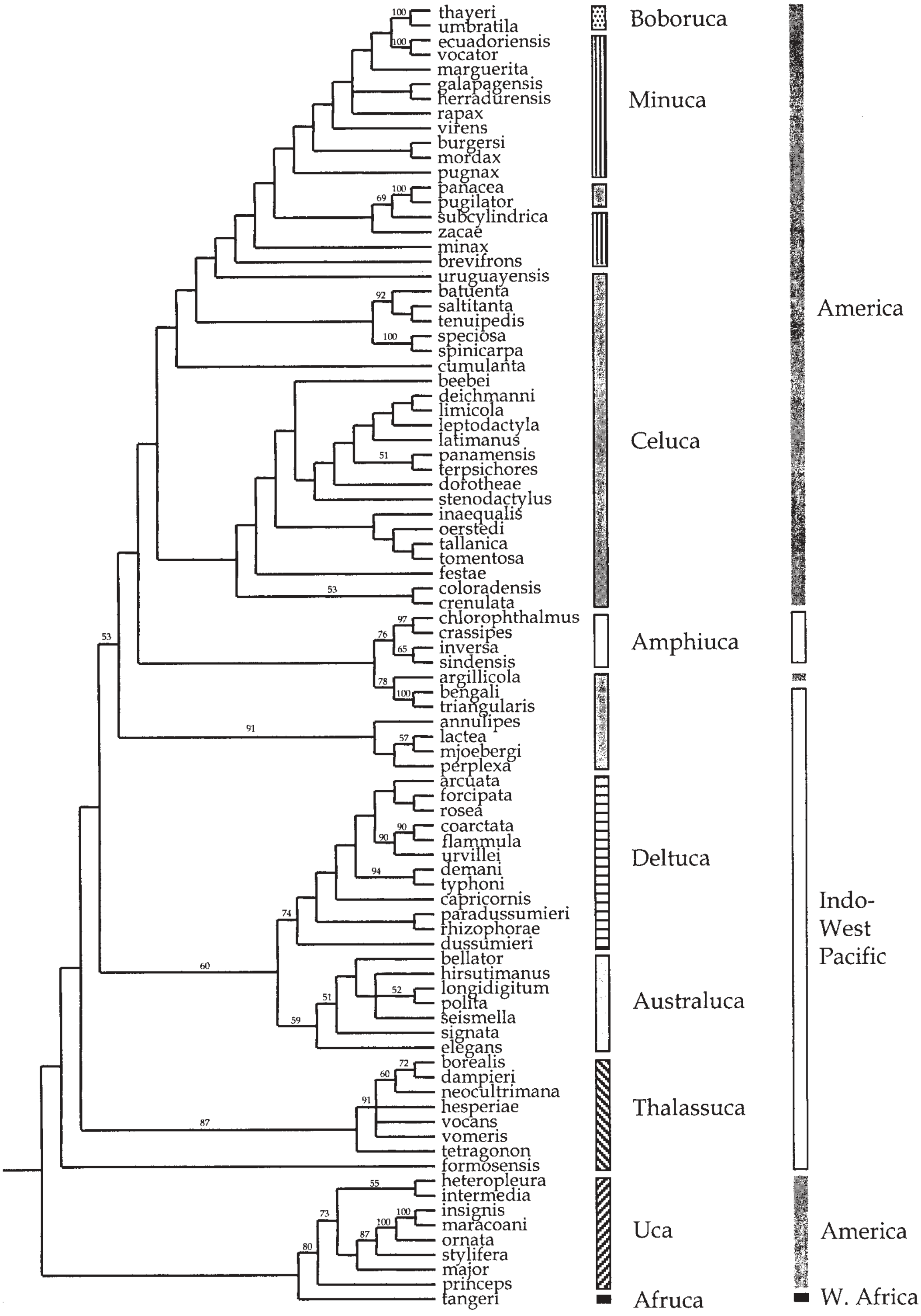

Fig. 4. Strict consensus of 12 most-parsimonious trees (length = 1,517, CI = 0.161, RI = 0.660) from unconstrained analysis. Numbers above branches are bootstrap values.

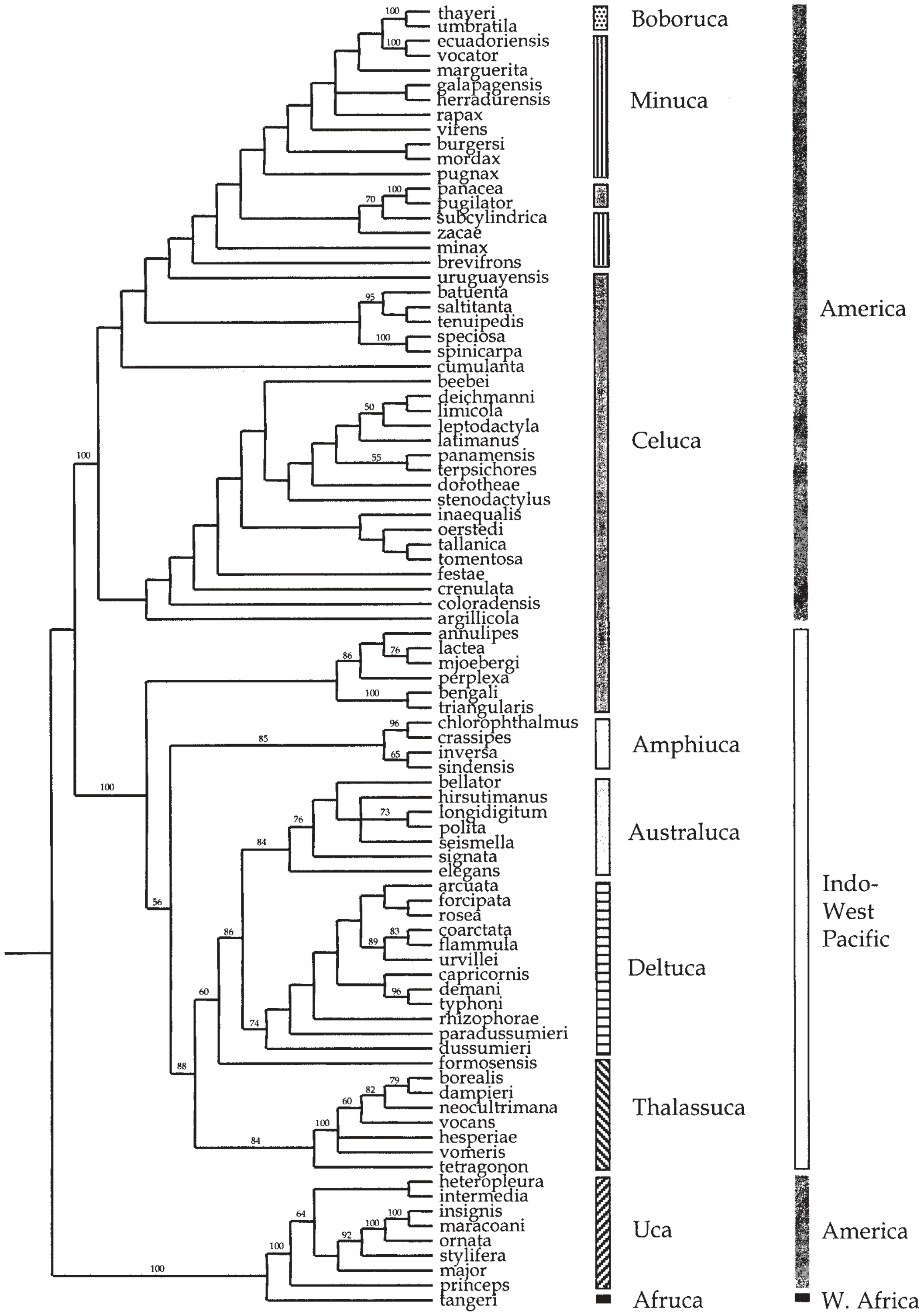

Fig. 5. Strict consensus of 8 most-parsimonious trees (length = 1,538.5, CI = 0.158, RI = 0.655) from constrained parsimony analysis, using the second constraint tree (see Fig. 3b). Numbers above branches are bootstrap values.

Table 6. Reassessment of *Uca* subgeneric nomenclature.

| Subgenus | Author | Type | Consists primarily of Crane's (1975) |
|---|---|---|---|
| *Uca* | Leach, 1814 | *U. major* | *Uca* and *Afruca* |
| *Minuca* | Bott, 1954 | *U. mordax* | *Minuca* and *Boboruca* |
| *Gelasimus* | Latreille, 1817 | *U. vocans* | *Thalassuca* |
| *Paraleptuca* | Bott, 1973b | *U. chlorophthalmus* | *Amphiuca* |
| *Tubuca* | Bott, 1973b | *U. urvillei* | *Deltuca* |
| *Leptuca* | Bott, 1973b | *U. stenodactylus* | *Celuca* |
| *Australuca* | Crane, 1975 | *U. bellator* | *Australuca* |

clasping structure in the abdominal cavity. Within the clade, the *Amphiuca* have a trench on the major palm, a depression on the outside of the major pollex, and a large gill on the third maxilliped. The other subgenera are not very well distinguished.

The first constrained search (Fig. 3a) found 40 MPTs of length 1,535 (CI = 0.159, RI = 0.656); this is 18 steps (1.2%) longer than the unconstrained search. The second constrained search (Fig. 3b) found 8 MPTs (Fig. 5) of length 1,538.5 (CI = 0.158, RI = 0.655); this is only 21 steps (1.4%) longer than the unconstrained search and just 3.5 steps (0.2%) longer than the first constrained search. Because the results were so similar, only those from the second constrained search are shown (Fig. 5). Other than constraining the Indo-West Pacific and derived American species to be monophyletic, there are virtually no differences between the constrained and unconstrained trees. Almost all of the ingroup topologies are identical. One interesting difference is the placement of *Uca formosensis* at the base of the *Deltuca* and *Australuca* subgenera, rather than with the *Thalassuca*. The bootstrap support for the relationships within the Indo-West Pacific clade are as strong or stronger than in the unconstrained tree; the support within the American clade is slightly weaker.

The Wilcoxon signed-rank test was significant ($n = 52$, $T_s = 413.5$, $t_s = -2.51$, $P < 0.02$), indicating that the character distribution significantly supports the unconstrained topology more than the constrained topology.

## DISCUSSION

To a large extent, this work conforms to previous studies and hypotheses about the overall subdivision of the genus *Uca*. Most of Crane's (1975) subgeneric divisions hold up fairly well, with just a few aberrant species. Using the phylogeny, we can propose an application of the proper nomenclature for the recognizable subgroups (Table 6).

Because of the decision by the International Commission on Zoological Nomenclature to designate the holotype of *Gelasimus platydactylus* as a neotype of *Cancer vocans major* (see Holthuis, 1979; ICZN, 1983), *U. major* (*Cancer vocans major*) is now the type species of the genus *Uca*. Therefore, *Uca* should be applied as in Crane (1975) and not as in Bott (1973b). However, there seems little justification to having *U. tangeri* in its own subgenus (*Afruca sensu* Crane). Therefore, it should also be included among the *Uca*, which is the name of the subgenus in which Bott (1973b) had placed it anyway. As noted by Manning and Holthuis (1981), Bott's use of *Gelasimus* was misapplied and should refer to Crane's subgenus *Thalassuca*. Bott's names *Paraleptuca*, *Tubuca*, and *Leptuca* should replace Crane's subgenera *Amphiuca*, *Deltuca*, and *Celuca*, respectively. *Australuca* (Crane, 1975) and *Minuca* (Bott, 1954) remain more or less unchanged. The remainder of Bott's (1973b) names (*Mesuca*, *Latuca*, *Planuca*, *Heteruca*, and *Austruca*) have no status under the current classification (although see below).

A number of authors (von Hagen, 1987b; Salmon and Zucker, 1988) have proposed that the placement of *U. thayeri* and *U. umbratila* (actually a single species with two subspecies by Crane's treatment) into their own subgenus (*Boboruca*) was unwarranted and that they should simply be considered members of the *Minuca*. The above results strongly place these species in the midst of the *Minuca*, and there seems no reason for them to be considered a separate subgenus. If one wished to maintain them as a separate subgenus, the proper name would be *Planuca* (Bott, 1973b).

The exact status of the *Leptuca* (*Celuca sensu* Crane) is questionable. These species appear to represent a large, rapid radiation in the Americas, and their relationships have been difficult to resolve through phylogenetic analysis (Levinton *et al.,* 1996; Sturmbauer *et al.,* 1996; present study). The taxon is paraphyletic (if not polyphyletic), with the *Minuca* derived from within the *Celuca.* If the Indo-West Pacific species form a clade, the *lactea* and *triangularis* complexes would fall under the name *Austruca* (Bott, 1973b), leaving *Leptuca* for the American species.

Crane had placed *U. formosensis* in the clade *Thalassuca* (now *Gelasimus*). Recently, a detailed study of this species (Shih *et al.,* 1999) questioned this placement and tentatively proposed that the species be included in the subgenus *Deltuca* (now *Tubuca*). Upon direct examination of specimens, I did not see much similarity between *U. formosensis* and the other *Gelasimus.* The results of this study place *U. formosensis* outside of the *Thalassuca,* in between them and the basal clade. In the constrained search, *U. formosensis* falls at the base of the *Tubuca* and *Australuca.* I agree that *U. formosensis* does not appear to belong to *Gelasimus,* but I am loathe at this point to suggest placing it in its own subgenus (as has been proposed by others, see Shih *et al.,* 1999). The exact relationship of this species to the rest of the genus remains uncertain.

A number of the American broad-front species show somewhat strange relationships. *Uca argillicola* tends to group with the Indo-West Pacific species; *U. panacea* and *U. pugilator* group with *U. subcylindrica* within the *Minuca.* Crane (1975) hesitantly placed *U. subcylindrica* in the *Minuca;* other authors (Barnwell and Thurman, 1984; Thurman, 1984) have found it to be more similar to some of the *Celuca* (now *Leptuca*), especially somewhat aberrant species such as *U. pugilator* and *U. panacea;* this study confirms that relationship but puts all three species, along with *U. zacae,* towards the base of the *Minuca.* Another divergent species Crane hesitantly placed within the *Minuca* is *U. panamensis;* this study places it squarely among some of the *Celuca.* Both *U. argillicola* and *U. panamensis* are highly derived and on extremely long branches, so their odd placement may be a long-branch effect. Although many of the American species do form small, well-supported phylogenetic cohorts, it seems impossible to make solid statements about the fine-scale relationships of these species.

Some of the species that were not included in the analysis (Table 4) deserve further comment. Three of the species are thought to be sister taxa of species included in the analysis (Crane, 1975); for *U. musica* and *U. acuta* this certainly appears to be true. Whether *U. monolifera* and *U. princeps* are sister species is somewhat questionable; the major claw of *U. monolifera* appears to be much more similar to the derived shear-like claw of *U. ornata, U. maracoani,* and *U. insignis* than it is to the simpler claw of *U. princeps.* Furthermore, *U. princeps* shows a lot of behavioral and color variation over its range along the Pacific coast of Central America (Crane, 1941, 1975; Peters, 1955; von Hagen, 1968), and may represent a series of cryptic species. Certainly, a study of the variation within this species over its geographic range could yield quite interesting results.

At various times, *Uca longisignalis* has been considered a subspecies of both *U. rapax* (see Crane, 1975) and *U. minax* (see von Hagen, 1980). Thurman (1982) found *U. longisignalis* to be a distinct species. Furthermore, he felt it was more closely related to a species group containing *U. burgersi, U. mordax, U. minax,* and *U. pugnax,* rather than a group containing *U. galapagensis, U. herradurensis, U. marguerita,* and *U. rapax.* In the current study, the later species group forms a clade with a few additional species; the members of the former species group all have basal positions within the *Minuca.* Although its exact position cannot be determined, it is likely that *U. longisignalis* is also among the basal species of the *Minuca.*

The current results are compatible with previous small-scale studies (Albrecht and von Hagen, 1981; von Hagen and Jones, 1989; Suzawa *et al.,* 1993). The relationships of the major clades are the same, and only the occasional detailed relationship between closely related species differs.

One of the most interesting results of earlier work (Levinton *et al.,* 1996; Sturmbauer *et al.,* 1996) was the division of the Indo-West Pacific and American clades. The critical question is whether the broad-front species in the Indo-West Pacific and the Americas represent convergence. Front-width is probably not adaptive *per se,* but is rather a side-effect of selection on eyestalk length (Gould and Lewontin, 1979). There are ecological correlations with eyestalk length within the

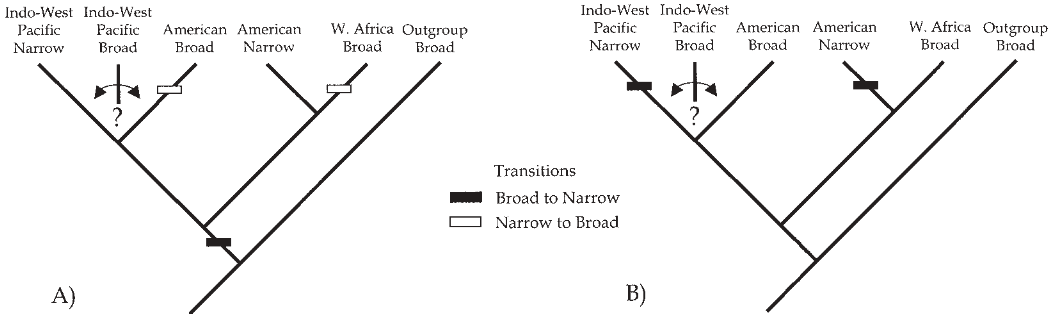

Fig. 6. Proposed biogeographic history of the genus *Uca*. A) Assumes a narrow-front ancestral fiddler crab; B) Assumes a broad-front ancestral fiddler crab. Black symbols represent transitions from broad to narrow; white symbols represent transitions from narrow to broad.

genus, e.g., species with longer eyestalks (*ergo* narrower fronts) tend to live on more open mudflats, while those with shorter eyestalks (broad-fronts) live in more closed mangroves (Crane, 1975). For example, all of the members of the subgenus *Uca* live on open mudflats and have extremely narrow fronts; the closely related species, *U. tangeri*, lives in an extremely complex habitat of closed mangroves and is essentially a broad-front species. Narrow-front crabs, with their eyes close together on long, narrow eyestalks, tend to have acute vertical resolving power along the horizon; this leads to better vision and depth and size perception in open, flat, featureless habitats (Zeil *et al.*, 1986). Although there are differences in visual acuity related to eyestalk length (and therefore broad- and narrow-front crabs) (Zeil *et al.*, 1986), these differences are on scales much greater than the difference seen between broad- and narrow-front *Uca* (Salmon and Zucker, 1988).

It is easily conceivable that this suite of characters could be convergent. However, the broad-front species all share another unique trait, that being a specialized pleonal clasping apparatus (Guinot, 1979) (this is a specialized structure in the abdominal cavity that helps hold the telson in place). This was one of the first shared-derived characters to adequately diagnose the broad-front *Celuca* and *Minuca* (*sensu* Crane) in the Americas as separate from the narrow-front *Uca* (see Albrecht and von Hagen, 1981). It was not realized earlier that this character is also found on all of the broad-front Indo-West Pacific species, including the Indo-West Pacific *Celuca* as well as the *Amphiuca* (now *Paraleptuca*). That this character could be convergent is possible, but that its convergence would perfectly parallel that of front width would be quite surprising. This character is missing from all of the narrow-front species, *U. tangeri* (which clearly belongs with the American narrow-fronts), and from all other Ocypodidae (Guinot, 1979) and strongly supports the monophyly of the broad-front fiddler crabs.

Biogeographically, the evolution of the genus is hard to explain simply by the tree presented in Fig. 4. The branch separating the two Indo-West Pacific narrow-front clades at the base of the tree (the *Gelasimus* and the clade containing the *Australuca* and *Tubuca*) has little bootstrap support and is supported by only a few characters that all show a large degree of homoplasy across the tree. Collapsing this single branch (along with the branch containing the lone species, *Uca formosensis*) to form a single Indo-West Pacific narrow-front clade leads to a geographically likely scenario for the evolution of the genus (Fig. 6), quite similar to that proposed by Levinton *et al.* (1996) and Sturmbauer *et al.* (1996).

In this scenario, the ancestral crabs were most likely broad-fronted (relative to the *Uca*), living in the Americas; this is supported by both molecular and the rather minimal fossil evidence (Rathbun, 1926; Brito, 1972). Although a narrow-front ancestry was hypothesized by Crane (1975), all of the potential outgroups in the family (e.g., *Ocypode* or *Macrophthalmus*) have broad fronts relative to *Uca* (the entire family Ocypodidae is narrow-fronted relative to most other crabs, e.g., Grapsidae or Portunidae). This would imply evolution from broad-front ancestral crabs. An early split led to two fiddler crab clades,

Table 7. Number of changes required under different scenarios of front-breadth evolution, treating front-breadth as a single character.

| | Indo-West Pacific Broad-Fronts | |
|---|---|---|
| Ancestral *Uca* | Indo-West Pacific clade | American clade |
| Narrow-front | 4 | 3 |
| Broad-front | 2 | 2 |

one containing the large American/West African fiddlers and the other the remainder of the species. Species from the later clade crossed what is now the Pacific Ocean to form the narrow-front Indo-West Pacific subgenera; the rest remained in the Americas to form the broad-front American subgenera.

Reconstructing front-width evolution under this scenario is quite illustrative (Fig. 6). Ignoring the Indo-West Pacific broad-front taxa for the moment, there are two possibilities: first, the early fiddler crab taxa evolved narrow fronts (Fig. 6a), with the broad front returning twice (once in West Africa for *Uca tangeri* and once for the American broad-front subgenera). Second, the narrow front evolved twice (Fig. 6b), once in the American *Uca* and once in the Indo-West Pacific subgenera. The second scenario is more parsimonious because it only requires two evolutionary events, rather than the three of the first scenario.

When you consider the Indo-West Pacific broad-front species the situation becomes more interesting (Table 7). If the Indo-West Pacific broad-front species are related to the American broad-front clade (as the morphological data suggests) and represent a second trans-oceanic invasion, the two front-width scenarios remain unchanged. However, if all of the Indo-West Pacific species form a clade, one of the outlined scenarios is affected. If the ancestral fiddler crabs were broad-fronts, there is no change (as long as the Indo-West Pacific broad-fronts are basal, which the morphological evidence suggests). If the ancestral fiddler crabs were narrow-fronts, we now require at least four evolutionary events to explain the pattern.

Although this does not resolve the placement of the Indo-West Pacific broad-front species with respect to the derived clades, it certainly suggests that front-width evolution within the genus has proceeded from broad to narrow and not the other way around as previously suggested (Crane, 1975). Furthermore, it adds support to the proposal (Levinton *et al.*, 1996; Sturmbauer *et al.*, 1996) that there has not been a general evolutionary trend in fiddler crabs toward complexity and the invasion of the extreme high intertidal environment, but rather that many of the hypothesized advanced characters were already present in the ancestors.

## CONCLUSIONS

Although there have been a number of small changes to the genus since the publication of her monograph, most of Crane's (1975) subgenera hold up quite well under phylogenetic analysis. These morphological based results are at odds with previous molecular analyses (Levinton *et al.*, 1996; Sturmbauer *et al.*, 1996) with respect to the placement of the set of broad-front taxa from the Indo-West Pacific. Otherwise, we can assign the proper taxonomic name to most of the fiddler crab subgenera, with only the resolution of the broad-front radiation in the Americas still causing a problem. Although many of the species-level relationships are only weakly supported, especially for the American broad-front species, this phylogeny can provide a framework for future comparative studies.

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APPENDIX I. SPECIMENS EXAMINED.

| Species | Collection |
|---|---|
| *Uca annulipes* | USNM 128591 |
| *Uca arcuata* | USNM 64953 |
| *Uca argillicola* | MSR–Diablo, Panama, Fall 1997 |
| *Uca batuenta* | MSR–Rodman N.B., Panama, Fall 1997 |
| *Uca beebei* | MSR–Rodman N.B., Panama, Fall 1997 |
| *Uca bellator* | USNM 137932 |
| *Uca bengali* | USNM 138168 |
| *Uca borealis* | To JL–Starfish Bay, Hong Kong, July 1995 |
| *Uca brevifrons* | USNM 138483 |
| *Uca burgersi* | USNM 126959 |
| *Uca capricornis* | DJ–Grove, N.T., Australia, May 1982 |
| *Uca chlorophthalmus* | To JL–Durban Harbour, South Africa, Feb. 1993 |
| *Uca coarctata* | USNM 137965 |
| *Uca coloradensis* | USNM (no number) |
| *Uca crassipes* | USNM 137964 |
| *Uca crenulata* | JL–Catalina Island, San Diego, California |
| *Uca cumulanta* | USNM 137516 |
| *Uca dampieri* | DJ–Barred Creek, Broome, Australia, May 1978 |
| *Uca deichmanni* | MSR–Rodman N.B., Panama, Fall 1997 |
| *Uca demani* | USNM 137982 |
| *Uca dorotheae* | USNM 138534 |
| *Uca dussumieri* | USNM 125711 |
| *Uca ecuadoriensis* | MSR–Diablo, Panama, Fall 1997 |
| *Uca elegans* | DJ–New Mangrove Bay, Australia, June 1980 |
| *Uca festae* | MSR–Diablo, Panama, Fall 1997 |
| *Uca flammula* | USNM 137980 |
| *Uca forcipata* | USNM 138010 |
| *Uca formosensis* | USNM 138015 |
| *Uca galapagensis* | USNM 138536 |
| *Uca herradurensis* | MSR–Diablo, Panama, Fall 1997 |
| *Uca hesperiae* | USNM 138189 |
| *Uca heteropleura* | MSR–Rodman N.B., Panama, Fall 1997 |
| *Uca hirsutimanus* | DJ–Derby, Australia, April 1983 |
| *Uca inaequalis* | MSR–Rodman N.B., Panama, Fall 1997 |
| *Uca insignis* | USNM 138577 |
| *Uca intermedia* | MSR–Rodman N.B., Panama, Fall 1997 |
| *Uca inversa* | USNM 138044 |
| *Uca lactea* | To JL–Starfish Bay, Hong Kong, Aug. 1995 |
| *Uca latimanus* | USNM 138562 |
| *Uca leptodactyla* | USNM 138568 |
| *Uca limicola* | USNM 138573 |
| *Uca longidigitum* | USNM 137942 |
| *Uca major* | USNM 137748 |
| *Uca maracoani* | USNM 138580 |
| *Uca marguerita* | USNM 180443 |
| *Uca minax* | To JL–Beaufort, North Carolina, Oct. 1992 |
| *Uca mjoebergi* | USNM 138072 |
| *Uca mordax* | USNM 138589 |
| *Uca neocultrimana* | USNM 138196 |
| *Uca oerstedi* | USNM 138610 |
| *Uca ornata* | MSR–Rodman N.B., Panama, Fall 1997 |
| *Uca panacea* | To JL–Panacea, Florida, Oct. 1992 |
| *Uca panamensis* | MSR–Naos, Panama, Fall 1997 |
| *Uca paradussumieri* | USNM 138001 |
| *Uca perplexa* | DJ–Batangas Bay, Australia, Aug. 1965 |
| *Uca polita* | USNM 138096 |
| *Uca princeps* | MSR–Rodman N.B., Panama, Fall 1997 |
| *Uca pugilator* | MSR–Flax Pond, Long Island, New York, July 1998 |
| *Uca pugnax* | MSR–Flax Pond, Long Island, New York, July 1998 |
| *Uca rapax* | USNM 93084 |
| *Uca rhizophorae* | USNM 137924 |
| *Uca rosea* | USNM 138099 |
| *Uca saltitanta* | MSR–Rodman N.B., Panama, Fall 1997 |
| *Uca seismella* | USNM 138103 |
| *Uca signata* | USNM 137946 |
| *Uca sindensis* | USNM 138046 |
| *Uca speciosa* | USNM 138824 |
| *Uca spinicarpa* | USNM 139174 |
| *Uca stenodactylus* | MSR–Rodman N.B., Panama, Fall 1997 |
| *Uca stylifera* | MSR–Rodman N.B., Panama, Fall 1997 |
| *Uca subcylindrica* | JL-DF–Kingsville, Texas, July 1995 |
| *Uca tallanica* | USNM 138838 |
| *Uca tangeri* | JL-JP–Mira Estuary, Portugal, July 1993 |
| *Uca tenuipedis* | MSR–Rodman N.B., Panama, Fall 1997 |
| *Uca terpsichores* | MSR–Rodman N.B., Panama, Fall 1997 |
| *Uca tetragonon* | USNM 138120 |
| *Uca thayeri* | JL-MS–Boca Raton, Florida, Sept. 1993 |
| *Uca tomentosa* | USNM 138840 |
| *Uca triangularis* | USNM 138173 |
| *Uca typhoni* | USNM 138874 |
| *Uca umbratila* | MSR–Diablo, Panama, Fall 1997 |
| *Uca uruguayensis* | USNM 138876 |
| *Uca urvillei* | To JL–Durban Harbour, South Africa, Feb. 1993 |
| *Uca virens* | USNM 128129 |
| *Uca vocans* | USNM 210843 |
| *Uca vocator* | USNM 137753 |
| *Uca vomeris* | USNM 138206 |
| *Uca zacae* | USNM 138871 |

Key:
DJ–Specimens provided to author by Diana Jones.
JL–Personal collection by Jeff Levinton.
JL-DF–Specimens provided to Jeff Levinton by Don Felder.
JL-MS–Specimens provided to Jeff Levinton by Michael Salmon.
JL-JP–Specimens provided to Jeff Levinton by José Paula.
MSR–Personal collection by the author.
To JL–Specimens provided to Jeff Levinton.
USNM–Collection of the United States National Museum of Natural History.

APPENDIX II. CHARACTER LIST.

1. Epibranchial region without (0) or with (1) pile.
2. Epibranchial region without (0) or with (1) setae.
3. Epibranchial region setae are sparse (0) or numerous (1).
4. Epibranchial region without (0) or with (1) tuberculation.
5. Epibranchial region ridge below orbit is without (0) or with (1) tuberculation.
6. Antennae are long (0) or short (1).
7. Antennular flagella are hidden beneath the front (0) or are not hidden (1).
8. Gill on 3rd maxilliped is large with many books (0) or small and leaflike (1) (Crane, 1975).
9. Spoon-shaped setae of 2nd maxilliped without (0) or with (1) basal process (Crane, 1975).
10. Highly dimorphic chelipeds are found only in the males (0) or in both sexes (1).
11. Minor ischium without (0) or with (1) a large tubercle on the distal ventral anterior margin.
12. Large teeth absent (0) or present (1) on the posteroventral margin of the minor merus.
13. Posterior surface of minor merus without (0) or with (1) longitudinal row of tubercles above posteroventral margin (Crane, 1975; George and Jones, 1982).
14. Posterior surface of minor merus rounded (0) or flattened (1) (Crane, 1975).
15. Chela length of minor cheliped are shorter than/equal to (0) or longer than (1) the manus (Crane, 1975).
16. Minor gape width is narrower than half of adjacent dactyl (0), between half and full width of adjacent dactyl (1), or greater than the width of the adjacent dactyl (2).
17. Minor pollex without (0) or with (1) an enlarged tooth.
18. Minor dactyl without (0) or with (1) an enlarged tooth.
19. Minor pollex without (0) or with (1) a ridge along the ventral margin.
20. Minor dactyl without (0) or with (1) a ridge along the dorsal margin.
21. Minor cheliped without (0) or with (1) serrations in the gape (George and Jones, 1982; von Hagen and Jones, 1989).
22. Minor cheliped serrations are small and similar in size (0) or large and unequal (1) (Crane, 1975).
23. Minor cheliped tip shape is forceps-like (0) or spooned (1) (Collins *et al.*, 1984).
24. Major cheliped is found approximately equally on the left and right side (0) or is found predominantly (greater than 80%) on the right side (1).
25. Major ischium without (0) or with (1) a stridulating ridge.
26. Major ischium without (0) or with (1) a large tubercle on the distal ventral anterior margin.
27. Anteroventral margin of major merus is without (0) or with (1) tuberculation.
28. Anterodorsal margin of major merus is without (0) or with (1) tuberculation (Crane, 1975).
29. Anterodorsal margin of major merus without (0) or with (1) a distal tooth (Jones and Morton, 1994).
30. Anterodorsal margin of major merus without (0) or with (1) a large convex flange (Crane, 1975).
31. Anterodorsal margin of major merus without (0) or with (1) a long crest (Crane, 1975).
32. Dorsal margin of major merus is without (0) or with (1) pile.
33. Ventral margin of major merus is without (0) or with (1) pile.
34. Large tooth absent (0) or present (1) on inner anterior surface of major carpus.
35. Large tooth absent (0) or present (1) from proximal anterodorsal margin of major carpus.
36. Vertical row of tubercles absent (0) or present (1) from anterior surface of major carpus.
37. Anterodorsal margin of major carpus without (0) or with (1) tuberculation.
38. Major carpus without (0) or with (1) dorsal margin pile.
39. Dorsal part of major carpal cavity without (0) or with (1) pile.
40. Pile absent (0) or present (1) in the gape of the major cheliped.
41. Outer major manus without (0) or with (1) depression at the base of the pollex (George and Jones, 1982).
42. Outer major manus dorsal margin is smooth (0) or rough (1) (Collins *et al.*, 1984).
43. Outer major manus without (0) or with (1) a groove along the dorsal margin.
44. Outer major manus without (0) or with (1) a groove outside the dactyl cusp.
45. Outer major manus without (0) or with (1) a ventral supramarginal groove.
46. Ventral supramarginal groove of outer major manus extends to base of pollex (0) or well onto pollex (1).
47. Ventral supramarginal groove of outer major manus without (0) or with (1) pile.
48. Outer major manus ventral margin armature is weak (0) or strong (1).
49. Outer major manus without (0) or with (1) tuberculation.
50. Outer major manus with small (0) or large (1) tubercles on the upper surface.
51. Outer major manus with small (0) or large (1) tubercles on the lower surface.
52. Base of major cheliped palm without (0) or with (1) a stridulating ridge.
53. Major cheliped palm without (0) or with (1) oblique tubercle ridge.
54. Oblique ridge of the major cheliped consists of small (0) or large (1) tubercles.
55. Oblique ridge of major palm ends without (0) or with (1) a large tubercle.
56. Tubercles of oblique ridge of palm are in a single row (0) or multiple rows (1) (Hendrickx, 1984).
57. Oblique ridge of the major cheliped terminates at the carpal cavity (0) or the ventral margin (1).
58. Dorsal margin of major palm is without (0) or with (1) a beaded ridge along the carpal cavity.
59. Predactyl ridge(s) along palm of major cheliped are parallel to (0) or diverging from (1) the palm-dactyl joint (Crane, 1975; Thurman, 1979; von Hagen, 1980).
60. Major palm has one (0) or two (1) predactyl ridges (Crane, 1975).

APPENDIX II. CHARACTER LIST. Continued.

61. Major palm without (0) or with (1) a trench at the base of the pollex.
62. Trench at base of major palm is linear (0) or trifid (1).
63. Major palm without (0) or with (1) a tuberculate ridge running between the oblique ridge and the dactyl.
64. Major palm without (0) or with (1) tuberculation (Thurman, 1979).
65. Middle tubercle row on major pollex is without (0) or with (1) a large median tooth.
66. Outer tubercle row on major pollex is without (0) or with (1) a median tooth.
67. Middle tubercle row on major pollex is without (0) or with (1) a large subdistal tooth.
68. Outer tubercle row on major pollex is without (0) or with (1) a large subdistal tooth.
69. Middle tubercle row on major pollex is without (0) or with (1) a proximal tooth.
70. Outer tubercle row on major pollex is without (0) or with (1) a proximal tooth.
71. Middle tubercle row on major dactyl is without (0) or with (1) a median tooth.
72. Outer tubercle row on major dactyl is without (0) or with (1) a median tooth.
73. Middle tubercle row on major dactyl is without (0) or with (1) a small subdistal tooth.
74. Middle tubercle row on major dactyl is without (0) or with (1) a large proximal tooth.
75. Inner tubercle row on major dactyl is without (0) or with (1) an extra large tubercle on the inside edge of the dactyl.
76. Inner tubercle row on major dactyl is absent (0) or present (1) distally.
77. Inner tubercle row on major dactyl is absent (0) or present (1) proximally.
78. Outer tubercle row on major dactyl is absent (0) or present (1) distally.
79. Outer tubercle row on major dactyl is absent (0) or present (1) proximally.
80. Major pollex without (0) or with (1) little teeth on its distal cutting edge (George and Jones, 1982).
81. Major dactyl without (0) or with (1) little teeth on its distal cutting edge (George and Jones, 1982).
82. Inner tubercle row of major pollex extends to the base of the dactyl (0) or past the base of the dactyl (1).
83. Outer tubercle row of major pollex does not (0) or does (1) start at the dactyl base.
84. Length of the major dactyl is less than or equal to the length of the manus (0), between one and two times as long as the manus (1), twice as long or greater than the length of the manus (2).
85. Major pollex without (0) or with (1) an outer median groove.
86. Outer median groove of major pollex without (0) or with (1) pile.
87. Outer median groove of major pollex curves up to center of pollex base (0) or stays close to ventral margin (1).
88. Major dactyl without (0) or with (1) an outer median groove (George and Jones, 1982).
89. Major dactyl without (0) or with (1) an outer subdorsal groove (George and Jones, 1982).
90. Outer subdorsal groove of major dactyl short (0) or long (1) (Bairagi and Misra, 1988).
91. Major pollex shape not triangular (0) or strongly triangular (1).
92. Major pollex is the same width or wider than the dactyl (0) or narrower than the dactyl (1).
93. Major pollex tip is simple (0) or bifid/trifid (1).
94. Major dactyl tip is simple (0) or bifurcate (1).
95. Major chela tips are not (0) or are (1) forceps-like.
96. Major dactyl and pollex without (0) or with (1) thin sharp, inward spines.
97. Major pollex without (0) or with (1) a ventral marginal carina.
98. Major pollex without (0) or with (1) outer surface tuberculation.
99. Major dactyl without (0) or with (1) outer surface tuberculation.
100. Outside of major pollex without (0) or with (1) pits (Crane, 1975).
101. Pits on outer pollex without (0) or with (1) pile.
102. Ambulatory legs are short (0) or long (1) (Crane, 1975).
103. Merus of the 1st ambulatory leg is slender (0) or broad (1).
104. Merus of the 2nd ambulatory leg is slender (0) or broad (1).
105. Merus of the 3rd ambulatory leg is slender (0) or broad (1).
106. Merus of the 4th ambulatory leg is slender (0) or broad (1).
107. Dorsal margin curvature of the merus of the 2nd ambulatory leg is straight (0) or convex (1).
108. Dorsal margin curvature of the merus of the 3rd ambulatory leg is straight (0) or convex (1).
109. Dorsal margin curvature of the merus of the 4th ambulatory leg is straight (0) or convex (1).
110. Posterior surface of 1st ambulatory leg without (0) or with (1) tuberculation (Collins *et al.*, 1984).
111. Longitudinal row of setae absent (0) or present (1) on anterior surface of the merus of the 1st ambulatory leg.
112. Ambulatory meri without (0) or with (1) tubercles on striae.
113. Anterior tubercles on the manus of the 1st ambulatory leg are absent (0) or present (1).
114. Anterior tubercles on the merus of the 1st ambulatory leg are absent (0) or present (1).
115. Anterior tubercles on the carpus of the 1st ambulatory leg are absent (0) or present (1).
116. Pile absent (0) or present (1) on the manus of the 1st ambulatory leg.
117. Pile absent (0) or present (1) on the carpus of the 1st ambulatory leg.
118. Pile absent (0) or present (1) on the merus of the 1st ambulatory leg.
119. Pile absent (0) or present (1) on the carpus of the 2nd ambulatory leg.
120. Pile absent (0) or present (1) on the manus of the 2nd ambulatory leg.
121. Pile absent (0) or present (1) on the merus of the 2nd ambulatory leg.
122. Pile absent (0) or present (1) on the carpus of the 3rd ambulatory leg.

APPENDIX II. CHARACTER LIST. Continued.

123. Pile absent (0) or present (1) on the manus of the 3rd ambulatory leg.
124. Pile absent (0) or present (1) on the merus of the 3rd ambulatory leg.
125. Pile absent (0) or present (1) on the carpus of the 4th ambulatory leg.
126. Pile absent (0) or present (1) on the merus of the 4th ambulatory leg.
127. Large teeth absent (0) or present (1) on posteroventral margin of the merus of the 1st ambulatory leg.
128. Large teeth absent (0) or present (1) on posteroventral margin of the merus of the 2nd ambulatory leg.
129. Large teeth absent (0) or present (1) on posteroventral margin of the merus of the 3rd ambulatory leg.
130. Large teeth absent (0) or present (1) on posteroventral margin of the merus of the 4th ambulatory leg.
131. Anteroventral margin serration absent (0) or present (1) distally on the merus of the 1st ambulatory leg.
132. Anteroventral margin serration absent (0) or present (1) proximally on the merus of the 1st ambulatory leg.
133. Posteroventral margin serration absent (0) or present (1) on the merus of the 1st ambulatory leg.
134. Dorsal margin serration absent (0) or present (1) on the merus of the 1st ambulatory leg.
135. Anteroventral margin serration absent (0) or present (1) distally on the merus of the 2nd ambulatory leg.
136. Anteroventral margin serration absent (0) or present (1) proximally on the merus of the 2nd ambulatory leg.
137. Posteroventral margin serration absent (0) or present (1) on the merus of the 2nd ambulatory leg.
138. Dorsal margin serration absent (0) or present (1) on the merus of the 2nd ambulatory leg.
139. Anteroventral margin serration absent (0) or present (1) distally on the merus of the 3rd ambulatory leg.
140. Anteroventral margin serration absent (0) or present (1) proximally on the merus of the 3rd ambulatory leg.
141. Posteroventral margin serration absent (0) or present (1) on the merus of the 3rd ambulatory leg.
142. Dorsal margin serration absent (0) or present (1) on the merus of the 3rd ambulatory leg.
143. Anteroventral margin serration absent (0) or present (1) distally on the merus of the 4th ambulatory leg.
144. Anteroventral margin serration absent (0) or present (1) proximally on the merus of the 4th ambulatory leg.
145. Posteroventral margin serration absent (0) or present (1) on the merus of the 4th ambulatory leg.
146. Dorsal margin serration absent (0) or present (1) on the merus of the 4th ambulatory leg.
147. Setae absent (0) or present (1) on ventral margin of the merus of the ambulatory legs.
148. Setae absent (0) or present (1) on dorsal margin of the merus of the ambulatory legs.
149. Setae on ventral margin of 1st ambulatory-leg merus are sparse (0) or numerous (1).
150. Setae on ventral margin of 1st ambulatory-leg merus are short (0) or long (1).
151. Setae on dorsal margin of 1st ambulatory-leg merus are sparse (0) or numerous (1).
152. Setae on dorsal margin of 1st ambulatory-leg merus are short (0) or long (1).
153. Setae on ventral margin of 2nd ambulatory-leg merus are sparse (0) or numerous (1).
154. Setae on ventral margin of 2nd ambulatory-leg merus are short (0) or long (1).
155. Setae on dorsal margin of 2nd ambulatory-leg merus are sparse (0) or numerous (1).
156. Setae on dorsal margin of 2nd ambulatory-leg merus are short (0) or long (1).
157. Setae on ventral margin of 3rd ambulatory-leg merus are sparse (0) or numerous (1).
158. Setae on ventral margin of 3rd ambulatory-leg merus are short (0) or long (1).
159. Setae on dorsal margin of 3rd ambulatory-leg merus are sparse (0) or numerous (1).
160. Setae on dorsal margin of 3rd ambulatory-leg merus are short (0) or long (1).
161. Setae on ventral margin of 4th ambulatory-leg merus are sparse (0) or numerous (1).
162. Setae on ventral margin of 4th ambulatory-leg merus are short (0) or long (1).
163. Setae on dorsal margin of 4th ambulatory-leg merus are sparse (0) or numerous (1).
164. Setae on dorsal margin of 4th ambulatory-leg merus are short (0) or long (1).
165. Ambulatory legs without (0) or with (1) long setae on the carpus and merus.
166. Orbital region with a large tubercle absent (0) or present (1) at the base of the eyestalk.
167. Style absent (0) or present (1) on eyestalk on major side in adults.
168. Style absent (0) or present (1) on eyestalk on major side in juveniles.
169. Eyebrow inclination is vertical (0) or inclined (1) (Rathbun, 1900a; von Hagen, 1980).
170. Lower margin of the eyebrow is absent (0) or present (1).
171. Width of the eyebrow is narrower (0) or equal/wider (1) than the eyestalk (Crane, 1975).
172. Cornea is equal to (0) or greater than (1) the width of the eyestalk (Crane, 1975).
173. Eyestalk is thin (0) or thick (1) (Rathbun, 1900a; Dai and Yang, 1991).
174. Base of front width is less than (0) or greater than (1) the diameter of the eyestalk (Crane, 1975).
175. Eye shape is round (0) or elongate (1).
176. Eye length is longer than half of the eyestalk (0) or shorter than half of the eyestalk (1).
177. Suborbital crenulations are evenly sized (0) or largest at outer margin (1).
178. Suborbital crenulations are small (0) or large (1) (Crane, 1975).
179. Suborbital crenulations are fused/missing from the entire margin (0) or run the full length of the margin (1) (Collins *et al.*, 1984).
180. Floor of orbit without (0) or with (1) a row of setae running behind the crenulations.
181. Floor of orbit without (0) or with (1) a line of accessory granules behind crenulations (George and Jones, 1982; von Hagen and Jones, 1989).
182. Floor of orbit without (0) or with (1) a ridge.
183. Floor of orbit without (0) or with (1) tuberculation.
184. Floor of orbits without (0) or with (1) numerous setae.
185. Frontal margin is thin (0) or thick (1).

APPENDIX II. CHARACTER LIST. Continued.

186. Frontal groove does not (0) or does (1) extend onto frontal V (George and Jones, 1982).
187. Frontal V is deep and narrow (0) or wide and shallow (1) (George and Jones, 1982).
188. Suborbital margin is rolled out (0) or erect (1) (Crane, 1975).
189. Orbital region without (0) or with (1) a tuft of setae below the anterolateral angle.
190. Outer corner or suborbital margin is not (0) or is (1) an upward crest.
191. Outer corner of suborbital margin without (0) or with (1) a square notch.
192. General shape of carapace from dorsal view is square (0) or trapezoidal (1).
193. Carapace without (0) or with (1) pile.
194. Vertical lateral margin of carapace extends subdorsally (0) or to dorsal surface (1).
195. Front width is narrow (0) or broad (1).
196. Carapace convexity is gently rounded (0), flat (1), or strongly convex (2).
197. Slope of orbits is straight/slightly oblique (0) or strongly oblique (1).
198. Anterolateral margins of carapace are absent (0) or present (1).
199. Anterolateral margins of carapace are convergent (0), parallel (1), or divergent (2).
200. Anterolateral margins of carapace are short (0) or long (1).
201. Anterolateral angles of carapace shape is acute (0) or square (1) (Bairagi and Misra, 1988).
202. Anterolateral angles point toward the front (0), at an angle (1), or to the side (2).
203. Anterolateral/dorsolateral junction of carapace is curved (0) or sharply angled (1).
204. Dorsolateral margins of carapace are absent (0) or present (1) (George and Jones, 1982).
205. Dorsolateral margins of carapace are short (0) or long (1).
206. Dorsolateral margins of carapace are curved (0) or straight (1) (Thurman, 1979).
207. Dorsolateral margins converge slightly (0) or strongly (1) (Thurman, 1979).
208. Dorsolateral margin spines are absent (0) or present (1) (Crane, 1975).
209. Dorsolateral margins of carapace consist of a microscopically beaded line of tubercles (0) or large, widely spaced tubercles (1) (von Hagen and Jones, 1989).
210. Posterolateral striae are absent (0), 1 pair (1), or 2 pair (2) (George and Jones, 1982; von Hagen, 1984).
211. Posterolateral striae are without (0) or with (1) hairs (von Hagen, 1980).
212. Posterolateral striae are without (0) or with (1) tubercles (George and Jones, 1982).
213. Anterior margin of front of carapace is faint (0) or distinct (1) (Crane, 1975).
214. Caparace is smooth (0) or rough (1) (Thurman, 1979).
215. Carapace without (0) or with (1) a row of setae running directly beneath the anterolateral and vertical-lateral margins.
216. Large tubercle absent (0) or present (1) at anterolateral–dorsal-lateral junction.
217. Large tubercle absent (0) or present (1) at posterior end of dorsal-lateral margins.
218. 3rd and 4th segments of the abdomen are distinct (0) or fused (1).
219. 4th and 5th segments of the abdomen are distinct (0) or fused (1).
220. 5th and 6th segments of the abdomen are distinct (0) or fused (1).
221. Specialized pleonal clasping apparatus is absent (0) or present (1) (Guinot, 1979).
222. Gonopod has no/slight (0) or strong (1) torsion.
223. Gonopod thumb is absent (0) or present (1).
224. Gonopod thumb is a flat shelf (0), ends below the flange base (1), or ends above the flange base (2).
225. Gonopod flanges are absent (0) or present (1).
226. Anterior flange of gonopod is small (0) or large (1).
227. Posterior flange of gonopod is small (0) or large (1).
228. Anterior flange of gonopod ends at pore (0) or above pore (1).
229. Posterior flange of gonopod ends at pore (0) or above pore (1).
230. Gonopod flange without (0) or with (1) chitinous spine.
231. Gonopod tip is not (0) or is (1) calcified.
232. Gonopod tip is a blunt (0) or a projecting tube (1).
233. Inner process of gonopod is a sharp spine (0), fleshy and tumid (1), or a flat triangular shelf (2).
234. Gonopod without (0) or with (1) large flat projection below the base of the tube.
235. Gonopod without (0) or with (1) a tubercle at the base of the anterior flange.
236. Gonopod without (0) or with (1) tubercle on inner edge of the pore.

## APPENDIX III. DATA MATRIX.

Data matrix used in the analysis of fiddler crabs. ? = missing data; N = unscorable/inapplicable conditions; P = polymorphism.

| | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000001 | 1111111111 | 1111111111 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0000000001 | 1111111112 | 2222222223 | 3333333334 | 4444444445 | 5555555556 | 6666666667 | 7777777778 | 8888888889 | 9999999990 | 0000000001 | 1111111112 |
| | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 |
| *Uca annulipes* | 0100011100 | 0000120010 | 0N10001100 | 0000001110 | 0001100010 | 0011100001 | 0N00101000 | 1000011111 | 11110NN00N | 0000000000 | N001101100 | 0100000000 |
| *Uca arcuata* | 0110011100 | 0000100000 | 1110011100 | 0000001110 | 0111101111 | 1011000000 | 1100101000 | 1011001011 | 1101101110 | 0000100000 | N011111110 | 0000000000 |
| *Uca argillicola* | 1110011100 | 0000110010 | 1010001100 | 0000001110 | 0111101011 | 000NNNN001 | 0N00001000 | 0001001111 | 11000NN011 | 0010001010 | N011111111 | 0100100000 |
| *Uca batuenta* | 0100011100 | 0000110011 | 1110001000 | 0000010110 | 00110NN010 | 0011101000 | 0N01100000 | 1001000011 | 01110NN00N | 0000000000 | N011101100 | 0100011011 |
| *Uca beebei* | 0110011100 | 0000111111 | 1110001100 | 0000001111 | 00010NN010 | 0011001000 | 0N01100000 | 0000001011 | 01110NN00N | 0000001000 | N001101100 | 0111100000 |
| *Uca bellator* | 1100011100 | 0000111110 | 1110011100 | 1010001111 | 0001101011 | 1011000001 | 0N01100000 | 1001001011 | 111110010N | 0000101100 | N011101100 | 0000000100 |
| *Uca bengali* | 0110011100 | 0011110011 | 1010001100 | 0010001111 | 0111100010 | 0011000000 | 0N01001010 | 0011011111 | 10010NN00N | 0000001000 | N001111111 | 0100000000 |
| *Uca borealis* | 00N0011000 | 0000110011 | 0N11011110 | 0000101110 | 11110NN111 | 1011100001 | 0N01101001 | 1000011011 | 110111100N | 0100000100 | N001101000 | 1000000000 |
| *Uca brevifrons* | 1110011100 | 0000100011 | 1110000100 | 0000001110 | 01110NN011 | 0011000011 | 0N01101000 | 0001011111 | 11110NN00N | 0010000000 | N000000001 | 0100000100 |
| *Uca burgersi* | 0110011100 | 0000100011 | 1010001100 | 0100010111 | 0111100011 | 0011011111 | 0N01101000 | 0000011111 | 11110NN010 | 0010000000 | N000000001 | 0100011111 |
| *Uca capricornis* | 1110011100 | 0000100010 | 1110011100 | 0000001110 | 0111101111 | 1011000000 | 1100100000 | 1000001011 | 1101110111 | 0000000100 | N011111110 | 0000000000 |
| *Uca chlorophthalmus* | 0110011000 | 0000110010 | 1010001010 | 0000001110 | 1011101010 | 0010000011 | 1000010110 | 0111011111 | 11010NN010 | 0000000000 | N011101111 | 0100000000 |
| *Uca coarctata* | 0110011100 | 0000100010 | 1010011110 | 0010001001 | 0111101111 | 1011000000 | 1100100000 | 1011000011 | 110110110N | 0000000000 | N011111110 | 0000000000 |
| *Uca coloradensis* | 0110011100 | 0000110011 | 1010001100 | 0000001110 | 00110NN010 | 0011001001 | 0N00100000 | 0001011111 | 10110NN00N | 0010000110 | N000000001 | 0100000000 |
| *Uca crassipes* | 0110011000 | 0000110010 | 1010001010 | 0000001110 | 1011101010 | 0010000011 | 1000101010 | 0001011111 | 11010NN010 | 0000000000 | N011111111 | 0100000000 |
| *Uca crenulata* | 0100011100 | 0000110011 | 1010001100 | 0000001110 | 00110NN010 | 0011001001 | 0N00100000 | 0001011111 | 11110NN00N | 0010000110 | N001101101 | 0100000000 |
| *Uca cumulanta* | 1110011100 | 0000110010 | 1010001100 | 0000000110 | 00110NN010 | 0011001001 | 0N01101000 | 0000010111 | 10110NN00N | 0000000000 | N011101101 | 0100000000 |
| *Uca dampieri* | 0100011000 | 0000120011 | 0N11011010 | 0000101110 | 11110NN111 | 1011000001 | 0N01000000 | 1000011011 | 1101110010 | 0100000110 | N000001100 | 0000000000 |
| *Uca deichmanni* | 0100011100 | 0000120011 | 0N10001100 | 0000000110 | 00010NN011 | 1011001001 | 0N00000000 | 1000011111 | 01110NN00N | 0000000110 | N000000000 | 0100000000 |
| *Uca demani* | 0110011100 | 0000120010 | 1110011100 | 0000001111 | 0111101111 | 1010000001 | 1100000000 | 1010001011 | 1100101111 | 0000100110 | N011111110 | 0000000000 |
| *Uca dorotheae* | 0100011100 | 0000120011 | 1010001100 | 0000001111 | 00010NN010 | 0011001001 | 0N01100000 | 1000001011 | 11110NN00N | 0000000000 | N000000000 | 0111100000 |
| *Uca dussumieri* | 1110011100 | 0000110011 | 1010011100 | 0000001111 | 0111110111 | 1011000001 | 1101100000 | 1000001111 | 1101111111 | 0000000100 | N011101100 | 0000000000 |
| *Uca ecuadoriensis* | 1110011100 | 0000100011 | 1010001100 | 0100001110 | 0011100010 | 0010100111 | 0N01101000 | 0000011110 | 01010NN010 | 0010000000 | N011101101 | 0100011111 |
| *Uca elegans* | 1100011100 | 0000120010 | 1010011100 | 1000001011 | 0111110011 | 1011000001 | 0N00100000 | 0000001011 | 1112101111 | 0000100100 | N000001100 | 0000000000 |
| *Uca festae* | 0110011100 | 0000110011 | 1010001100 | 0100001111 | 00010NN010 | 0011001001 | 0N00000000 | 1001001010 | 00120NN00N | 0010000100 | N001101100 | 0100000000 |
| *Uca flammula* | 0110011100 | 0000110010 | 1010011110 | 0000001110 | 0111101111 | 1011000001 | 1100100000 | 1001000011 | 110210110N | 0000000000 | N011111110 | 0000000000 |
| *Uca forcipata* | 1110011100 | 0000110011 | 1110011100 | 0000001111 | 0111101111 | 1011000001 | 1101001000 | 0010001011 | 110110110N | 0000100000 | N011111110 | 0000000100 |
| *Uca formosensis* | 0101011000 | 0000110011 | 1010011100 | 0000001110 | 1111100111 | 1010000001 | 0N00100000 | 1001011011 | 111110000N | 0000000110 | N011111110 | 0000000000 |
| *Uca galapagensis* | 1110011100 | 0000100011 | 1010001100 | 0100011110 | 0111100011 | 0011001101 | 0N01101000 | 0000011111 | 11110NN010 | 0010000000 | N011111111 | 0100001111 |
| *Uca herradurensis* | 1110011100 | 0000110011 | 1010001100 | 0100011110 | 0111100011 | 0011001101 | 0N01101000 | 0000011111 | 11110NN010 | 0010000000 | N011111111 | 0100011111 |
| *Uca hesperiae* | 0100011000 | 0000120011 | 0N11001110 | 0000101110 | 11110NN111 | 1011100001 | 0N01101001 | 1001011011 | 111111100N | 0100000000 | N001101100 | 1000000000 |
| *Uca heteropleura* | 0100011010 | 0000110011 | 1010011101 | 0100001111 | 01010NN111 | 1011100000 | 0N00001000 | 0010110111 | 111110100N | 0000001010 | N011101100 | 0000000000 |
| *Uca hirsutimanus* | 1110011100 | 0000101110 | 1110011100 | 1110001111 | 0111111011 | 0011000001 | 0N00100000 | 1000001011 | 111111110N | 0000100000 | N011111100 | 0000000000 |
| *Uca inaequalis* | 1110111100 | 0000110011 | 1010001100 | 0000001111 | 00010NN111 | 0011000000 | 0N00100000 | 1000001011 | 10100NN00N | 1000000000 | N001101110 | 0100100011 |
| *Uca insignis* | 00N0011010 | 1000100011 | 0N10011110 | 0000100110 | 01010NN111 | 1011100000 | 0N10000000 | 1000011111 | 101211100N | 0100011001 | 1011101100 | 0000011111 |
| *Uca intermedia* | 0100011010 | 0000110011 | 1110011101 | 0100001111 | 01000NN111 | 1011000000 | 0N10001000 | 0010101010 | 111011100N | 0000001010 | N011101100 | 0000000000 |
| *Uca inversa* | 0110011000 | 0000120010 | 0N10001100 | 1000001110 | 10110NN010 | 000NNNN011 | 1000100000 | 1010011111 | 01110NN010 | 0000000100 | N000000001 | 0100000000 |
| *Uca lactea* | 0100011100 | 0000120010 | 1010001100 | 0000001110 | 0001100010 | 0011000001 | 0N00100000 | 1000001111 | 11110NN00N | 0000000010 | N000001100 | 0100000000 |
| *Uca latimanus* | 0100011100 | 0000120000 | 0N10001100 | 0000001111 | 0111100111 | 100NNNN000 | 0N00000000 | 0000011111 | 11100NN00N | 0000001110 | N000000001 | 0100000000 |
| *Uca leptodactyla* | 0100011100 | 0000120010 | 0N10001100 | 0010000111 | 00010NN010 | 0011001000 | 0N00000000 | 1001010111 | 10120NN00N | 0000000000 | N000000001 | 0100000000 |
| *Uca limicola* | 1100011100 | 0000110010 | 1010001100 | 0110000111 | 00010NN010 | 0011001001 | 0N00100000 | 1000011111 | 10110NN00N | 0000000000 | N000000001 | 0100000000 |
| *Uca longidigitum* | 1100011100 | 0000110010 | 1010011100 | 1010001011 | 00000NN010 | 0010010001 | 0N01100000 | 1000001011 | 11120NN10N | 0000100000 | N011101100 | 0000000000 |
| *Uca major* | 0100011010 | 0000100011 | 0N10011101 | 0000001110 | 01010NN111 | 1011101001 | 0N10100000 | 1000110111 | 111111100N | 0000001110 | N001101100 | 0000000000 |
| *Uca maracoani* | 00N0011010 | 1000100011 | 0N10011110 | 0000101110 | 01010NN111 | 1011100000 | 0N10000000 | 1000011111 | 101211100N | 0100011001 | 1011101100 | 0000011111 |
| *Uca marguerita* | 0110111100 | 0000110011 | 1010001100 | 0110011111 | 0111100011 | 0011011101 | 0N01101000 | 0000011111 | 11010NN010 | 0010000000 | N011111111 | 0100011111 |
| *Uca minax* | 0110011100 | 0000110011 | 1010001100 | 0000011010 | 01110NN011 | 0011010100 | 0N01101000 | 0000011111 | 11110NN00N | 0010000000 | N000000001 | 0000001010 |
| *Uca mjoebergi* | 0100011100 | 0000120010 | 1010001100 | 0000001110 | 0001100010 | 0011100001 | 0N00100000 | 1000001111 | 11110NN00N | 0000000010 | N001101100 | 0100000000 |
| *Uca mordax* | 1110011100 | 0000110011 | 1010001100 | 0100011110 | 0111100011 | 0011010111 | 0N01101000 | 0000011111 | 11010NN010 | 0010000000 | N000000001 | 0100011111 |
| *Uca neocultrimana* | 0100011000 | 0000110011 | 0N11011110 | 0000101110 | 11110NN111 | 1011100001 | 0N01101001 | 0001010011 | 110111100N | 0100000110 | N000000000 | 1000000000 |
| *Uca oerstedi* | 0100011100 | 0010110011 | 1110001100 | 0010001111 | 01110NN111 | 1011101001 | 0N00100000 | 1000001011 | 11110NN00N | 0000000000 | N001101110 | 0100000100 |
| *Uca ornata* | 0100011010 | 1100100011 | 0N10011110 | 0000101111 | 00010NN111 | 0011100000 | 0N00000000 | 0000011111 | 101211100N | 0100011001 | 1011101100 | 0000001110 |
| *Uca panacea* | 0110011100 | 0000110010 | 1010001100 | 0000001110 | 0011100011 | 100NNNN001 | 0N01101000 | 0000011111 | 1111100010 | 0010000100 | N000000001 | 0101100000 |
| *Uca panamensis* | 1100011100 | 0000000011 | 0N10001100 | 0000000010 | 00000NN00N | N00NNNN100 | 0N00100000 | 0000000000 | 00010NN00N | 0000000000 | N000000000 | 0100000000 |
| *Uca paradussumieri* | 1010011100 | 0000100011 | 1010011100 | 0010101111 | 0111111111 | 1011100001 | 1101100000 | 1001001110 | 0102111111 | 0000000000 | N001101100 | 0000000100 |
| *Uca perplexa* | 0100011100 | 0000110010 | 1010001100 | 0000001110 | 0001100010 | 0011100001 | 0N00101010 | 1001011111 | 11010NN00N | 0100000000 | N001101100 | 0100000000 |
| *Uca polita* | 1110011100 | 0000101110 | 1010011100 | 1010001111 | 00010NN010 | 0010010001 | 0N00100000 | 1000001011 | 11110NN10N | 0000000000 | N011101100 | 0000000000 |
| *Uca princeps* | 0100011010 | 0000110011 | 1010011100 | 1000001111 | 01000NN111 | 1011100000 | 0N10100000 | 1000110111 | 111110100N | 0000001010 | N001101100 | 0000000000 |
| *Uca pugilator* | 0110011100 | 0000110010 | 1010001100 | 0000001110 | 0011100011 | 100NNNN001 | 0N01101000 | 0000011111 | 1111100010 | 0010000100 | N000000000 | 0111100000 |

APPENDIX III. EXTENDED

| 1111111111 | 1111111111 | 1111111111 | 1111111111 | 1111111111 | 1111111111 | 1111111111 | 1111111112 | 2222222222 | 2222222222 | 2222222222 | 222222 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2222222223 | 3333333334 | 4444444445 | 5555555556 | 666666666 | 7777777777 | 8888888889 | 9999999990 | 0000000001 | 1111111112 | 2222222223 | 333333 |
| 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 123456 |
| 0000000000 | 0011011101 | 1101011101 | 0001000100 | 0000000011 | 0111011110 | 0000101110 | 0101120100 | 0001110001 | 0010000000 | 1011111110 | 002000 |
| 0000000000 | 1011111101 | 1101011100 | 0001100110 | 0000000001 | 1100010000 | 0000110011 | 0100020100 | 0101101000 | NN10000000 | 0011101000 | 000000 |
| 0000000000 | 1111011101 | 1101011101 | 0001000100 | 0100000011 | 0011011011 | 0000111010 | 0101101100 | 0101111002 | 0010000000 | 1011111110 | 112000 |
| 0110000000 | 0000000000 | 0100011101 | 0001000100 | 0000000011 | 0011011000 | 0000111100 | 0100100111 | 1101101001 | 0010000000 | 1010100110 | 112000 |
| 0000000000 | 1111111111 | 1100111101 | 0001100110 | 0100000011 | 1011011111 | 0000111010 | 0100100120 | 1211100001 | 0010000111 | 10100NNNN0 | 112000 |
| 1001010000 | 1111011101 | 11011101NN | 00NN00NN00 | NN00000000 | 0101010000 | 1100111010 | 0100000101 | 0101101001 | 0110000000 | 00120NNNN0 | 110000 |
| 0000000000 | 1011111101 | 1101111101 | 0001000100 | 0100000011 | 0011011110 | 0000101110 | 0101101100 | 0101101000 | NN10000000 | 1012100110 | 112000 |
| 0000000000 | 0010011001 | 10011001NN | 11NN11NN11 | NN00000001 | 0101010110 | 0000110110 | 0100000100 | 0001010000 | NN10000000 | 0012111000 | 001000 |
| 1001000000 | 0001000100 | 0100011101 | 0001000100 | 0000100011 | 1011011011 | 0001111010 | 0101100121 | 1011100001 | 0010000000 | 1012110000 | 001000 |
| 1111100000 | 0001000100 | 0100011101 | 0001000100 | 0100100011 | 1011011111 | 0001111010 | 0101100121 | 1001111002 | 0010000000 | 1011111100 | 001000 |
| 0000000000 | 1111111111 | 1101111100 | 1000100010 | 0000000001 | 0100010000 | 0000110011 | 0100000100 | 0101101000 | NN10000000 | 0012110000 | 001000 |
| 0000000000 | 0111011101 | 1101111100 | 0000000000 | 0000000011 | 0101010010 | 0000111110 | 0101100100 | 0001101001 | 0110000000 | 10110NNNN0 | 112000 |
| 0000000000 | 1011101110 | 1100011101 | 1001100110 | 0000000001 | 0100010000 | 1000110011 | 0100000100 | 0101101000 | NN10000000 | 00120NNNN0 | 110000 |
| 0000000000 | 1111111101 | 1101111101 | 0001000100 | 0000000011 | 1011011111 | 0000111110 | 0101100121 | 0011111001 | 0010100000 | 1011111110 | 112000 |
| 0000000000 | 0111011101 | 1101111101 | 0001000100 | 0000000011 | 0101010010 | 0000111110 | 0101100100 | 0001101001 | 0110000000 | 10110NNNN0 | 112000 |
| 0000000000 | 1111111101 | 1101111101 | 0001000100 | 0000000011 | 1011011111 | 0000111110 | 0101100111 | 0011101001 | 0010100000 | 1012111110 | 112000 |
| 0000000000 | 0001000100 | 0100011101 | 0001000100 | 0100000011 | 0011011110 | 0000111110 | 0101100100 | 1011111001 | 0010100000 | 10110NNNN0 | 112001 |
| 0000000000 | 0010011001 | 10011001NN | 11NN11NN11 | NN00000001 | 0101010110 | 0000110110 | 0101000100 | 0001010000 | NN10000000 | 0111100000 | 001000 |
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| 0000000000 | 1111111101 | 1101111101 | 0001100110 | 0000000001 | 0100010001 | 1010110011 | 0100000100 | 0101101000 | NN10000000 | 0011111100 | 001000 |
| 0000000000 | 0111111111 | 1101111101 | 0001000100 | 0000000011 | 1011011110 | 0000111100 | 0101100110 | 1211010001 | 0010000111 | 10100NNNN0 | 112000 |
| 0000000000 | 0011111111 | 1101111101 | 0001000100 | 0000000001 | 1100010000 | 0000100011 | 0100000100 | 0101101000 | NN10000000 | 0012110000 | 001000 |
| 1111110000 | 0011001111 | 11111101NN | 00NN00NN00 | NN00100011 | 0011010011 | 0000101110 | 0111100121 | 1001111001 | 0010000000 | 1012111000 | 001010 |
| 0000000000 | 0011011101 | 1101111101 | 1001100100 | 0000000000 | 0101010000 | 0000111010 | 0100000101 | 0101101000 | NN10000000 | 0011?????0 | 110000 |
| 0000000000 | 1111111111 | 1101111100 | 0001100110 | 0000000011 | 1011011110 | 0000101110 | 0101100121 | 1111101001 | 0110100000 | 10110NNNN0 | 112000 |
| 0000000000 | 1011101110 | 1100011101 | 1001100110 | 0000000001 | 1100010000 | 0000110011 | 0100000100 | 0101101000 | NN10000000 | 00120NNNN0 | 110000 |
| 1001010000 | 1011111111 | 1101011101 | 0001000100 | 0000000001 | 0100010011 | 0000110011 | 0100001100 | 0101101000 | NN10000000 | 0012100000 | 010000 |
| 0000000000 | 1011111111 | 11011101NN | 00NN00NN00 | NN00000001 | 0101010100 | 0000110110 | 0101000111 | 0001101000 | NN10100000 | 0011101000 | 001000 |
| 1111110000 | 0001000100 | 0101011101 | 0001000100 | 0100100011 | 1011010111 | 0000111010 | 0101100121 | 1001111002 | 0010000000 | 1012111010 | 001000 |
| 1111110000 | 0001000100 | 0101011101 | 0001000100 | 0100100011 | 1011010111 | 0000101000 | 0101100121 | 1001111002 | 1010000000 | 1012111100 | 001000 |
| 0000000000 | 0011011101 | 1101111101 | 1100110011 | 0011000001 | 0101010110 | 0000110110 | 0101000100 | 0001010000 | NN10000000 | 0111101000 | 001000 |
| 0000000000 | 0011111111 | 11111101NN | 00NN00NN00 | NN0001PP00 | 0100010110 | 0000110110 | 0100000100 | 1101100000 | NN10000000 | 000N100000 | 01N100 |
| 0000000000 | 0111011101 | 1101111101 | 0001000100 | 0000000001 | 0101010000 | 1100111010 | 0100000100 | 0101101001 | 0010000000 | 00110NNNN0 | 110000 |
| 0110000000 | 1011111111 | 1100111101 | 0001000100 | 0000000011 | 0011010000 | 0000111000 | 0111101101 | 1111111001 | 0110000000 | 10100NNNN0 | 112001 |
| 1111110000 | 0000000000 | 00000001NN | 00NN00NN00 | NN00010?00 | 1100010110 | 0000110110 | 0101010110 | 0101100000 | NN11011000 | 000N11N1N0 | 001000 |
| 0000000000 | 0011001100 | 11001001NN | 00NN00NN00 | NN00010P00 | 0100010110 | 0000110110 | 0101000110 | 1111100000 | NN10000000 | 010N100000 | 01N000 |
| 0000000000 | 0111011101 | 1101111101 | 0001000100 | 0000000011 | 0101010000 | 0000111110 | 1100100100 | 0001001000 | NN10000000 | 100N111000 | 112000 |
| 0000000000 | 0011001100 | 1101111101 | 0001000100 | 0000000011 | 0111011110 | 0000101110 | 0101120100 | 0101110001 | 0010100000 | 1012111110 | 002000 |
| 0000000000 | 0111011101 | 1101111101 | 0001000100 | 0100000011 | 1011011111 | 0000111010 | 0101100120 | 1001110001 | 0010000111 | 1011111000 | 002000 |
| 0000000000 | 0001000100 | 0101111101 | 0101010101 | 0101000011 | 0011011111 | 0000111100 | 0101120120 | 1101100001 | 0010000111 | 1011111110 | 002000 |
| 0000000000 | 0001000100 | 0101101101 | 1101110111 | 0101000011 | 0011011111 | 0000111110 | 0101100111 | 1211110001 | 0010100111 | 10110NNNN0 | 112000 |
| 0000000000 | 0011001100 | 1100111101 | 0001000100 | 0000000000 | 0101010000 | 0100111010 | 0100000101 | 0101001000 | NN10000000 | 00100NNNN0 | 110000 |
| 0000000000 | 0111011101 | 11011101NN | 00NN00NN00 | NN00010000 | 0100010110 | 0000110110 | 0101000100 | 0101100000 | NN10100000 | 010N100010 | 01N000 |
| 1111110000 | 0000000000 | 00000001NN | 10NN10NN10 | NN10010P00 | 1100010110 | 0000110110 | 0101010110 | 0101100010 | NN11001000 | 000N11N1N0 | 001000 |
| 1111110000 | 0011001100 | 1100011101 | 0001000100 | 0100100011 | 1011011111 | 0001111010 | 0101100121 | 1001111002 | 0010000000 | 1011111000 | 001000 |
| 0101000000 | 0000000000 | 0000001111 | 1111111111 | 1111100011 | 1011010111 | 0000101010 | 0101100121 | 1001111001 | 1010000000 | 1011111010 | 002000 |
| 0000000000 | 0011001101 | 1101011101 | 0001000100 | 0000000011 | 0111011110 | 0000101110 | 0101120100 | 0101110001 | 0010000000 | 1010111110 | 002000 |
| 1111100000 | 0001001100 | 1100111101 | 0001000100 | 0000100011 | 1011011111 | 0001111010 | 0111100121 | 1001101001 | 0010000000 | 1011111000 | 002000 |
| 0000000000 | 0011001101 | 11011101NN | 11NN11NN11 | NN00000001 | 0101010010 | 0000110110 | 0100000100 | 0001010000 | NN10000000 | 0012111000 | 001000 |
| 1000010000 | 1111111111 | 1101111101 | 0001000100 | 0000100011 | 0011011110 | 0000111010 | 0111100121 | 1011101001 | 0110100000 | 10100NNNN0 | 112000 |
| 1101111110 | 0000000000 | 00000001NN | 00NN00NN00 | NN00010000 | 1100010100 | 0000110110 | 0100010100 | 0101100010 | NN11001000 | 000N100000 | 010000 |
| 0000000000 | 0001111111 | 1101111101 | 1101110111 | 0111100011 | 1011010111 | 0000111010 | 0101100121 | 1001111001 | 0110100000 | 1011?????0 | 01?000 |
| 0000000000 | 1111111111 | 1111111100 | 0000000000 | 0000000011 | 1011011111 | 0000101100 | 0101110111 | 0001101001 | 0010100000 | 1011111000 | 001000 |
| 1001010000 | 1111111101 | 1101011100 | 1000100010 | 0000000001 | 0100011000 | 0000110010 | 0100000100 | 0101011000 | NN10000000 | 0012110001 | 001000 |
| 0000000000 | 0011001100 | 1101111101 | 0001000100 | 0000000011 | 0111011110 | 0000101110 | 0101120100 | 0101110001 | 0010000000 | 1112111110 | 002000 |
| 0000000000 | 0011001100 | 1101111100 | 1000100010 | 0000000000 | 0101010000 | 0100111010 | 0100000101 | 0011101001 | 0010000000 | 00100NNNN0 | 110000 |
| 0000000000 | 0011111111 | 11111101NN | 00NN00NN00 | NN00010P00 | 1100010110 | 0000110110 | 0101000100 | 0001101000 | NN10000000 | 0011110000 | 000100 |
| 0000000000 | 1111111111 | 1101111101 | 1101110111 | 0111100011 | 1011010111 | 0000111010 | 0101100121 | 1001101001 | 0110100000 | 1011111110 | 012000 |

APPENDIX III. DATA MATRIX. Continued.

| | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000000 | 0000000001 | 1111111111 | 1111111111 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0000000001 | 1111111112 | 2222222223 | 3333333334 | 4444444445 | 5555555556 | 6666666667 | 7777777778 | 8888888889 | 9999999990 | 0000000001 | 1111111112 |
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| *Uca pugnax* | 1110111100 | 0000110011 | 1010001100 | 0100011110 | 0111100011 | 0010010101 | 0N01100000 | 0000011111 | 11110NN00N | 0010000000 | N000000001 | 0100011111 |
| *Uca rapax* | 1110011100 | 0000100011 | 1010001100 | 0110001110 | 0111100011 | 0011011101 | 0N01101000 | 0000011111 | 11110NN010 | 0010000000 | N011111111 | 0100011111 |
| *Uca rhizophorae* | 1110011100 | 0000100010 | 1010011100 | 0010001111 | 0111101111 | 1011000001 | 1001101000 | 1000000011 | 100111110N | 0000100000 | N011111110 | 0000000000 |
| *Uca rosea* | 0110011100 | 0000100011 | 1010011100 | 0000001111 | 0111101111 | 1011000000 | 1000101000 | 0011001011 | 1101111111 | 0000100010 | N011111110 | 0000000000 |
| *Uca saltitanta* | 0100011100 | 0000010011 | 1110001100 | 0000001110 | 00010NN011 | 1010000000 | 0N00100000 | 1001000011 | 10110NN00N | 1000001000 | N000000000 | 0100001011 |
| *Uca seismella* | 0100011100 | 0000101110 | 1110011100 | 1010001111 | 0101101011 | 0011100001 | 0N01100000 | 1001001011 | 11110NN10N | 0000001000 | N011101100 | 0000000000 |
| *Uca signata* | 0100011100 | 0000110010 | 1010011100 | 1000001111 | 0101100011 | 1011010001 | 0N01100000 | 1001001011 | 111110010N | 0000101100 | N011111110 | 0000000000 |
| *Uca sindensis* | 0110011000 | 0000110010 | 1010001000 | 1000001110 | 10010NN010 | 000NNNN011 | 1000100000 | 0000011111 | 11110NN010 | 0000000000 | N011111110 | 0100000000 |
| *Uca speciosa* | 1110011100 | 0000110011 | 1010001100 | 0110001110 | 00110NN010 | 0011101001 | 0N00100000 | 0001011111 | 11110NN00N | 0000000000 | N000001101 | 0100011111 |
| *Uca spinicarpa* | 1110011100 | 0000110011 | 1010001100 | 0101001110 | 00110NN010 | 0011101001 | 0N00100000 | 0001011111 | 11110NN00N | 0000000000 | N000001101 | 0100011111 |
| *Uca stenodactylus* | 0110011100 | 0000111111 | 1110001100 | 0000001111 | 0001100010 | 0011001000 | 0N01100000 | 0000001111 | 11120NN00N | 0000000000 | N000000000 | 0100000000 |
| *Uca stylifera* | 00N0011010 | 0000100011 | 0N10011001 | 0000101010 | 01010NN111 | 1011101000 | 0N10100000 | 1000110011 | 111210100N | 0000001001 | 0011101100 | 0000000000 |
| *Uca subcylindrica* | 0110011100 | 0000100011 | 1110001100 | 0000101111 | 1111100111 | 100NNNN001 | 0N01101000 | 0001011111 | 1101101010 | 0010000000 | N000000000 | 0000000000 |
| *Uca tallanica* | 0100111100 | 0000110011 | 1110001100 | 0110001111 | 0111101110 | 0010000001 | 0N01100000 | 1000000011 | 1111111010 | 0000001000 | N011111101 | 0100100100 |
| *Uca tangeri* | 00N1011110 | 1000100011 | 1010011101 | 0000001010 | 00000NN011 | 1011100000 | 0N00000000 | 0000011111 | 11110NN00N | 0000000100 | N000000001 | 0100000000 |
| *Uca tenuipedis* | 0100011100 | 0000110011 | 1110000000 | 0000001010 | 00010NN10N | N00NNNN000 | 0N01100000 | 0000000011 | 11100NN00N | 1000000000 | N000000000 | 0100011011 |
| *Uca terpsichores* | 0110011100 | 0000120000 | 0N10000100 | 0000001110 | 00010NN010 | 0111001000 | 0N00100000 | 0001010110 | 10120NN00N | 0000000000 | N000000000 | 0101100000 |
| *Uca tetragonon* | 0100011000 | 0000110011 | 1011001110 | 0000001110 | 11010NN011 | 1010000011 | 0N01101000 | 0000011011 | 111110100N | 0000000110 | N000000000 | 0100000000 |
| *Uca thayeri* | 1110111100 | 0000110011 | 1010001100 | 0111001111 | 0111100110 | 0011000001 | 0N00101000 | 1001011111 | 11120NN010 | 0010000000 | N011111110 | 0100011111 |
| *Uca tomentosa* | 1100011100 | 0000110010 | 1010001100 | 0110011111 | 0111100111 | 0010001001 | 0N00100000 | 1000001011 | 11000NN010 | 1000001010 | N01111111? | 0100000000 |
| *Uca triangularis* | 0110111100 | 0011110011 | 1010001100 | 0010001111 | 0111100010 | 0011000000 | 0N01001010 | 0011011111 | 10010NN010 | 0000001000 | N000111111 | 0100000000 |
| *Uca typhoni* | 0110011100 | ?0001????? | 11?0011100 | 0000001110 | 0111101111 | 1010000001 | 1101100000 | 100000?011 | 1100101111 | 0000100110 | N011111110 | 0000000000 |
| *Uca umbratila* | 1110111100 | 0000100011 | 1010001100 | 0111001111 | 0111100110 | 0010000001 | 0N00101000 | 1001001011 | 11110NN010 | 0010000000 | N011111110 | 0100011111 |
| *Uca uruguayensis* | 0110011100 | 0000110011 | 1010001100 | 0110001111 | 00110NN010 | 0010000001 | 0N01000000 | 0001011111 | 11000NN00N | 0011001000 | N001101101 | 0100000000 |
| *Uca urvillei* | 0110011100 | 0000100010 | 1110011110 | 0000001110 | 01110NN111 | 1011000001 | 1100100000 | 1001000110 | 1002100110 | 0000000000 | N011111110 | 0000000000 |
| *Uca virens* | 1110011100 | 0000100011 | 1010001100 | 0100011110 | 0011100011 | 0011010101 | 0N01101000 | 0000011111 | 11110NN00N | 0010000000 | N000001101 | 0100011111 |
| *Uca vocans* | 0100011000 | 0000110011 | 0N11011010 | 0000101110 | 11110NN111 | 1011000001 | 0N01101001 | 1001011011 | 111111100N | 0100000110 | N000001000 | 1000000000 |
| *Uca vocator* | 1110011100 | 0000100011 | 1010001100 | 0100001110 | 0011100010 | 0010100111 | 0N01101000 | 0000011110 | 01010NN010 | 0010000000 | N011101101 | 0100011111 |
| *Uca vomeris* | 0100011000 | 0000120011 | 0N11001010 | 0000101110 | 11110NN111 | 1011000001 | 0N01100000 | 1001011011 | 111111100N | 0100000110 | N000001100 | 1000000000 |
| *Uca zacae* | 0110011100 | 0010110011 | 1010001100 | 0110001111 | 1111101011 | 000NNNN101 | 0N01000000 | 0000000011 | 11100NN010 | 0010000000 | N000000001 | 0100001010 |

Appendix III. Extended.

| 1111111111 | 1111111111 | 1111111111 | 1111111111 | 1111111111 | 1111111111 | 1111111111 | 1111111112 | 2222222222 | 2222222222 | 2222222222 | 222222 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 2222222223 | 333333333 | 44444444445 | 5555555556 | 666666666 | 7777777777 | 88888888889 | 9999999990 | 0000000001 | 1111111112 | 2222222223 | 333333 |
| 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 1234567890 | 123456 |
| 1111000000 | 0011001100 | 1101011101 | 1001100110 | 0100100011 | 0011011111 | 0000111010 | 0101100121 | 1001111002 | 0010000000 | 1011111110 | 002000 |
| 1111110000 | 0001000100 | 0100011101 | 1001100110 | 0100100011 | 1011010111 | 0000111010 | 0101100121 | 1001111002 | 0010000000 | 1011111110 | 001000 |
| 0000000000 | 0011001101 | 1101111101 | 1001100110 | 0000000001 | 0100011000 | 0000100011 | 0100000100 | 0111101000 | NN10000000 | 0012110000 | 001000 |
| 0000000000 | 1011111111 | 1101011100 | 0000000000 | 0000000001 | 0100011000 | 0000110011 | 01000010NN | 02N1111000 | NN10000000 | 0012111000 | 001000 |
| 1111010000 | 0001000100 | 0100011101 | 0001000100 | 0100000011 | 0011011000 | 0000111000 | 0101100121 | 1011100001 | 0110000PPP | 1010111110 | 112000 |
| 0000010000 | 0111011101 | 1101111100 | 0000000000 | 0000000000 | 0101010000 | 0100111010 | 0100000101 | 1001001011 | 0010000000 | 00100NNNN0 | 110000 |
| 0000000000 | 0011001100 | 1101011101 | 0001000100 | 0000000001 | 0101010000 | 1100111010 | 0100000101 | 0101101001 | 0010000000 | 00100NNNN0 | 110000 |
| 0000000000 | 0111011101 | 1101111101 | 0001000100 | 0000000011 | 0101010010 | 0000111110 | 0100100100 | 0001101000 | NN10000000 | 1011111000 | 112000 |
| 1111110000 | 0001000100 | 0101011101 | 1001100110 | 0000100011 | 0011011111 | 0000111110 | 0111100111 | 0011111001 | 0111100000 | 1011111110 | 112000 |
| 1111000000 | 0001000100 | 0101011101 | 1001100110 | 0000100011 | 0011011111 | 0000111110 | 0111100111 | 0011111001 | 0111100000 | 1011111110 | 112000 |
| 0000000000 | 1111111111 | 1111111101 | 0001000100 | 0100000011 | 1011011110 | 0000101010 | 0101100111 | 0111100001 | 0010000111 | 10100NNNN0 | 112000 |
| 0000000000 | 0010001000 | 10001001NN | 00NN00NN00 | NN00011100 | 0100010110 | 0000110110 | 0100000100 | 1101100000 | NN10000000 | 010N100000 | 01N000 |
| 0000000000 | 0001000100 | 0101111101 | 1111111111 | 0100100011 | 0011010111 | 0000111010 | 0101120121 | 1001100002 | 0010000000 | 1010101010 | 001000 |
| 1001010000 | 1111111111 | 1111111101 | 0001000100 | 0000100011 | 0011011110 | 0000111100 | 0111100100 | 1101111001 | 0110000000 | 10100NNNN0 | 112000 |
| 0000000000 | 1011101110 | 11101101NN | 00NN00NN00 | NN00010000 | 1101010110 | 0010111100 | 0101100120 | 1001100000 | NN11000000 | 0011111110 | 001000 |
| 0110000000 | 0001000100 | 0100011101 | 0001000100 | 0000000011 | 0011011100 | 0000111000 | 0101100111 | 1101111001 | 0110000000 | 1010111110 | 002000 |
| 0000000000 | 1111111111 | 1111111101 | 0001000100 | 0100000011 | 1011011111 | 0000111000 | 0101100100 | 0101101002 | 0100000111 | 101111N1N0 | 102000 |
| 0000000000 | 0011001101 | 1101111101 | 1101110000 | 0000000001 | 0101010110 | 0000110110 | 0101000100 | 0001101000 | NN10000000 | 0011111000 | 001000 |
| 1111110000 | 1011111111 | 1101111100 | 1100110011 | 0011000011 | 1111011111 | 0000111110 | 0111100111 | 1101101002 | 0110100000 | 1011111000 | 012000 |
| 0000000000 | ??11111111 | 11011111?? | ??01000100 | 0000000011 | 0011011110 | 0000111000 | 0111100111 | 1111101001 | 0110000000 | 10110NNNN0 | 112000 |
| 0000000000 | 1011111101 | 1101111101 | 0001000100 | 0100000011 | 0011011110 | 1110101110 | 0100101100 | 0101101000 | NN10000000 | 1012100110 | 112000 |
| 0000000000 | 1111111111 | 1101111101 | 1101110111 | 0100000001 | 0100010001 | 1010110011 | 0100000100 | 0101101000 | NN10000000 | 0011110100 | 001000 |
| 1111110000 | 1011111111 | 1101111101 | 1001100110 | 0110000011 | 1111011111 | 0000111110 | 0111100111 | 1101101002 | 0010100000 | 1011111000 | 012000 |
| 0000000000 | 0001000100 | 0100011110 | 0110011001 | 0001100011 | 0011011111 | 0000111000 | 0101100110 | 1011111001 | 0010000011 | 1011111000 | 002000 |
| 0000000000 | 1111111101 | 1101011101 | 1101110010 | 0000000001 | 0100010000 | 1010110011 | 0101000101 | 0101101000 | NN10000000 | 00120NNNN0 | 110000 |
| 1111110000 | 0001000100 | 0100011111 | 1011101110 | 0110100011 | 1011011111 | 0000111010 | 0101100121 | 1001111002 | 0010100000 | 1011111110 | 002000 |
| 0000000000 | 0011001101 | 1101111100 | 1100110011 | 0000000001 | 0101010110 | 0000110110 | 0100000100 | 0001010000 | NN10000000 | 0112111000 | 001000 |
| 1111110000 | 0011001100 | 11001101NN | 10NN10NN10 | NN10100011 | 0011010011 | 0000101110 | 0111100121 | 1001111001 | 1010100000 | 1012111000 | 001010 |
| 0000000000 | 0011001101 | 1101111101 | 1101110011 | 0010000001 | 0101010110 | 0000110110 | 0101000100 | 0001010000 | NN10000000 | 0112111000 | 001000 |
| 0100100000 | 0001000100 | 0100011101 | 0001000100 | 0000100011 | 1011011111 | 0000101010 | 0111101100 | 1001111002 | 0010000000 | 1011111110 | 002000 |