THE COMPARATIVE CLAW MORPHOLOGY, PHYLOGENY, AND BEHAVIOR OF FIDDLER CRABS (GENUS *UCA*)

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Abstract of the Dissertation

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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 organism, having a large major claw containing a third to half of the animal's body mass and a small minor claw. The morphology of major and minor claws varies tremendously across species. These studies are concerned with understanding the phylogenetic history of the genus, describing patterns of claw shape within and across species, and exploring the relationship of claw morphology with behavior and ecology.

The systematic and phylogenetic history of the genus is explored in some detail before a morphological phylogenetic analysis was performed on 88 of the 97 recognized species. These results were compared to a molecular study of 16S ribosomal DNA for 28 species. The results resolve most of the subgeneric taxonomic conflicts and allow one to perform interspecific analyses in a comparative methodological framework.

Geometric morphometrics was used to study claw shape across the genus. Within species, major claws show allometric growth in both shape and size; minor claw growth is isometric. Both major and minor claws are isometric for size and allometric for shape across species; accounting for phylogenetic dependence has little effect on the analyses. There is evidence for evolutionary allometry explaining some of the diversity of claw forms seen within the genus.

Four behaviors are associated with claw use: visual signaling, acoustic signaling, combat, and feeding. The first three are examined with respect to major claw morphology; the later with minor claw morphology. Only combat can explain a significant amount of variation in major claw morphology. Differences in habitat choice are able to explain some variation in minor claw morphology. Species in sandy habitats have minor claws with wider gapes and longer chela than those in muddy habitats.

Dedication

This work is dedicated to Albert and Deborah Rosenberg,
for their love and support…

…to those who have gone before and those who will come after…

…to the continual wonder and amazement that is nature…

…and finally,
to those wonderful little fiddlers.

We may not understand why you do what you do,
but we continue to be
fascinated, delighted, and entranced
by it none the less.

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CHAPTER 1

INTRODUCTION

Attempting to understand how evolution has shaped the morphology of a structure is often confounded by the multiple functions of that structure. The difficulty in understanding all of the functions and how selection may act within this complex web has made understanding the evolution of most morphological characters extremely difficult. One set of characters that have often been recognized to have dual function are those which serve both as signals in sexual selection (ornaments) as well as in direct intrasexual competition (armaments) (Berglund *et al.* 1996). Sexual selection is considered to be one of the most important evolutionary forces (Andersson 1994); it can act indirectly through mate choice or directly through competition. It is invoked to explain sexual dimorphism, the evolution of extravagant morphological features, bright coloration, and complex mating behaviors. All of these are represented in fiddler crabs.

Male fiddler crabs (Brachyura, Ocypodidae, genus *Uca*) show an extreme form of cheliped asymmetry; they have a smaller (minor) claw used for feeding and a larger (major) claw used for waving display and agonistic interactions. The large size of the major claw has been considered a classic example of sexual selection since Darwin (1874). Because the few functions served by the major claw have predictable constraints, it should be possible to study male fiddler crab behavior as a means of understanding how evolution has shaped the major claw.

1.1 WHAT ARE FIDDLER CRABS?

Fiddler crabs are small, intertidal marine crabs of the genus *Uca*. There are currently 97 recognized species, found all around the globe. Although primarily concentrated in the tropics, fiddler crabs can be found deep in the temperate zone, ranging as far north as Massachusetts and as far south as South Africa. They live on sandy beaches, open mudflats, and dense mangroves; one species even lives along rocky shores. They are active during low tide; during this time they feed, construct burrows, fight, and mate. They descend into burrows as high tide approaches and stay safely within until the next low tide. Although primarily diurnal, some species are active at night as well as during the day.

The name *Fiddler Crab* is often misinterpreted as somehow referring to the waving. The name comes from the appearance of the male while feeding; the continual motion of the minor claw from the substrate to the mouth and back to the substrate resembles a violinist moving a bow across a fiddle (the large claw). In much of South America and Mexico, they are known as *Congrejos Violinistas*, which is a direct translation of the English name. In Germany, they are *Winkerkrabbe*, which means "waving crabs." The most poetic general name is Japanese, where they are known as *Siho Maneki*, which means "beckoning for the return of the tide" (Ricketts and Calvin 1948). They have also been called by such colorful names as *Deaf Ear Crabs* in Jamaica (Rathbun 1918; Barnwell 1986) and *Fever Crabs* in Barbados (Jones 1968).

Fiddler crabs are best known to naturalists for the extreme sexual dimorphism and body asymmetry in males. The male fiddler crab has a minor claw used for feeding and a major claw used for display and combat. The major claw is usually 4-5 times longer than the minor claw and contains a third (occasionally as much as half) of the crab's body mass. The major claw is usually brightly colored and conspicuous; often the rest of the crab is as well. Females have two small claws which resemble the minor claw of the male. They are almost always cryptic. Most species have equal numbers of left- and right-handed males (handedness refers to the side with the major claw); a single Indo-West Pacific clade of seven species is predominantly right handed (Barnwell 1982; Jones and George 1982; Shih *et al.* 1999).

Fiddler crabs are specialized deposit feeders. They scoop sediment from the substrate (with the minor claw if male, with both claws if female) and use their mouth parts to scrape organic matter (e.g. algae or diatoms) away from the sand or mud. The remaining inorganic sediment is then dropped as a tiny pellet; these pellets often litter the area around burrows and in some species can be used to determine feeding activity or the gender of the crab. Because they only have one claw with which to feed, male crabs feed longer and scoop faster than do females (Caravello and Cameron 1987; Weissburg 1990, 1992, 1993); once the major claw reaches a certain size, it is an extremely ineffective feeding tool (Merz *et al.* 1999). On very rare occasions male fiddler crabs in a few species have been seen to hunt smaller crabs with the major claw (Koga *et al.* 1995), but this cannot be considered a major or normal component of feeding.

Male fiddler crabs show complex visual and acoustic displays. Males of each species have unique display characteristics that serve a function in both male-male aggression and male-female species recognition and mate choice (Crane 1975; Salmon *et al.* 1978; Hagen 1983, 1984; Pope 1997). In the field, many species can be recognized by their wave pattern alone. Some species are so morphologically similar that they can virtually only be distinguished by display differences.

The two major functions of the major claw, waving and combat, have opposing constraints. Because of its extreme size, one would expect selection for waving display to have reduced the mass of the major claw; it should become a weak, flimsy, gaudy structure, used to get attention but not much else. It has been proposed in the past that combat between male fiddler crabs is completely ritualized and injury results in only rare instances (Huxley 1932; Crane 1967), with display being the driving force in its evolution (Calman 1911; Huxley 1932; Crane 1975). The fact that the major claw retains functionality at all sizes (Levinton and Judge 1993; Levinton *et al.* 1995) and frequently show signs of injury due to intraspecific interactions (J. Christy, personal communication; Powers 1975; Jones 1980), suggests that combat behavior must have played an important role in maintaining the structure of the claw. Furthermore, game theory suggests that selection would support honest signaling in structures which function as both ornaments and armaments (Berglund *et al.* 1996).

The relationship between the major cheliped and predation risk seem to be very dependent on predator type. The primary threat response by a fiddler crab is to run and hide in a burrow; when cornered, fiddler crabs will stand in a threatening posture and (if male) will sometimes attempt to snap at offending objects with their major claw (Crane 1975). Different predators show different preferences in prey choice (Iribarne and Martinez 1999); some prefer females or males missing a major cheliped (Altevogt 1955; Begg 1981; Bildstein *et al.* 1989), some prefer juveniles (Boshe 1982), and others show no preference (Altevogt 1955). Some birds specifically catch fiddler crabs by grabbing the major claw with their beaks (Raut 1943), although males can escape predation by automotizing the claw (Lee and Kneib 1994). Bildstein *et al.* (1989) reported that it took ibises longer to eat male crabs with an intact major cheliped than females or males missing a major cheliped. On the other hand, possession of an enlarged cheliped can make a male crab easier for predators to see or catch (Raut 1943; Crane 1975). If there is an effect of the major claw on predation risk, it is clear that size, and not function, has the greatest effect (Backwell *et al.* 1998). Males may also be more at risk due to increased time spent on the surface feeding and courting (Ens *et al.* 1993; Backwell *et al.* 1998); this is an indirect effect of claw size.

Although all species of fiddler crab show extreme cheliped dimorphism, there is considerable variation in major cheliped morphology and shape among species (e.g. see Crane 1975). While evolutionary allometry (Klingenberg 1996) may play a role in explaining some of the differences in major claw shape among species (Crane 1975; Frith and Brunemeister 1983), it cannot explain all of these differences. The driving force behind claw shape is likely to be functional. Because the major claw is used for only two functions, display and combat, it should be possible to tease apart the importance of these behaviors in controlling claw shape. Because the minor claw is a specialized feeding appendage, there may be morphological correlates between minor claw structure and substrate type (Crane 1975). Other behavioral patterns in *Uca* have shown a strong tendency to follow grades from simple to primitive to complex (Crane 1975; Christy and Salmon 1984) and are related to degrees of terrestriality. A number of morphological characters are correlated with visual display characteristics. For example, thoracic muscle sarcomere length is inversely correlated with the speed and duration of waving (Rhodes 1986); species with lateral waving show more asymmetry in the ambulatories than those with vertical waving (Takeda and Murai 1993). A study of combat and morphology may unveil similar patterns.

> Contrary to my earlier conclusions, it is now clear that interspecific distinctions in combat are numerous enough to make their comparative study highly rewarding. While the differences are not nearly as striking as in display there is no question but that they both illuminate evolutionary trends in species groups and show most interesting steps in the development of combat ritualization. (Crane 1967:74).

1.2 OVERVIEW OF STUDY

The aim of this research was to explore the interspecific relationship between claw variation and behavior across the genus. In order to put the analyses in the proper framework, a genus-wide phylogenetic analysis was necessary. Modern morphometric methods were used to analyze and describe patterns of claw shape within and across species. These shapes were then analyzed with respect to ecological differences in waving display, combat behavior, and habitat choice.

In Chapter 2, I review the systematic and phylogenetic history of fiddler crabs, perform a phylogenetic analysis of the genus based on morphological characters, and discuss the implications these results have on the systematics and biogeographic history of *Uca*.

In Chapter 3 (Rosenberg 1997), I report the results of a pilot study using geometric morphometrics to examine the shapes of the major and minor claws of *Uca pugnax*, comparing the shape and multivariate allometric trajectories of the claws.

In Chapter 4, I analyze the evolutionary patterns of claw shape across the genus *Uca*. Using geometric morphometrics and elliptical Fourier analysis, I explore the intra- and interspecific allometry of major and minor claw size and shape, the major patterns of shape variation, the correlation of major and minor claw shape, and the correlation between outline and landmark based shape descriptions.

In Chapter 5, I review the visual, acoustic, combat, and feeding behaviors of fiddler crabs, and analyze their relationship with claw morphology. The structure of the major claw is examined with respect to its dual functions of display and combat. The structure of the minor claw is examined with respect to habitat choice.

LITERATURE CITED

Altevogt, R. 1955. Beobachtungen und Untersuchungen an indischen Winkerkrabben. *Zeitschrift für Morphologie und Ökologie der Tiere* 43:501-522.

Andersson, M. 1994. *Sexual Selection*. Princeton University Press: Princeton, NJ.

Backwell, P. R. Y., P. D. O'Hara, and J. H. Christy. 1998. Prey availability and selective foraging in shorebirds. *Animal Behaviour* 55:1659-1667.

Barnwell, F. H. 1982. The prevalence of male right-handedness in the Indo-West Pacific fiddler crabs *Uca vocans* (Linnaeus) and *U. tetrogonon* (Herbst) (Decapoda: Ocypodidae). *Journal of Crustacean Biology* 2:70-83.

Barnwell, F. H. 1986. Fiddler crabs of Jamaica (Decapoda, Brachyura, Ocypodidae, genus *Uca*). *Crustaceana* 50:146-165.

Begg, G. W. 1981. Cape Wagtail eating fiddler crabs. *Ostrich* 52:250.

Berglund, A., A. Bisazza, and A. Pilastro. 1996. Armaments and ornaments: An evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society* 58:385-399.

Bildstein, K. L., S. G. McDowell, and I. L. Brisbin. 1989. Consequences of sexual dimorphism in sand fiddler crabs, *Uca pugilator*: Differential vulnerability to avian predation. *Animal Behaviour* 37:133-139.

Boshe, J. I. 1982. Predation of fiddler crabs *Uca stenodactyla* (Ocypodidae) by the common shore birds in Pangani Beach, Tanzania. *African Journal of Ecology* 20:237-240.

Calman, W. T. 1911. *The Life of Crustacea*. Methuen & Co. Ltd.: London.

Caravello, H. E., and G. N. Cameron. 1987. The effects of sexual selection on the foraging behaviour of the gulf coast fiddler crab, *Uca panacea*. *Animal Behaviour* 35:1864-1874.

Christy, J. H., and M. Salmon. 1984. Ecology and evolution of mating systems of fiddler crabs (genus *Uca*). *Biological Reviews* 59:483-509.

Crane, J. 1967. Combat and its ritualization in fiddler crabs (Ocypodidae) with special reference to *Uca rapax* (Smith). *Zoologica NY* 52:49-77.

Crane, J. 1975. *Fiddler Crabs of the World: Ocypodidae: Genus Uca*. Princeton University Press: Princeton, NJ.

Darwin, C. 1874. *The Descent of Man and Selection in Relation to Sex*. 2nd Edition. A. L. Burt Company: New York.

Ens, B. J., M. Klaassen, and L. Zwarts. 1993. Flocking and feeding in the fiddler crab (*Uca tangeri*): Prey availability as risk-taking behaviour. *Netherlands Journal of Sea Research* 31:477-494.

Frith, D. W., and S. Brunemeister. 1983. Fiddler crab (Ocypodidae: Genus *Uca*) size, allometry and male major chela handedness and morphism on a Thailand mangrove shore. *Phuket Marine Biological Center Research Bulletin* 29:1-16.

Hagen, H.-O. v. 1983. Visual and acoustic display in *Uca mordax* and *U. burgersi*, sibling species of neotropical fiddler crabs. I. Waving display. *Behaviour* 83:229-250.

Hagen, H.-O. v. 1984. Visual and acoustic display in *Uca mordax* and *U. burgersi*, sibling species of neotropical fiddler crabs. II. Vibration signals. *Behaviour* 91:204-228.

Huxley, J. S. 1932. *Problems of Relative Growth*. Dial Press: London.

Iribarne, O. O., and M. M. Martinez. 1999. Predation on the southwestern Atlantic fiddler crab (*Uca uruguayensis*) by migratory shorebirds (*Pluvialis dominica*, *P. squatarola*, *Arenaria interpres*, and *Numenius phaeopus*). *Estuaries* 22:47-54.

Jones, A. R. 1980. Chela injuries in the fiddler crab, *Uca burgersi* Holthius. *Marine Behavior and Physiology* 7:47-56.

Jones, D. S., and R. W. George. 1982. Handedness in Fiddler Crabs as an aid in taxonomic grouping of the genus *Uca* (Decapoda, Ocypodidae). *Crustaceana* 43:100-102.

Jones, H. G. 1968. Preliminary studies on the brachyuran Crustacea of Barbados. II. *Journal of the Barbados Museum and Historical Society* 32:187-189.

Klingenberg, C. P. 1996. Multivariate allometry. Pp. 23-49 in *Advances in Morphometrics*, L. F. Marcus, M. Corti, A. Loy, G. J. P. Naylor and D. E. Slice, eds. Plenum Press: New York.

Koga, T., S. Goshima, M. Murai, and S. Poovachiranon. 1995. Predation and cannibalism by the male fiddler crab *Uca tetragonon*. *Journal of Ethology* 13:181-183.

Lee, S. Y., and R. T. Kneib. 1994. Effects of biogenic structure on prey consumption by the xanthid crabs *Eurytium limosum* and *Panopeus herbstii* in a salt marsh. *Marine Ecology Progress Series* 104:39-47.

Levinton, J. S., and M. L. Judge. 1993. The relationship of closing force to body size for the major claw of *Uca pugnax* (Decapoda: Ocypodidae). *Functional Ecology* 7:339-345.

Levinton, J. S., M. L. Judge, and J. P. Kurdziel. 1995. Functional differences between the major and minor claws of fiddler crabs (*Uca*, family Ocypodidae, order Decapoda, subphylum Crustacea): A result of selection or developmental constraint? *Journal of Experimental Marine Biology and Ecology* 193:147-160.

Merz, R. A., S. B. Altsculer, and K. C. Hauser. 1999. Growing ploughshares into swords: The morphological and functional transition of feeding to display claws in maturing male fiddler crabs. *American Zoologist* 39:40A.

Pope, D. S. 1997. Fiddler crab claw waving: A signal to males, females, or both? *American Zoologist* 37:95A.

Powers, L. W. 1975. *The Fiddler Crab Burrow: A Study in Behavioral Ecology*. Ph.D Thesis. University of Texas at Austin.

Rathbun, M. J. 1918. The grapsoid crabs of America. *United States National Museum Bulletin* 97:1-461.

Raut, M. R. 1943. Whimbrel and fiddler crabs. *Journal of the Bombay Natural History Society* 44:300.

Rhodes, W. R. 1986. A comparative study of thoracic and cheliped muscle asymmetry in male Fiddler Crabs (Genus: *Uca*). *Biological Bulletin* 170:335-349.

Ricketts, E. F., and J. Calvin. 1948. *Between Pacific Tides*. Revised Edition. Stanford University Press: Stanford, CA.

Rosenberg, M. S. 1997. Evolution of shape differences between the major and minor chelipeds of *Uca pugnax* (Decapoda: Ocypodidae). *Journal of Crustacean Biology* 17:52-59.

Salmon, M., G. W. Hyatt, K. McCarthy, and J. D. Costlow, Jr. 1978. Display specificity and reproductive isolation in the fiddler crabs, *Uca panacea* and *U. pugilator*. *Zeitschrift für Tierpsychologie* 48:251-276.

Shih, H.-T., H.-K. Mok, H.-W. Chang, and S.-C. Lee. 1999. Morphology of *Uca formosensis* Rathbun, 1921 (Crustacea: Decapoda: Ocypodidae), an endemic fiddler crab from Taiwan, with notes on its ecology. *Zoological Studies* 38:164-177.

Takeda, S., and M. Murai. 1993. Asymmetry in male fiddler crabs is related to the basic pattern of claw-waving display. *Biological Bulletin* 184:203-208.

Weissburg, M. J. 1990. *The Foraging Biology of Uca pugnax: Mechanics, Functional Morphology and Feeding Strategies*. Ph.D. Thesis. Department of Ecology and Evolution, State University of New York at Stony Brook.

Weissburg, M. J. 1992. Functional analysis of fiddler crab foraging: Sex-specific mechanics and constraints in *Uca pugnax* (Smith). *Journal of Experimental Marine Biology and Ecology* 156:105-124.

Weissburg, M. J. 1993. Sex and the single forager: Gender-specific energy maximization strategies in fiddler crabs. *Ecology* 74:279-291.

CHAPTER 2

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

2.1 ABSTRACT

Although fiddler crabs (genus *Uca*) have been among the most widely studied organisms with respect to sexual selection, asymmetry, and visual and acoustic signaling, the phylogenetic relationships within the genus have remained 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.

2.2 INTRODUCTION

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 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 which resemble the males' 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 they range from as far north as Massachusetts and 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 1968; Hyatt 1977; 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; 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.

2.3 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.

The Genus *Uca*

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 Holthius 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 official type specimen 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), when *U. heterochelos* was commonly adopted as the name. Almost 50 years later, Holthius (1962) pointed out that *U. heterochelos* was an objective junior synonym of *U. major*, and the type species has been known 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*. Correcting this error would have caused a somewhat painful change of names (Holthius 1979; Manning and Holthius 1981). The type species would still be called *U. major*, but would refer to the West African/Portuguese species rather than the American one; the American species, which has been called *U. major* since 1962, would be called *U. platydactylus*, a name unused since 1918.

To deal with this dilemma, the Society of Zoological Nomenclature officially designated the holotype of *Gelasimus platydactylus* as a neotype of *Cancer vocans major* (Holthius 1979; Opinion 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/Portuguese 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 that sits between the eyestalks (Figure 2.1). Relative front-width and eyestalk length are necessarily inversely proportional, since the eyestalks are constrained to fit within the orbital cavity of the carapace; the longer the eyestalks, the narrower the front must be.

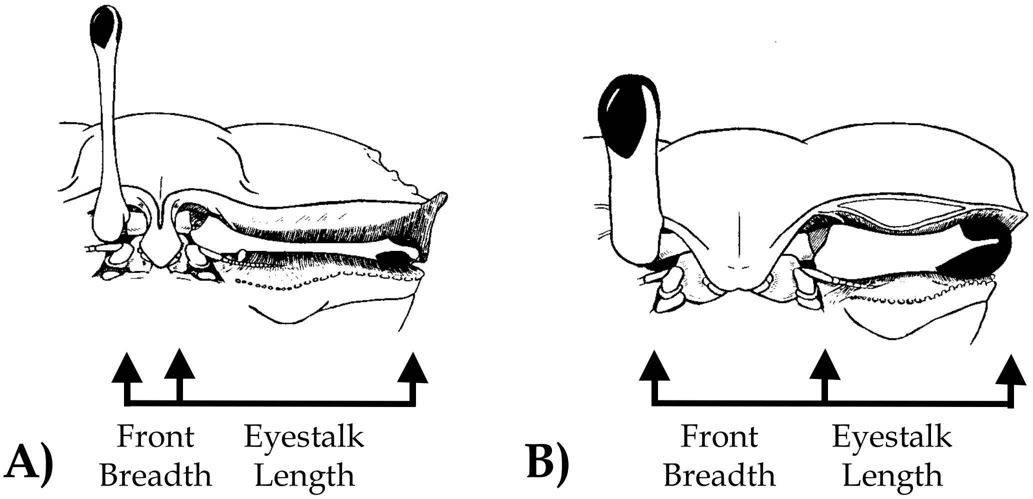

Figure 2.1. Examples of narrow-front and broad-front morphologies. A) *U. ornata*; B) *U. terpsichores*. Figure modified from Crane (1975).

In the mid-1970's the subdivisions became much more complicated. In 1975, Jocelyn Crane's long overdue 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 2.1).

Subgenus	**Author**	**Species**	**Subspecies**
Deltuca	Crane, 1975	*forcipata**	
		rosea	
		dussumieri	*dussumieri, capricornis, spinata*
		demani	*demani, typhoni, australiae*
		arcuata	
		coarctata	*coarctata, flammula*
		urvillei	
		acuta	*actua, rhizophorae*
Australuca	Crane, 1975	*bellator**	*bellator, signata, minima, longidigita*
		seismella	
		polita	
Thalassuca	Crane, 1975	*tetragonon**	
		formosensis	
		vocans	*vocans, borealis, herperiae, pacificensis, dampieri vomeris*
Amphiuca	Crane, 1975	*chlorophthalmus**	*chlorophthalmus, crassipes*
		inversa	*inversa, sindensis*
Boboruca	Crane, 1975	*thayeri**	*thayeri, umbratila*
Afruca	Crane, 1975	*tangeri**	
Uca	Leach (*sensu* Bott, 1954)	*maracoani**	*maracoani, insignis*
		heteropleura	

		major	
		stylifera	
		princeps	*princeps, monilifera*
		ornata	
Minuca	Bott, 1954	*mordax**	
		pygmaea	
		vocator	*vocator, ecuadoriensis*
		burgersi	
		panamensis	
		minax	
		brevifrons	
		galapagensis	*galapagensis, herradurensis*
		rapax	*rapax, longisignalis*
		pugnax	*pugnax, virens*
		zacae	
		subcylindrica	
Celuca	Crane, 1975	*deichmanni**	
		argillicola	
		pugilator	
		uruguayensis	
		crenulata	*crenulata, coloradensis*
		speciosa	*speciosa, spinicarpa*
		cumulanta	
		batuenta	
		saltitanta	
		oerstedi	
		inaqeuqlis	

	tenuipedis	
	tomentosa	
	tallanica	
	featae	
	helleri	
	leptochela	
	dorotheae	
	beebei	
	stenodactylus	
	triangularis	*triangularis, bengali*
	lactea	*lactea, annulipes, perplexa, mjobergi*
	leptodactyla	
	limicola	
	musica	*musica, terpsichores*
	latimanus	

Table 2.1. Subdivisions of the genus *Uca* according to Crane (1975). An asterisk indicates the type species.

Unfortunately, while Crane's book was in press, Bott (1973b) published his own division of the genus. In a short (11 pages), somewhat obscure 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 2.2). Bott only recognized 52 taxa (half as many as Crane); many of the names he used turn out to be junior subsynonyms 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 (Hagen 1976;

Manning and Holthius 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 Hagen (1976), Crane's subgenera *Thalassuca*, *Amphiuca*, and *Boboruca* should be called (after Bott) *Mesuca*, *Paraleptuca*, and *Plaunca*, 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 Holthius (1981), Crane's *Thalassuca* should not be replaced by *Mesuca* as suggested by 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.

Genus	**Subgenus**	**Author**	**Species**
African/Indo-West Pacific Genera			
Uca		Leach, 1814	*tangeri**
			marionis (*vocans*)
Mesuca	*Mesuca*	Bott, 1973b	*tetragonon**
			forcipatus
			coarctata
			brevipes (*arcuata*)
			rhizophorae
	Latuca	Bott, 1973b	*neocultrimana** (*pacificensis*)
			paradussumieri (*spinata*)
			rosea
			dussumieri
Tubuca		Bott, 1973b	*urvillei**
			forceps (*lactea*)
Austruca		Bott, 1973b	*annulipes**
			lactea

		inversa
		orientalis (*perplexa*)
		sindensis
Paraleptuca	Bott, 1973b	*chlorophthalmus**
		gaimardi (*crassipes*)
American Genera		
Minuca	Bott, 1954	*mordax**
		burgersi
		lanigera (*ecuadoriensis*)
		panamensis
		herradurensis
		rapax
		brevifrons
		murifecenta (*vocator*)
Planuca	Bott, 1973b	*thayeri**
		zilchi (*umbratila*)
		deichmanni
		galapagensis
		macrodactyla (*galapagensis*)
		uruguayensis
		pugilator
Leptuca	Bott, 1973b	*stenodactylus**
		leptochela
		leptodactyla
		festae
		coloradensis
		beebei
		oerstedti

Gelasimus	Latreille, 1817	*inaequalis*
		saltitanta
		terpsichores
		mertensi (*tomentosa*)
		*maracoani**
		platydactylus (*major*)
		stylifera
		insignis
		princeps
Heteruca	Bott, 1973b	*heteropleurus**

Table 2.2. Divisions of the genus *Uca* according to Bott (1973b). An asterisk indicates the type species; names in parentheses indicate the correct species name as revised by Crane (1975) (the exceptions being *U. neocultrimana* and *U. paradussumieri*, see below).

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; Prahl 1982; Hogarth 1986).

The Species of *Uca*

The best place to start 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 seniority and take precedence. These changes are summarized in Table 2.3.

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	Prahl and Toro (1985)
Uca victoriana	Hagen (1987b)

Junior Subsynonym	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*	

Incorrect Spelling	Correct Spelling	Reference
Uca longidigita	*Uca longidigitum*	Hagen and Jones (1989)
Uca mjobergi	*Uca mjoebergi*	Hagen and Jones (1989)

Table 2.3. Changes to the species level taxonomy of the genus *Uca* since Crane (1975). †The newly described species *Uca pavo* George and Jones, 1982, is a junior subsynonym of *Uca capricornis* (Hagen and Jones 1989).

Crane tended to lump related taxa into subspecies rather than treat them as distinct species. A number of studies since that time have raised some of her subspecies to specific status (Salmon *et al.* 1979; Thurman 1979, 1982; Barnwell 1980; Green 1980; Barnwell and Thurman 1984; Collins *et al.* 1984; Salmon and Kettler 1987; Hagen and Jones 1989); in fact, virtually every subspecies that has been studied since the publication of Crane's monograph has been raised to specific status. 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; Hagen and Jones 1989; Jones and Morton 1995). Because it appears that Crane was overly conservative in her designation of subspecies, I shall follow this practice.

The Phylogeny of *Uca*

The genus *Uca* is in 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 Holthius 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 hypothesis 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. 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 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, 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 lineage. One narrow-front lineage migrated to the New World and gave rise to the American (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, were 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.

Very little molecular phylogenetic work has been conducted on *Uca* (Albrecht and Hagen 1981; Suzawa *et al.* 1993; Levinton *et al.* 1996; Sturmbauer *et al.* 1996). Albrecht and 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 Hagen found *Boboruca* to be a more advanced clade nestled 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 Hagen (1981) 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 geocarcinid species, and a grapsid species as outgroups. Their work revealed three interesting results (Figure 2.2).

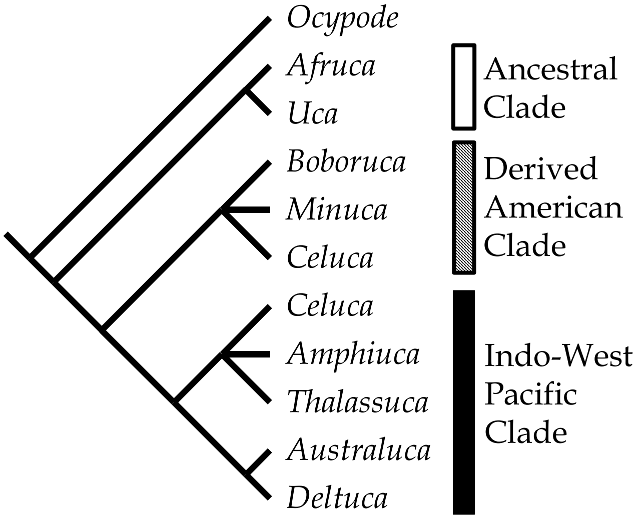

Figure 2.2. Phylogenetic relationships of Crane's (1975) subgenera, according to Sturmbauer *et al.* (1996) and Levinton *et al.* (1996).

First, it confirmed that the *Ocypode* are 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* was 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.

2.4 MATERIAL AND METHODS

An initial morphological character list was generated by combing through numerous species descriptions, comparisons, and identification keys (Rathbun 1933; 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; Prahl 1982; Barnwell and Thurman 1984; Collins *et al.* 1984; Hendrickx 1984; Prahl and Toro 1985; Abele and Kim 1986; Bairagi and Misra 1988; 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.

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 (> 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 by myself and others and from museum collections (Appendix I). Of the ninety-seven recognized fiddler crab species, eighty-eight were included in the analysis; the remaining nine were unavailable for examination and are listed in Table 2.4. The missing species are spread across the genus and their exclusion should not change any 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 phylogeny, although the ingroup relationships were largely unaffected (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 ambulatories (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* (Levinton *et al.* 1996). Because of this problem, the results of the Levinton *et al.* (1996) and Sturmbauer *et al.* (1996) studies will be followed; the subgenera *Uca* and *Afruca sensu* Crane will be 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.

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

Table 2.4. Species of *Uca* not included in the phylogenetic analysis. Subgenera refer to Crane (1975).

A matrix with two hundred thirty-six 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; 1000 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 which bears heavily on this data set, is how to treat inapplicable characters (Platnick *et al.* 1991; Maddison 1993; Pleijel 1995; Hawkins *et al.* 1997). This is not the same as missing data: inapplicable characters refers to when a set of characters does not exist for certain taxa, not when the information about those characters is 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 eleven species that do not have this ridge at all; all of the characters that refer to aspects of the ridge have no meaning for these 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 which 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 since 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 which was missing from some taxa. Characters which contained this alternate character state were downweighted based on the number of characters which referred to the missing feature. All of the characters with adjusted weights are listed in Table 2.5.

Morphological Feature	Character #'s	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
Postero-lateral striae of carapace	211-212	0.500
Gonopod thumb	224	0.750
Gonopod flanges	226-227	0.500

Table 2.5. Suites of characters which were inapplicable for some taxa. Characters which are not listed had a weight of 1.

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

(Figure 2.3a). 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 (Figure 2.3b). 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).

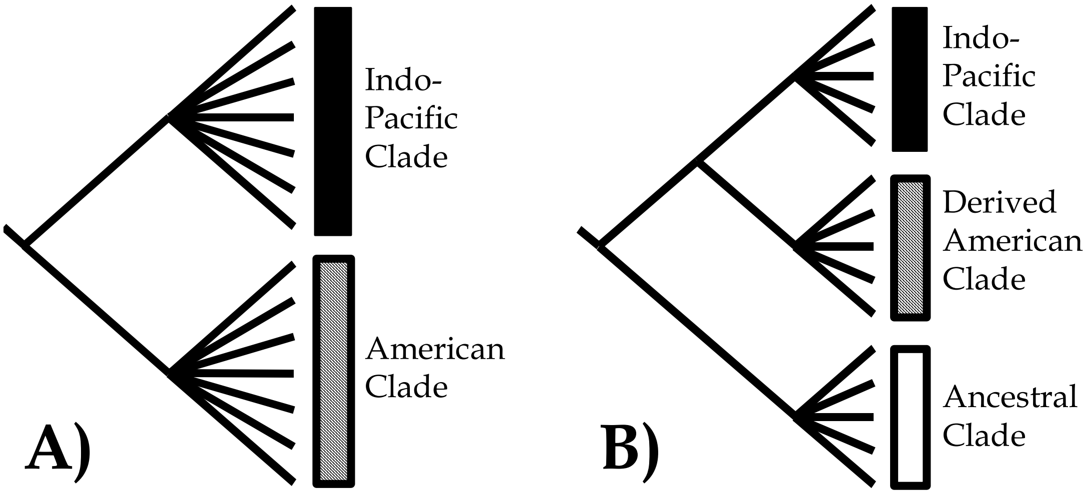

Figure 2.3. Conceptualization of constraint trees used to compare these analyses to other hypotheses. A) Indo-West Pacific vs. American dichotomy; B) Indo-West Pacific vs. crown American dichotomy, with basal American outgroup.

2.5 RESULTS

Two hundred and four of the two hundred and thirty-six characters were parsimony informative. The heuristic search found 12 MPTs of length 1517 (consistency index (CI) = 0.161, retention index (RI) = 0.660) (Figure 2.4). Referring to the subgenera *sensu* Crane, 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 nearly 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 *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 antero-dorsal margin of the major merus.

The *Deltuca* and *Australuca* clade is supported by their narrow front, the presence of a median groove on the dactyl, small suborbital crennelations which are fused or missing along the length of the margin, and a vertical lateral margin which does not reach the dorsal surface of the carapace. The separation between

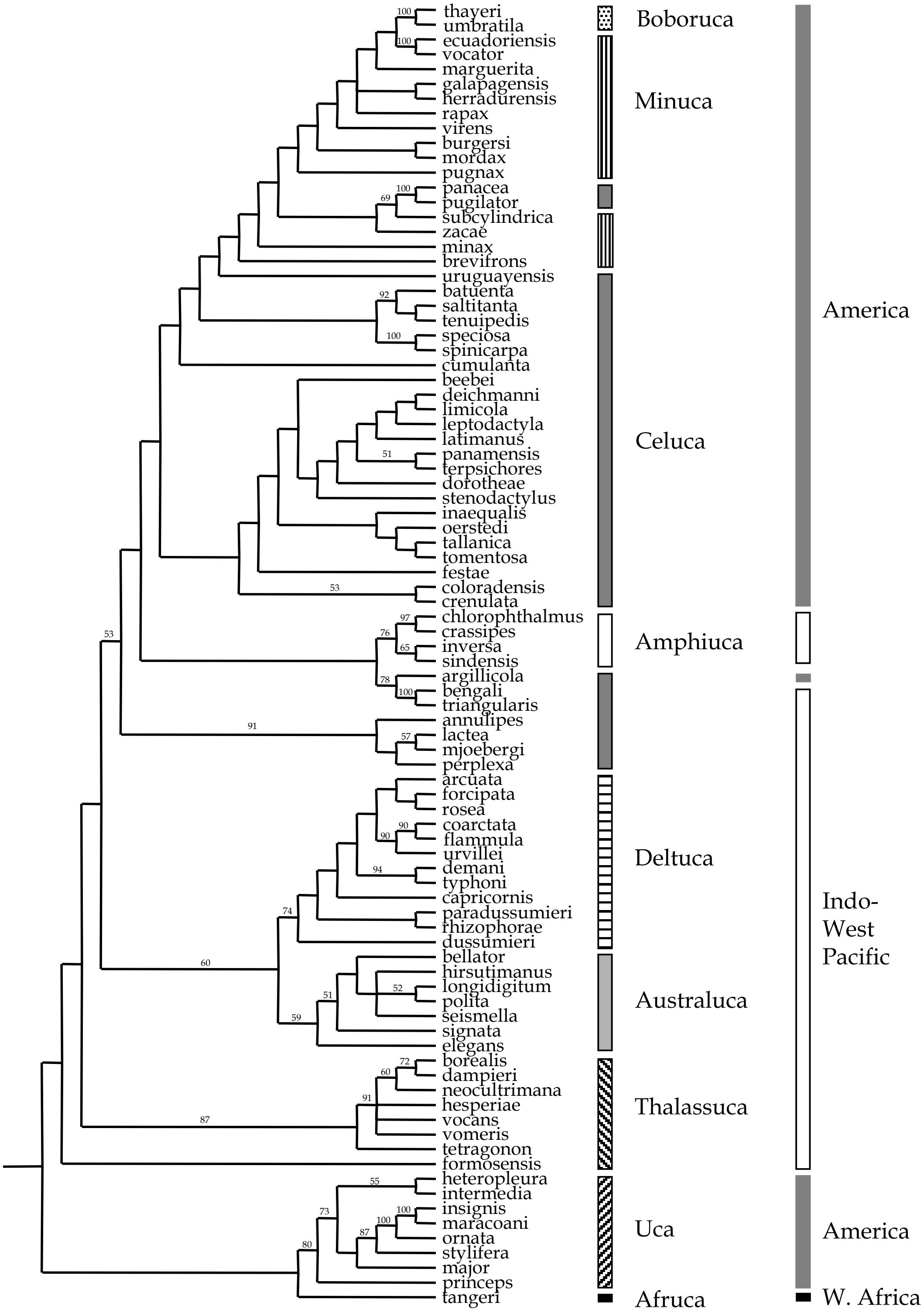

Figure 2.4. Strict consensus of 12 most-parsimonious trees (length = 1517, CI = 0.161, RI = 0.660) from unconstrained analysis. Numbers above branches are bootstrap values.

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 antero-dorsal margin of the major merus.

There are eighteen character changes at the base of the clade containing the *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 stria on the ambulatori meri, an inclined eyebrow, postero-lateral stria on the carapace of most species, and a specialized pleonal 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 (Figure 2.3a) found 40 MPTs of length 1535 (CI = 0.159, RI = 0.656); this is 18 steps (1.2%) longer than the unconstrained search. The second constrained search (Figure 2.3b) found 8 MPTs (Figure 2.5) of length 1538.5 (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 (Figure 2.5). 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.

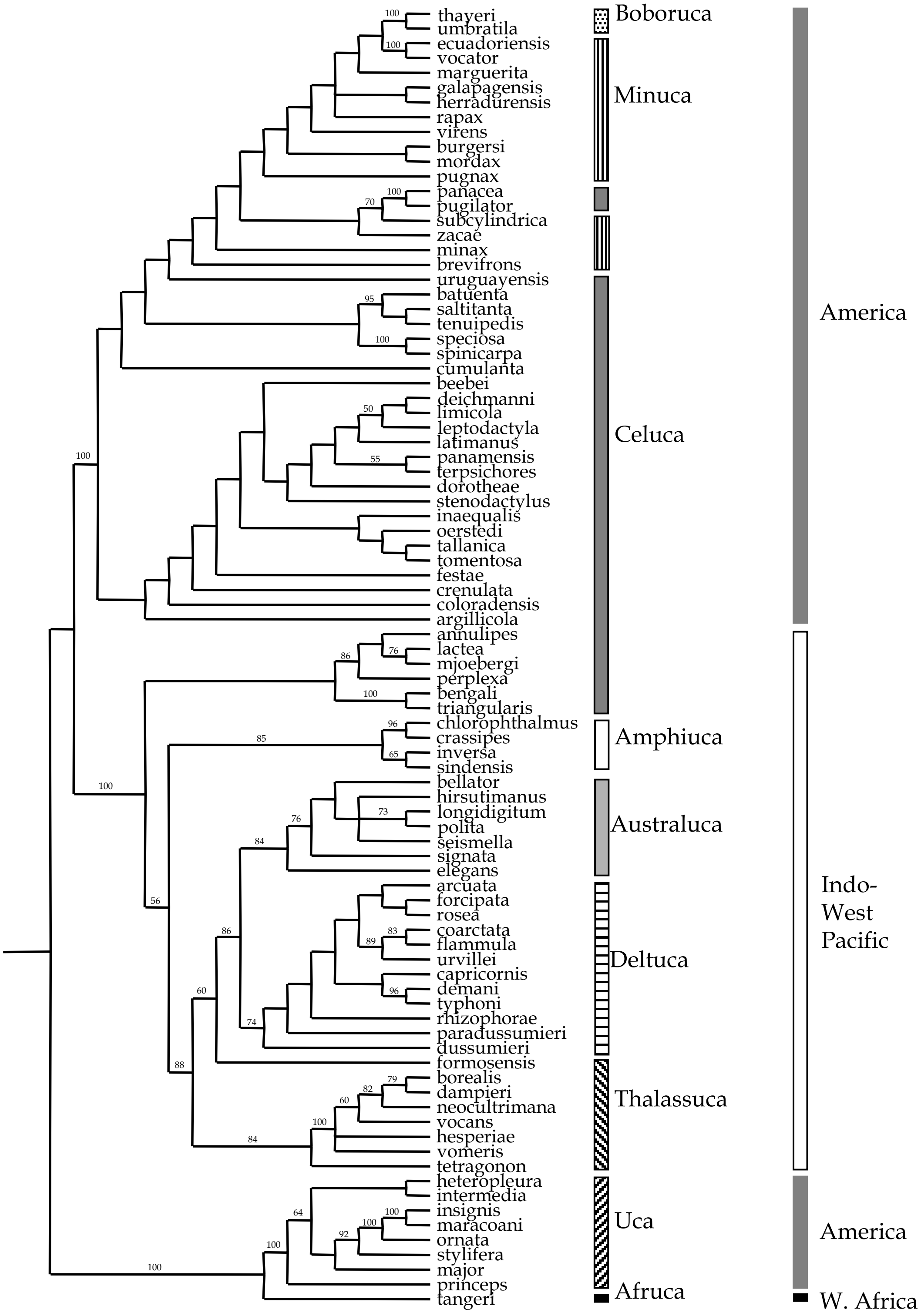

Figure 2.5. Strict consensus of 8 most-parsimonious trees (length = 1538.5, CI = 0.158, RI = 0.655) from constrained parsimony analysis, using the second constraint tree (Figure 2.3b). Numbers above branches are bootstrap values.

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.

2.6 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 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 2.6).

Subgenus	Author	Type	Consists primarily of Crane's (1975)
Uca	Leach, 1814	*U. major*	*Uca* & *Afruca*
Minuca	Bott, 1954	*U. mordax*	*Minuca* & *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*

Table 2.6. Reassessment of *Uca* subgeneric nomenclature.

Because of the decision by the Society of Zoological Nomenclature to designate the holotype of *Gelasimus platydactylus* as a neotype of *Cancer vocans major* (Holthius 1979; Opinion 1983), *U. major* (*Cancer vocans major*) is still the official 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 Bott (1973b) had placed it in anyway. As noted by Manning and Holthius (1981), Bott's use of *Gelasimus* was misapplied and should refer to the 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 (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 (present study, Levinton *et al.* 1996; Sturmbauer *et al.* 1996). The taxon is paraphyletic (if not polyphyletic), with the *Minuca* branching off in the middle. 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*. Upon direct examination of specimens, I did not see much similarity between *U. formosensis* and the other *Thalassuca*. 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 *Deltuca* and *Australuca*. This author agrees that *U. formosensis* does not appear to belong to the *Thalassuca*, but is loath to 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*, 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 which were not included in the analysis (Table 2.4) 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; 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* (Crane 1975) and *U. minax* (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 Hagen 1981; 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 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 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 which 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* (Albrecht and 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*. 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 Figure 2.4. The pectinate branching pattern at the base of the narrow-front subgenera has no bootstrap support and is supported by only a few characters which all show a large degree of homoplasy across the tree. Therefore, we might assume the Indo-West Pacific narrow-front species form a clade and propose a more likely scenario for the evolution of the genus (Figure 2.6), quite similar to that proposed by Levinton *et al.* (1996) and Sturmbauer *et al.* (1996).

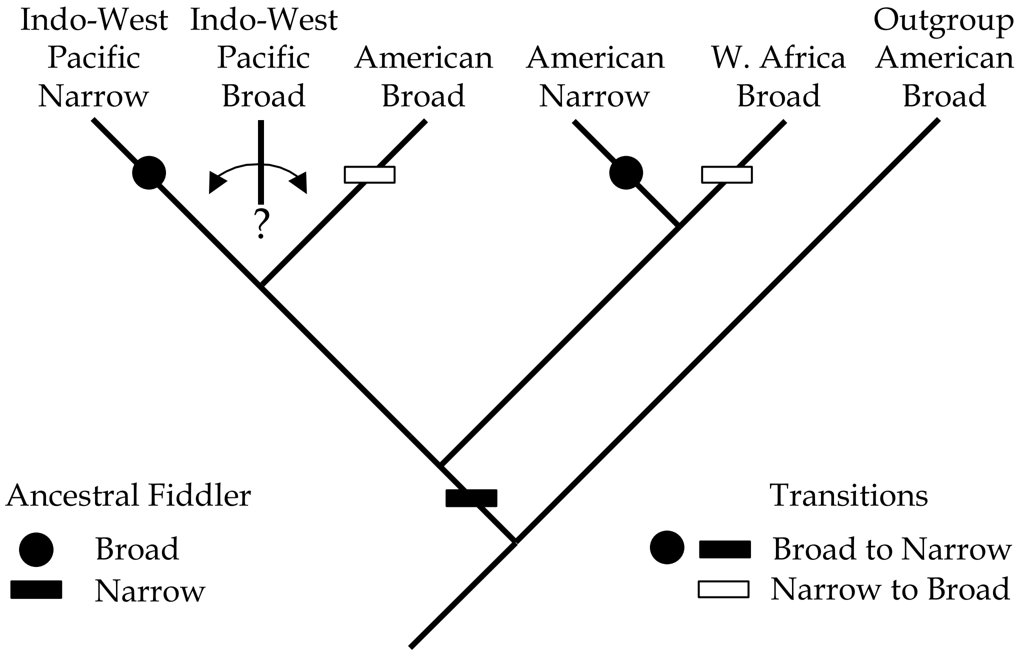

Figure 2.6. Proposed biogeographic history of the genus *Uca*. Circles represent transitions assuming a broad-front ancestral fiddler crab; rectangles assume a narrow-front ancestral fiddler crab. Black symbols represent transitions from broad to narrow; white symbols represent transitions from narrow to broad.

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, one containing the large American/West African *Uca* and the other the remainder of the species. Species from the later clade crossed the 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 (Figure 2.6). Ignoring the Indo-West Pacific broad-front taxa for the moment, there are two possibilities: first, the early fiddler crab taxa evolved narrow-fronts, 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, once in the American *Uca* and once in the Indo-West Pacific subgenera. The second scenario is more parsimonious since 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 2.7).

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

Table 2.7. Number of changes required under different scenarios of front-breadth evolution, treating front-breadth as a single character.

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.

2.7 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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LITERATURE CITED

Abele, L. G., and W. Kim. 1986. *An Illustrated Guide to the Marine Decapod Crustaceans of Florida*. State of Florida Department of Environmental Regulation: Tallahassee, FL.

Albrecht, H., and H.-O. v. Hagen. 1981. Differential weighting of electrophoretic data in crayfish and fiddler crabs (Decapoda: Astacidae and Ocypodidae). *Comparative Biochemistry and Physiology* 70B:393-399.

Altevogt, R., and T. Davis, Antony. 1979. Shift of handedness in Indian populations of *Uca vocans* (Linné 1758) (Crustacea, Decapoda, Ocypodidae). *Zoologischer Anzeiger* 203:342-344.

Backwell, P. R. Y., M. D. Jennions, J. H. Christy, and N. I. Passmore. 1999. Female choice in the synchronously waving fiddler crab *Uca annulipes*. *Ethology* 105:415-421.

Bairagi, N., and A. Misra. 1988. On the taxonomic status of *Gelasimus acutus* Stimpson (Decapoda: Ocypodidae) present in the national collection of the Zoological Survey of India, Calcutta. *Journal of the Bombay Natural History Society* 85:449-451.

Barnwell, F. H. 1966. Daily and tidal patterns of activity in individual fiddler crab (genus *Uca*) from the Woods Hole region. *Biological Bulletin* 130:1-17.

Barnwell, F. H. 1968. The role of rhythmic systems in the adaptation of fiddler crabs to the intertidal zone. *American Zoologist* 8:569-583.

Barnwell, F. H. 1980. Taxonomic differentiation within the *lactea*-complex of fiddler crabs in the Sunda Shelf region. *American Zoologist* 20:957.

Barnwell, F. H. 1982. The prevalence of male right-handedness in the Indo-West Pacific fiddler crabs *Uca vocans* (Linnaeus) and *U. tetrogonon* (Herbst) (Decapoda: Ocypodidae). *Journal of Crustacean Biology* 2:70-83.

Barnwell, F. H., and C. L. Thurman, II. 1984. Taxonomy and biogeography of fiddler crabs (Ocypodidae: genus *Uca*) of the Atlantic and Gulf coasts of eastern North America. *Zoological Journal of the Linnean Society* 81:23-87.

Bott, R. 1954. Dekapoden (Crustacea) aus El Salvador. 1. Winkerkrabben (*Uca*). *Senckenbergiana biologica* 35:155-180.

Bott, R. 1973a. Die Typus-Art der Gattung *Uca* Leach 1814 (Decapoda: Ocypodidae). *Senckenbergiana biologica* 54:311-314.

Bott, R. 1973b. Die verwandtschaftlichen Beziehungen der *Uca*-Arten (Decapoda: Ocypodidae). *Senckenbergiana biologica* 54:315-325.

Brito, I. M. 1972. Contribuição ao conhecimento dos crustáceos decápodos da formação Pirabas. II—O gênero *Uca* (Brachyura-Ocypodidae). *Anais da Academia Brasileira de Ciências* 44:95-98.

Brown, F. A., Jr., M. F. Bennett, and H. M. Webb. 1954. Persistent daily and tidal rhythms of O_2-consumption in fiddler crabs. *Journal of Cellular and Comparative Physiology* 44:477-506.

Brown, F. A., Jr., and G. C. Stephens. 1951. Studies of the daily rhythmicity of the fiddler crab, *Uca*. Modifications by photoperiod. *Biological Bulletin* 101:71-83.

Brown, F. A., Jr., and H. M. Webb. 1949. Studies of the daily rhythmicity of the fiddler crab, *Uca*. Modifications by light. *Physiological Zoölogy* 22:136-148.

Christy, J. H. 1983. Female choice in the resource-defense mating system of the sand fiddler crab, *Uca pugilator*. *Behavioral Ecology and Sociobiology* 12:169-180.

Christy, J. H. 1987. Female choice and breeding behavior of the fiddler crab *Uca beebei*. *Journal of Crustacean Biology* 70:624-635.

Collins, M. J., D. A. Jones, and D. A. Clayton. 1984. Redescription of *Uca sindensis* (Alcock, 1900) (Brachyura: Ocypodidae) with notes on the ecology of a population from Kuwait. *Journal of Crustacean Biology* 4:318-328.

Coohill, T. P., C. K. Bartell, and M. Fingerman. 1970. Relative effectiveness of ultraviolet and visible light in eliciting pigment dispersion directly in melanophores of the fiddler crab, *Uca pugilator*. *Physiological Zoölogy* 43:232-239.

Crane, J. 1941. Crabs of the genus *Uca* from the west coast of Central America. *Zoologica NY* 26:145-208.

Crane, J. 1967. Combat and its ritualization in fiddler crabs (Ocypodidae) with special reference to *Uca rapax* (Smith). *Zoologica NY* 52:49-77.

Crane, J. 1975. *Fiddler Crabs of the World: Ocypodidae: Genus Uca*. Princeton University Press: Princeton, NJ.

Dai, A.-y., and S.-l. Yang. 1991. *Crabs of the China Seas*. Springer-Verlag: Berlin.

Devi, V. U. 1987. Heavy metal toxicity to fiddler crabs, *Uca annulipes* Latreille and *Uca triangularis* (Milne Edwards): Tolerance to copper, mercury, cadmium, and zinc. *Bulletin of Environmental Contamination and Toxicology* 39:1020-1027.

Felsenstein, J. 1985. Confidence limits on phylogenies with a molecular clock. *Systematic Zoology* 34:152-161.

Fingerman, M., and S. W. Fingerman. 1977. Antagonistic actions of dopamine and 5-hydroxytryptamine on color changes in the fiddler crab, *Uca pugilator*. *Comparative Biochemistry and Physiology* 58C:121-127.

George, R. W., and D. S. Jones. 1982. A revision of the fiddler crabs of Australia (Ocypodinae: *Uca*). *Record of the Western Australian Museum* Supplement:1-99.

Gould, S. J., and R. C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: A critique of the adapationist programme. *Proceedings of the Royal Society of London* 205B:581-598.

Green, C. J. R. 1980. Behavioral taxonomy resolves differences between Gulf of California *Uca* species (Brachyura, Ocypodidae). *American Zoologist* 20:957.

Green, J. P., and J. Schochet. 1972. Chela type in *Uca vocans*. *American Zoologist* 12:714-715.

Guinot, D. 1979. Données nouvelles sur la morphologie, la phylogenèse et la taxonomie des crustacés décapodes brachyoures. *Mémoires du Muséum National d'Histoire Naturelle* 112A:1-354.

Hagen, H.-O. v. 1968. Studien an peruanischen Winkerkrabben (*Uca*). *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere* 95:395-468.

Hagen, H.-O. v. 1976. (Book Review) Jocelyn Crane, Fiddler Crabs of the World. Ocypodidae: Genus *Uca*. *Crustaceana* 31:221-224.

Hagen, H.-O. v. 1980. A key to the "X-species" of North American fiddler crabs (genus *Uca*). *Zoölogische mededelingen* 55:88-96.

Hagen, H.-O. v. 1983. Visual and acoustic display in *Uca mordax* and *U. burgersi*, sibling species of neotropical fiddler crabs. I. Waving display. *Behaviour* 83:229-250.

Hagen, H.-O. v. 1984. Visual and acoustic display in *Uca mordax* and *U. burgersi*, sibling species of neotropical fiddler crabs. II. Vibration signals. *Behaviour* 91:204-228.

Hagen, H.-O. v. 1987a. Allometric growth in two populations of *Uca tangeri* from the Guadalquivir estuary (Andalusia). *Investigacíon Pesquera (Barcelona)* 51:443-452.

Hagen, H.-O. v. 1987b. Morphologie und Winkbalz einer neuen *Uca*-Art (Crustacea, Brachyura) aus dem Staat Espirito Santo (Brasilien). *Mitteilungen aus dem hamburgischen zoologischen Museum und Institut* 84:81-94.

Hagen, H.-O. v., and D. S. Jones. 1989. The fiddler crabs (Ocypodidae: *Uca*) of Darwin, Northern Territory, Australia. *Beagle, Records of the Northern Territory Museum of Arts and Sciences* 6:55-68.

Hanumante, M. M., and M. Fingerman. 1981. 5-hydroxytryptamine control of red pigment-dispersing hormone release in the fiddler crab, *Uca pugilator*: Effects of a 5-hydroxytryptamine uptake inhibitor and a 5-hydroxytryptamine receptor blocker on 5-hydroxytryptamine-induced and iproniazid-induced red pigment dispersion. *General and Comparative Endocrinology* 45:395-401.

Harvey, P. H., and M. D. Pagel. 1991. *The Comparative Method in Evolutionary Biology*. Oxford University Press: Oxford.

Hawkins, J. A., C. E. Hughes, and R. W. Scotland. 1997. Primary homology assessment, characters and character status. *Cladistics* 13:275-283.

Hendrickx, M. E. 1984. Studies of the coastal marine faunna of southern Sinaloa, Mexico. II. The decapod crustaceans of Estero el Verde. *Anales del Instituto de Ciencias del Mar y Limnología* 11:23-48.

Herbst, J. F. W. 1782-1804. *Versuch einer Naturgeschichte der Krabben und Krebse. Nebst einer systematischen Beschreibung ihrer verschiedenen Arten*. J. C. Fuessly: Zurich.

Hogarth, P. J. 1986. Occurence of *Uca* (*Deltuca*) *urvillei* (H. Milne Edwards, 1852) in the Saudi Red Sea (Decapoda, Ocypodidae). *Crustaceana* 51:222-223.

Holthius, L. B. 1962. Forty-seven genera of Decapoda (Crustacea); proposed addition to the official list. *Bulletin of Zoological Nomenclature* 19:232-252.

Holthius, L. B. 1979. *Cancer vocans major* Herbst, 1782 (Crustacea, Decapoda): Request for the use of the plenary powers to validate a neotype. Z.N.(S). 2235. *Bulletin of Zoological Nomenclature* 35:248-252.

Hopkins, P. M., A. C.-K. Chung, and D. S. Durica. 1999. Limb regeneration in the fiddler crab, *Uca pugilator*: Histological, physiological and molecular considerations. *American Zoologist* 39:513-526.

Huxley, J. S., and F. S. Callow. 1933. A note on the asymmetry of male fiddler-crabs (*Uca pugilator*). *Archiv für Entwicklungsmechanik der Organismen* 129:379-392.

Hyatt, G. W. 1977. Quantitative analysis of size-dependent variation in the fiddler crab wave display (*Uca pugilator*, Brachyura, Ocypodidae). *Marine Behaviour and Physiology* 5:19-36.

Hyatt, G. W., and M. Salmon. 1978. Combat in the fiddler crabs *Uca pugilator* and *U. pugnax*: A quantitative analysis. *Behaviour* 65:182-211.

Hyatt, G. W., and M. Salmon. 1979. Comparative statistical and information analysis of combat in fiddler crabs, *Uca pugilator* and *U. pugnax*. *Behaviour* 68:1-23.

Ismail, A., M. A. Badri, and M. N. Ramlan. 1991. Heavy metal contamination in fiddler crabs (*Uca annulipes*) and hermit crabs (*Clibanarius sp.*) in a coastal area of northern peninsular Malaysia. *Environmental Technology* 12:923-926.

Jennions, M. D., and P. R. Y. Backwell. 1996. Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. *Biological Journal of the Linnean Society* 57:293-306.

Jones, D. S., and R. W. George. 1982. Handedness in Fiddler Crabs as an aid in taxonomic grouping of the genus *Uca* (Decapoda, Ocypodidae). *Crustaceana* 43:100-102.

Jones, D. S., and B. Morton. 1995. The fiddler crabs (Ocypodidae: *Uca*) of Hong Kong. *Asian Marine Biology* 11:9-40.

Kingsley, J. S. 1880. Carcinological notes, No. II.-Revision of the Gelasimi. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1880:135-155.

Kitaura, J., K. Wada, and M. Nishida. 1998. Molecular phylogeny and evolution of unique mud-using territorial behavior in Ocypodid crabs (Crustacea: Brachyura: Ocypodidae). *Molecular Biology and Evolution* 15:626-637.

Lamarck, J. B. P. A. d. 1801. *Systeme des animaux sans vertebres*. Deterville: Paris.

Land, M., and J. Layne. 1995a. The visual control of behaviour in fiddler crabs I. Resolution, thresholds and the role of the horizon. *Journal of Comparative Physiology* 177A:81-90.

Land, M., and J. Layne. 1995b. The visual control of behaviour in fiddler crabs II. Tracking control systems in courtship and defense. *Journal of Comparative Physiology* 177A:91-103.

Larson, A. 1994. The comparison of morphological and molecular data in phylogenetic systematics. Pp. 371-390 in *Molecular Ecology and Evolution: Approaches and Applications*, B. Schierwater, B. Streit, G. P. Wagner and R. DeSalle, eds. Birkhäuser Verlag: Basel.

Latreille, P. A. 1817. Gélasime, *Gelasimus* (Buffon). Pp. 517-520 in *Nouveau dictionnaire d'histoire naturelle, appliquée aux arts, à l'agriculture, à l'économie rurale et domestique, à l'médecine, etc. Par une société de naturalistes et d'agriculteurs*, Volume XII. Deterville: Paris.

Layne, J. E. 1998. Retinal location is the key to identifying predators in fiddler crabs (*Uca pugilator*). *Journal of Experimental Biology* 201:2253-2261.

Leach, W. E. 1814. Crustaceology. Pp. 383-437 in *The Edinburgh Encyclopedia*, Volume VII. Brewster: Edinburgh.

Levinton, J., C. Sturmbauer, and J. H. Christy. 1996. Molecular data and biogeography: Resolution of a controversy over evolutionary history of a pan-tropical group of invertebrates. *Journal of Experimental Marine Biology and Ecology* 203:117-131.

Levinton, J. S., and M. L. Judge. 1993. The relationship of closing force to body size for the major claw of *Uca pugnax* (Decapoda: Ocypodidae). *Functional Ecology* 7:339-345.

Levinton, J. S., M. L. Judge, and J. P. Kurdziel. 1995. Functional differences between the major and minor claws of fiddler crabs (*Uca*, family Ocypodidae, order Decapoda, subphylum Crustacea): A result of selection or developmental constraint? *Journal of Experimental Marine Biology and Ecology* 193:147-160.

Maddison, D. R. 1991. The discovery and importance of multiple islands of most-parsimonious trees. *Systematic Zoology* 40:315-328.

Maddison, W. P. 1993. Missing data versus missing characters in phylogenetic analysis. *Systematic Biology* 42:576-581.

Manning, R. B., and L. B. Holthius. 1981. West African Brachyuran Crabs (Crustacea: Decapoda). *Smithsonian Contributions to Zoology* 306:1-379.

Miller, D. C. 1961. The feeding mechanism of fiddler crabs, with ecological considerations of feeding adaptations. *Zoologica NY* 46:89-100.

Milne-Edwards, H. 1837. *Historie naturelle des crustaces comprenant l-anatomie, la physiologie et las classification des ces animaux*. Volume 2. Paris.

Milne-Edwards, M. 1852. Observations sur les affinités zoologiques et la classification naturelle des crustacés. *Annales des Sciences Naturelles. Zoologie. Série 3* 18:109-166.

Nakasone, Y. 1982. Ecology of the fiddler crab *Uca* (*Thalassuca*) *vocans vocans* (Linnaeus) (Decapoda: Ocypodidae) I. Daily activity in warm and cold seasons. *Researches on Population Ecology* 24:97-109.

Novak, A., and M. Salmon. 1974. *Uca panacea*, a new species of fiddler crab from the Gulf coast of the United States. *Proceedings of the Biological Society of Washington* 87:313-326.

Opinion. 1983. *Cancer vocans major* Herbst, 1782 (Crustacea, Decapoda): Neotype designated under the plenary powers. *Bulletin of Zoological Nomenclature* 40:200-201.

Palmer, J. D. 1964. A persistent, light-preference rhythm in fiddler crab, *Uca pugnax* and its possible adaptive significance. *American Naturalist* 98:431-434.

Palmer, J. D. 1988. Comparative studies of tidal rhythms. VI. Several clocks govern the activity of two species of fiddler crabs. *Marine Behaviour and Physiology* 13:201-219.

Palmer, J. D. 1989. Comparative studies of tidal rhythms. VII. The circalunidian locomotor rhythm of the brackish-water fiddler crab, *Uca minax*. *Marine Behaviour and Physiology* 14:129-143.

Palmer, J. D. 1991. Contributions made to chronobiology by studies of fiddler crab rhythms. *Chronobiology International* 8:110-130.

Peters, H. M. 1955. Die Winkgebärde von *Uca* and *Minuca* (Brachyura) in vergleichend-ethologischer, -ökologischer und -morphologisch-anatomischer Betrachtung. *Zeitschrift für Morphologie und Ökologie der Tiere* 43:425-500.

Platnick, N. I., C. E. Griswold, and J. A. Coddington. 1991. On missing entries in cladistic analysis. *Cladistics* 7:337-343.

Pleijel, F. 1995. On character coding for phylogeny reconstruction. *Cladistics* 11:309-315.

Prahl, H. v. 1982. The distribution of the genus *Uca* (Crustacea: Ocypodidae) along the Colombian Pacific coast. *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere* 109:433-442.

Prahl, H. v., and N. Toro. 1985. *Uca* (*Uca*) *intermedia* (Crustacea: Brachyura: Ocypodidae) A new fiddler crab of the Pacific coast of Columbia. *Zoologischer Anzeiger* 215:274-278.

Rathbun, M. J. 1897. A revision of the nomenclature of the Brachyura. *Proceedings of the Biological Society of Washington* 11:153-167.

Rathbun, M. J. 1918. The grapsoid crabs of America. *United States National Museum Bulletin* 97:1-461.

Rathbun, M. J. 1926. The fossil stalk-eyed Crustacea of the Pacific slope of North America. *United States National Museum Bulletin* 138:1-155.

Rathbun, M. J. 1933. Brachyuran crabs of Porto Rico and the Virgin Islands. *Scientific Survey of Porto Rico and the Virgin Islands* 15:1-121.

Rosenberg, M. S. 1997. Evolution of shape differences between the major and minor chelipeds of *Uca pugnax* (Decapoda: Ocypodidae). *Journal of Crustacean Biology* 17:52-59.

Salmon, M. 1965. Waving display and sound production in the courtship behavior of *Uca pugilator*, with comparison to *U. minax* and *U. pugnax*. *Zoologica NY* 50:123-150.

Salmon, M., and S. P. Atsaides. 1968. Visual and acoustical signalling during courtship by fiddler crabs (genus *Uca*). *American Zoologist* 8:623-639.

Salmon, M., S. D. Ferris, D. Johnston, G. W. Hyatt, and G. S. Whitt. 1979. Behavioral and biochemical evidence for species distinctiveness in the fiddler crabs, *Uca speciosa* and *U. spinicarpa*. *Evolution* 33:182-191.

Salmon, M., G. W. Hyatt, K. McCarthy, and J. D. Costlow, Jr. 1978. Display specificity and reproductive isolation in the fiddler crabs, *Uca panacea* and *U. pugilator*. *Zeitschrift für Tierpsychologie* 48:251-276.

Salmon, M., and M. K. Kettler. 1987. The importance of behavioral and biochemical differences between fiddler crab taxa, with special reference to *Uca rapax* (Smith) and *U. virens* (Salmon & Atsaides). *Contributions in Marine Science* 30:63-76.

Salmon, M., and N. Zucker. 1988. Interpreting differences in the reproductive behavior of fiddler crabs (genus *Uca*). Pp. 387-407 in *Behavioral Adaptation to Intertidal Life*, G. Chelazzi and M. Vannini, eds. Plenum Press: New York.

Seba, A. 1758. *Locupletissimi rerum naturalium thesauri accurata descriptio, et iconibus artificiosissimis expressio, per universam physiees historiam. Opus, cui, in hoc rerum genere, nullum par exstitit*. Volume 3. Amsterdam.

Shaw, G., and E. R. Nodder. 1802. *The naturalist's miscellany*. Volume 14. London.

Shih, H.-T., H.-K. Mok, H.-W. Chang, and S.-C. Lee. 1999. Morphology of *Uca formosensis* Rathbun, 1921 (Crustacea: Decapoda: Ocypodidae), an endemic fiddler crab from Taiwan, with notes on its ecology. *Zoological Studies* 38:164-177.

Smith, S. I. 1870. Notes on American Crustacea. No. 1. Ocypodoidea. *Transactions of the Connecticut Academy of Arts and Science* 2:113-176.

Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*. Third Edition. W. H. Freeman and Company: New York.

Sturmbauer, C., J. S. Levinton, and J. H. Christy. 1996. Molecular phylogeny analysis of fiddler crabs: Test of the hypothesis of increasing behavioral complexity in evolution. *Proceedings of the National Academy of Sciences USA* 93:10855-10857.

Suzawa, Y., H. S. Yong, and M. Murai. 1993. Genetic differentiation of Malaysian fiddler crabs (genus *Uca*). *Comparative Bichemistry and Physiology* 105B:529-533.

Swofford, D. L. 1999. *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Version 4. Sinauer Associates: Sunderland, MA.

Takeda, S., and M. Murai. 1993. Asymmetry in male fiddler crabs is related to the basic pattern of claw-waving display. *Biological Bulletin* 184:203-208.

Templeton, A. R. 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference ot the evolution of humans and the apes. *Evolution* 37:221-244.

Thurman, C. L., II. 1979. *Fiddler crabs of the Gulf of Mexico*. Ph.D. Thesis. University of Minnesota.

Thurman, C. L., II. 1981. *Uca marguerita*, a new species of fiddler crab (Brachyura: Ocypodidae) from eastern Mexico. *Proceedings of the Biological Society of Washington* 94:169-180.

Thurman, C. L., II. 1982. On the distinctness of the fiddler crabs *Uca minax* (LeConte) and *Uca longsignalis* Salmon & Atsaides in their region of sympatry (Decapoda Brachyura, Ocypodidae). *Crustaceana* 43:37-50.

Thurman, C. L., II. 1984. Ecological notes on fiddler crabs of south Texas, with special reference to *Uca subcylindrica*. *Journal of Crustacean Biology* 4:665-681.

Trinkaus-Randall, V. E. 1982. Regeneration of transplanted chelae in two species of fiddler crabs (*Uca pugilator* and *Uca pugnax*). *Journal of Experimental Zoology* 224:13-24.

Veitch, L. G. 1978. Size, shape and allometry in *Uca*; A multivariate approach. *The Mathematical Scientist* 3:35-45.

Vernberg, F. J., and R. E. Tashian. 1959. Studies on the physiological variation between tropical and temperate zone fiddler crabs of the genus *Uca*. I. Thermal death limits. *Ecology* 40:589-593.

Vernberg, W. B., and J. O'Hara. 1972. Temperature-salinity stress and mercury uptake in the fiddler crab, *Uca pugilator*. *Journal of the Fisheries Research Board of Canada* 29:1491-1494.

Vernberg, W. B., and F. J. Vernberg. 1968. Studies on the physiological variation between tropical and temperate zone fiddler crabs of the genus *Uca*--X. The influence of temperature on cytochrome-C oxidase activity. *Comparative Biochemistry and Physiology* 26:499-508.

Weis, J. S. 1977. Regeneration of limbs autotomized at different times in the fiddler crab, *Uca pugilator*. *Canadian Journal of Zoology* 55:656-660.

Weis, J. S., and K. Kim. 1988. Tributyltin is a teratogen in producing deformities in limbs of the fiddler crab, *Uca pugilator*. *Archives of Environmental Contamination and Toxicology* 17:583-587.

Weissburg, M. J. 1992. Functional analysis of fiddler crab foraging: Sex-specific mechanics and constraints in *Uca pugnax* (Smith). *Journal of Experimental Marine Biology and Ecology* 156:105-124.

Weissburg, M. J. 1993. Sex and the single forager: Gender-specific energy maximization strategies in fiddler crabs. *Ecology* 74:279-291.

Wolfrath, B. 1992. Field experiments on feeding of European fiddler crab *Uca tangeri*. *Marine Ecology Progress Series* 90:39-43.

Yamaguchi, T. 1973. Asymmetry and dimorphism of chelipeds in the fiddler crab, *Uca lactea* De Haan. *Zoological Magazine* 82:154-158.

Yamaguchi, T. 1977. Studies on the handedness of the fiddler crab, *Uca lactea*. *Biological Bulletin* 152:424-436.

Zeil, J., and M. M. Al-Mutairi. 1996. The variation of resolution and of ommatidial dimensions in the compound eyes of the fiddler crab *Uca lactea annulipes* (Ocypodidae, Brachyura, Decapoda). *Journal of Experimental Biology* 199:1569-1577.

Zeil, J., G. Nalbach, and H.-O. Nalbach. 1986. Eyes, eye stalks and the visual world of semi-terrestrial crabs. *Journal of Comparative Physiology* 159A:801-811.

Zeil, J., and J. M. Zanker. 1997. A glimpse into crabworld. *Vision Research* 37:3417-3426.

CHAPTER 3

EVOLUTION OF SHAPE DIFFERENCES BETWEEN THE MAJOR AND MINOR CHELIPEDS OF *UCA PUGNAX* (DECAPODA: OCYPODIDAE)[1]

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EVOLUTION OF SHAPE DIFFERENCES BETWEEN THE MAJOR AND MINOR CHELIPEDS OF *UCA PUGNAX* (DECAPODA: OCYPODIDAE)

Michael S. Rosenberg

ABSTRACT

Geometric morphometrics were used to analyze shape differences between the major and minor chelipeds of the fiddler crab *Uca pugnax*. Although the major and minor chelipeds had similar allometric developmental trajectories, the form of the major cheliped was not an allometric extrapolation of the minor cheliped. The changes in shape associated with the formation of the major cheliped have functional relevance; they allow the major cheliped to produce relatively more power than the minor cheliped. This result suggests that selection for combat effectiveness has played an important role in the evolution of the major cheliped.

Sexual dimorphism and body asymmetry are common in many decapods, such as hermit crabs, snapping shrimps (Mellon and Stephens, 1978; Mellon, 1981), and lobsters (Govind, 1984, 1989). The most extreme case of cheliped sexual dimorphism in decapods is found in fiddler crabs in the genus *Uca*. Female fiddler crabs have two small chelipeds used in food gathering and sorting. Males have a single small (minor) cheliped that resembles those of the female, as well as a larger (major) cheliped that is used not for feeding, but rather for display and male-male agonistic interactions (Crane, 1975; Christy and Salmon, 1984). The major cheliped may be as much as 30 times more massive than the minor cheliped and can comprise almost half of the total body mass of the crab (Crane, 1975).

Many aspects of cheliped asymmetry in fiddler crabs have been studied in the past century, including development (Morgan, 1923, 1924; Vernberg and Costlow, 1966; Miller, 1973; Yamaguchi, 1977; Ahmed, 1978; Trinkaus-Randall and Govind, 1985), behavior (Valiela *et al.*, 1974; Caravello and Cameron, 1987; Takeda and Murai, 1993), form (Huxley, 1932; Miller, 1973; Rhodes, 1986), and function (Levinton and Judge, 1993; Levinton *et al.*, 1995). While Huxley (1932) demonstrated that both the minor and major cheliped grow allometrically with respect to carapace size, no one has been able to determine whether the shape of the major cheliped is an allometric extrapolation of the minor cheliped, or whether the major cheliped has a separate growth trajectory. This is a critical question in trying to perceive the selection pressures that have acted on the evolution of the major cheliped. The differentiation of major and minor cheliped function, as well as the extreme size dimorphism, allows us the opportunity to search for an answer.

The two functions of the major cheliped, display and combat, do not necessarily have the same morphological requirements. Development of the major cheliped may be combined with functional adaptations for increased closing force or speed for agnostic interactions. An alternative hypothesis (Huxley, 1932) is that the major cheliped is used primarily for display; as size increases, the functionality of the major cheliped decreases. The major cheliped is used in combat at all sizes (Crane, 1975). Most males, however, do not enter combat with much larger males; they retreat without physical contact. Therefore, the question may be raised as to whether males falsely advertise their ability to defeat their opponents in combat. Functional studies (Levinton *et al.*, 1995) have shown differences between the major and minor cheliped that are not related simply to size. Major chelipeds maintain functional ability, despite the high metabolic costs associated with such a large increase in size (Levinton and Judge, 1993). Although it has been shown (Levinton and Judge, 1993) that morphometric measurements can be good indicators of the underlying functional abilities, no comprehensive study of variation in cheliped shape has been performed on the fiddler crab. The newly emerging field of geometric morphometrics offers an excellent approach for analyzing shape variation between the chelipeds. These methods are more effective in capturing shape information than previous methods, provide more powerful statistical tests for differences in shape, and lend themselves toward useful graphical representations of the changes between one object and another (see Rohlf and Marcus (1993) for a basic review of geometric morphometrics).

A valid null hypothesis for the evolution of the major cheliped in the male is that it developed from an ancestral cheliped resembling the minor cheliped. There are two reasons that one might expect the major cheliped to retain the ancestral developmental pattern. The first is the possibility that development of the major cheliped would be restricted and canalized by the developmental growth pattern of the minor cheliped. If development is canalized, the form of the major cheliped should be a direct allometric extrapolation of the minor cheliped. Second, if the main selective pressure acting on the major cheliped came from sexual selection for display, with combat subsumed under the false advertisement by size, the hypothesis could be formed that there would be little selective pressure for the growth trajectory of the major cheliped to deviate from that of the minor cheliped.

The alternate hypothesis is that selection has acted upon population variation of the major cheliped and altered its structure to make it biomechanically more suitable for combat. The purpose of this study is to use geometric morphometrics to study subtle shape variation between the major and minor chelipeds of *Uca pugnax* (Smith) in order to test whether there has been a shift in the nonsize-related growth patterns of the major cheliped.

MATERIALS AND METHODS

Sixty-three male fiddler crabs of the species *U. pugnax* that had previously been collected from field populations at Flax Pond, New York, U.S.A., and stored in alcohol were used for the analysis. While some species of fiddler crabs (e.g., *Uca vocans* (L.)) have multiple forms of the major cheliped (Crane, 1975), *U. pugnax* appears to have only a single form. If there are multiple forms in *U. pugnax*, such as the constitutional form and regenerative form found in *Uca lactea* (de Haan) (see Yamaguchi, 1973), the differences are quite subtle and the variation between morphs is much less than that between major and minor chelipeds. Only individuals with complete major and minor chelipeds were used. Twenty-eight of the individuals had left major chelipeds; the remaining 35 had right major chelipeds. There was a large range in individual size, with cheliped length (as measured from the tip of the pollex to the back of the manus) ranging in major chelipeds from 9.55–34.05 mm and in minor chelipeds from 4.65–8.60 mm.

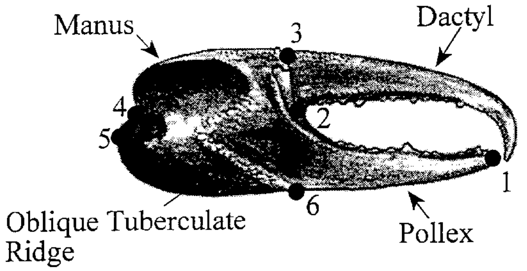

Fig. 1. Diagram of a cheliped with the six morphological landmarks labeled. The landmarks are as follows: 1, tip of the pollex; 2, lower junction between the dactyl and the manus; 3, upper junction between the dactyl and the manus; 4, top of the juncture between the carpus and the manus; 5, base of the juncture between the carpus and the manus; 6, the depression at the base of the pollex where (on the major cheliped) the oblique tuberculate ridge ends. Length was measured as the distance between landmarks 1 and 5. Height was measured as the distance between landmarks 3 and 6. (Figure from Crane, 1975).

The inner (palmar) surface of each cheliped was photographed using a 35-mm camera fitted with a 100-mm macrolens (for the major chelipeds) or a dissecting microscope at 60× (for the minor chelipeds) in order to obtain maximum resolution. The camera was locked in a vertical position and transparent tape was used to hold the chelipeds in a horizontal plane to minimize distortion. A small rule was photographed adjacent to each cheliped in order to provide a common scale. The photographs were projected onto a wall to obtain maximum magnification, and a GP–7 Grafbar Mark II sonic digitizer from Science Accessories Corporation was used to capture the coordinates of 6 morphological landmarks (in 2 dimensions) as well as 2 points on the rule for scaling purposes. The 6 landmarks (Fig. 1) were chosen for their relative ease in identification, their apparent homology between chelipeds, and the ability of the suite of landmarks to capture the general shape of the chelipeds. No points upon the dactyl were chosen because of the current inability of geometric morphometrics to deal with articulated movable structures.

A full, detailed, mathematical description of geometric morphometrics is beyond the scope of this paper. Rohlf and Bookstein (1990), Bookstein (1991), and Rohlf and Marcus (1993), as well as any other specific sources referenced in this paper, offer further details.

A Generalized Least-Squares (Procrustes) method (Rohlf and Slice, 1990) was used to superimpose all of the chelipeds and to create a single consensus configuration (Fig. 2) by scaling all of the chelipeds to the same centroid size and by translating, rotating, and reflecting them in order to optimally line up each group

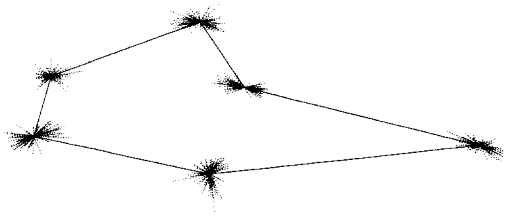

Fig. 2. Generalized Least-Squares superimposition of all 126 chelipeds showing variation at each landmark after the specimens have been scaled, translated, reflected, and rotated. The outline is formed by linking the average of the coordinates of each landmark and represents the consensus configuration. (Figure produced using GRF-ND, 1994).

of homologous landmarks. Because it is a more complete representation of the size of landmark-captured shapes, I used centroid size instead of more classical size measurements such as length or width in these analyses. Centroid size is the square root of the sum of squared deviations of the landmarks from the centroid (mathematical center of the landmarks) of the object (Sneath, 1967; Bookstein, 1991).

The consensus configuration was used to create a set of orthogonal shape axes, known as principal warps (Bookstein, 1991). The differences between each individual cheliped and the consensus configuration are projected onto the principal warps, yielding partial warp scores for each specimen. The partial warp scores represent the nonuniform deformations needed to transform the positions of the landmarks in the consensus configuration into those of each individual cheliped. Nonuniform components reflect variation such as nonlinear and localized variation (Bookstein, 1991). These scores are combined into a single matrix (**W**-matrix) from which a number of statistical analyses can be made (Rohlf, 1993). Two additional shape parameters describing uniform (affine) shape were calculated by a method proposed by Bookstein (1996), in order to reflect simple variation, such as linear shear and stretching.

A principal-component analysis of the **W**-matrix describes major trends of nonlinear shape variation (Rohlf, 1993). The first-principal component (also known as the first Relative Warp) represents the direction of maximum, nonuniform shape variation. The second Relative Warp represents the next largest direction of nonuniform shape variation orthogonal to the first, etc. Relative Warp scores for each individual cheliped represent how strong that form of variation is for an individual cheliped.

A multivariate analysis of variance (MANOVA) was performed on both the uniform and nonuniform (**W**-matrix) components of shape variation to determine whether shape differences exist between the major and minor chelipeds. To test whether these differences are due to size (allometry) or represent different ontogenetic growth patterns, multiple regressions of centroid size on the partial warps and uniform components, as well as multivariate analyses of covariance (MANCOVA), using major or minor cheliped as the categorical variable and centroid size as the covariate, were performed.

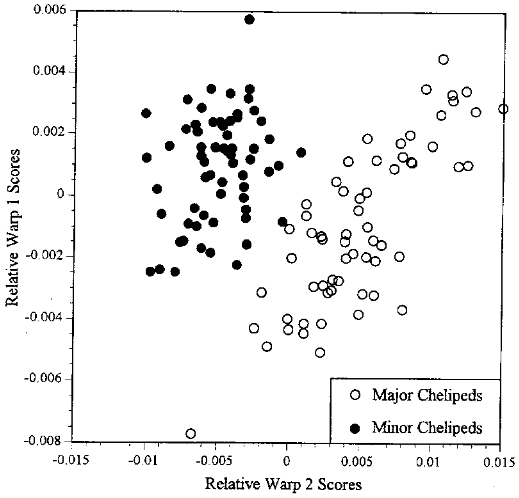

Fig. 3. Bivariate plot of Relative Warp 1 scores versus Relative Warp 2 scores. (Relative Warp scores were calculated by TPSRW, 1992).

Classical morphometric measures were created from the landmark data in order to compare the geometric morphometric results to traditional methods of analyzing allometry and growth, as well as to compare these results to other published studies (Levinton *et al*, 1995). The distance between landmarks 1 and 5 (the tip of the pollex to the base of the connection between the carpus and manus) was used as a measure of cheliped length (Fig. 1). The distance between landmarks 3 and 6 [the top of the joint between the dactyl and manus to the depression at the base of the pollex where (on the major cheliped) the oblique tuberculate ridge ends] was used as a measure of cheliped height. The distance between landmarks 1 and 6 (the tip of the pollex to the base of the pollex) was used as a measure of pollex length. While these are not the exact measures of length and height used by Levinton *et al.* (1995), they are close enough to be able to compare the results of the two methods.

RESULTS

A bivariate plot of Relative Warp 1 scores versus Relative Warp 2 scores (Fig. 3) shows a clear division between the two types of chelipeds, indicating that they can be distinguished by shape. Transformation grids showing the exaggerated effects of the first two Relative Warps display where most of the variation occurs (Figs. 4, 5). The first Relative Warp (Fig. 4), which represents the direction of maximal nonuniform shape variation, mostly shows variation along the length of the cheliped (the axis between landmarks 1 and 4). Deformation in one direction along this axis shows compression of the manus (distance between landmarks 2 and 4) and expansion of the pollex (dis-

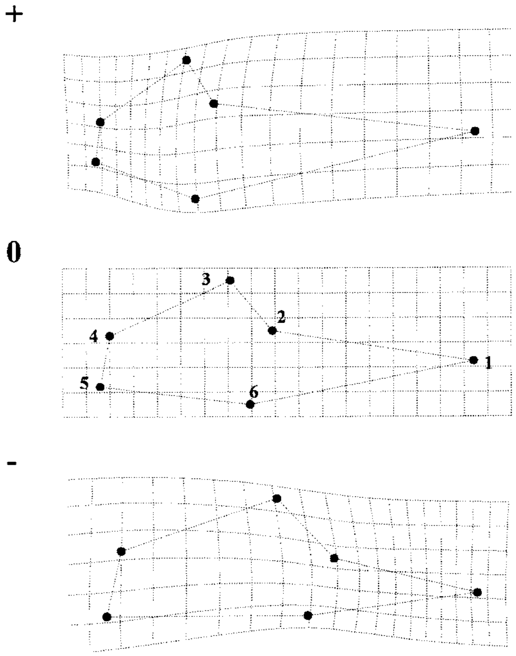

Fig. 4. Overall deformation of shape along the first Relative Warp for all 126 specimens. The first Relative Warp represents the direction of maximal nonuniform shape variation (obtained by a principal components analysis of the **W**-matrix). Positive deformations along this axis represent a short manus and a long pollex. Negative deformations represent a long manus and a short pollex. (Figures produced using TPSRW, 1992).

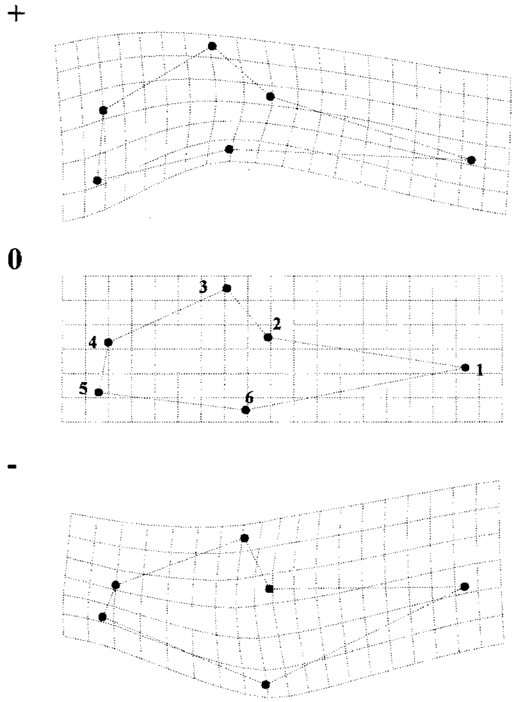

Fig. 5. Overall deformation of shape along the second Relative Warp for all 126 specimens. Positive deformations along this axis represent a narrow cheliped; negative deformations represent a broad cheliped. (Figures produced using TPSRW, 1992).

tance between landmarks 1 and 6). Deformation in the other direction shows compression of the pollex and expansion of the manus. The pollex also shows variation in the height of the base of the pollex (distance between landmarks 2 and 6). The second Relative Warp (Fig. 5) represents variation along the height of the cheliped (the axis between landmarks 3 and 6). Deformation along this axis mainly concerns the relative location of the ends of the cheliped (the tip of the pollex and the back of the manus where the carpus attaches) to the center of the cheliped (the juncture of the manus and the dactyl and the base of the pollex). Deformation in one direction shows the cheliped becoming straighter with landmarks 1, 5, and 6 becoming fairly linear, while deformation in the other direction shows a strongly curved cheliped with the tip of the pollex and the lower juncture of the carpus and manus moving closer to the dactyl with the bottom of the pollex moving farther away.

The results of the MANOVA (Table 1)

Table 1. Results of a two-way MANOVA of nonuniform (**W**-matrix) and uniform (affine) shape variables, comparing the effects of major versus minor cheliped and individuals.

Source	Wilk's Λ	*Fs*	*d.f.*	*P*
Nonuniform shape variables (**W**-matrix)				
Individuals	0.01092049	1.0622	372, 349.84	0.2838
Chelipeds	0.12885259	64.2277	6, 57	0.0001
Uniform (affine) shape variables				
Individuals	0.32664885	0.7376	124, 122	0.9537
Cheliped	0.15548838	165.6561	2, 61	0.0001

Table 2. Results of MANCOVAs on nonuniform (**W**-matrix) and uniform (affine) shape variables, using major and minor cheliped as categorical variables and centroid size as the covariates.

Source	Wilk's Λ	*Fs*	*d.f.*	*P*
Nonuniform shape variables (**W**-matrix)				
Cheliped	0.63924415	11.0988	6, 118	0.0001
Centroid size	0.81119511	4.5774	6, 118	0.0003
Uniform (affine) shape variables				
Cheliped	0.39158077	94.7788	2, 122	0.0001
Centroid size	0.45058051	74.3809	2, 122	0.0001

show a significant difference in both the uniform and nonuniform components of shape between the major and minor chelipeds, but find no difference in shape among individuals. The multiple regressions found a significant relationship between size and shape (nonuniform components of shape: $R^2 = 0.740$, $F = 51.52$, $d.f. = 6, 119$, $P < 0.0001$; uniform components of shape: $R^2 = 0.722$, $F = 174.86$, $d.f. = 2, 123$, $P < 0.0001$), suggesting an allometric growth trend in the chelipeds. In order to test whether the allometric trends in major and minor chelipeds were identical, a multivariate equivalent of a homogeneity of slopes test was performed by a MANOVA in which an interaction between cheliped and centroid size was examined. For both uniform and nonuniform components, there was no significant interaction (uniform components, $P < 0.2305$; nonuniform components $P < 0.8607$) between cheliped and centroid size, indicating that the multivariate "slopes" were equal (in a univariate case, this is equivalent to discovering that two linear regressions are parallel).

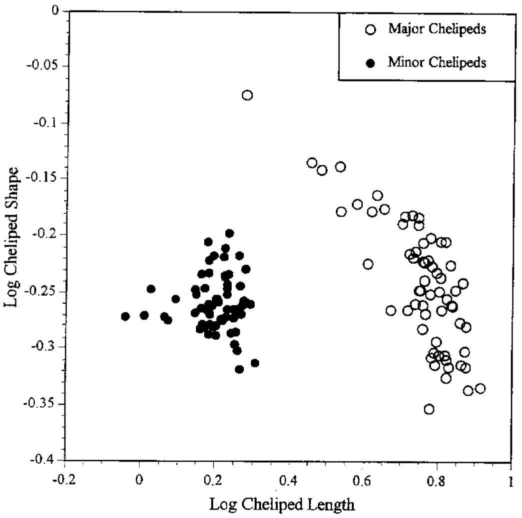

Fig. 6. Relationship between length and shape of chelipeds of *Uca pugnax*. Measurements were extrapolated from landmark data. Shape is the ratio of cheliped height to pollex length. The slope of the least-squares linear regression of shape on length for the major chelipeds is -0.396246 ($P < 0.0001$), while that of the minor chelipeds is -0.003270 ($P = 0.9449$).

These results validate the use of a MANCOVA to test whether the major and minor chelipeds are following the same allometric trend; if they are, then the major cheliped is simply an allometric projection of the minor cheliped. The results of the MANCOVA (Table 2) show a significant difference between the shape of the major and minor chelipeds, even when standardized for size. This result is equivalent to the usual ANCOVA case where both chelipeds have trajectories with the same slope but different *y*-intercepts.

A univariate measure of cheliped shape was defined as the ratio between cheliped height and pollex length; this measurement was chosen, because it can be used in the description of mechanical advantage in chelipeds of *Uca* (Levinton and Judge, 1993). This ratio was plotted against cheliped length in order to examine univariate measures of allometry (Fig. 6). Linear regression for major chelipeds showed a significant ($Fs = 95.6379$, $d.f. = 1, 61$, $P < 0.0001$) trend of decreasing mechanical advantage as size increased, while regression for minor chelipeds showed no significant ($Fs = 0.0048$, $d.f. = 1, 61$, $P = 0.9449$) trend. This result is identical to that obtained by Levinton *et al.* (1995).

DISCUSSION

The results indicate that both major and minor chelipeds not only show allometric growth trends, but show the same growth

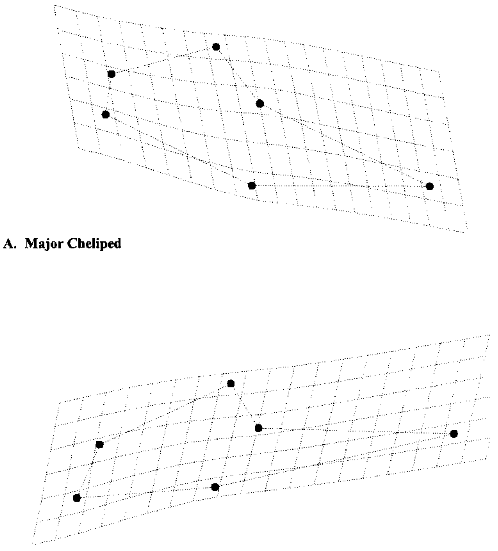

Fig. 7. Predicted cheliped shapes. These figures represent a projection of the exaggerated differences (including both uniform and nonuniform variation) between major (A) and minor (B) chelipeds. The major cheliped has a wider manus and pollex; the minor cheliped is more slender. (Figures produced using TPSREG, 1992).

trend. However, the major cheliped is not simply an allometric projection of the minor cheliped; the multivariate growth trajectories are parallel, but not coincident. These results indicate that the major cheliped is not restricted to the developmental pathway of the minor cheliped. It is also likely that selective pressures other than those for size were acting upon the major chelipeds. This agrees with previous findings that the major chelipeds are functionally active, despite high metabolic costs (Levinton and Judge, 1993).

It is possible to predict average shapes of the major and minor chelipeds from the **W**-matrix (Fig. 7) using the thin-plate spline-bending energy formulas that have been brought into geometric morphometrics (Rohlf and Marcus, 1993). The major cheliped has a taller manus and pollex than does the minor cheliped. The relative size between the cheliped and the diameter of the carpus is larger in the major cheliped than in the minor cheliped. The minor cheliped has a relatively longer pollex than does the major cheliped, as evidenced by the location of landmark 6. The minor cheliped also has a narrower dactyl (as evidenced by the distance between landmarks 2 and 3).

Mechanical advantage in crab chelipeds has been characterized by Warner and Jones (1976) and expanded by Levinton and Judge (1993) for *U. pugnax*; it is described by the ratio of cheliped height and pollex length. Because the major cheliped has both a relatively shorter pollex and taller manus (Fig. 7) than the minor cheliped, all other things being equal, the major cheliped has a greater mechanical advantage than the minor cheliped. Other factors which affect the functionality of the chelipeds include the cross-sectional muscle area (Levinton *et al.*, 1995), the muscle fiber composition (Trinkaus-Randall and Govind, 1985), and the angle of muscle insertion (Rhodes, 1986). Each of these factors shows the same trend: the major cheliped tends to be suited for relatively slower, more powerful crushing motions than is the minor cheliped. This is further evidence that natural selection for combat, and not display, has been a major force in the evolution of the major cheliped.

Levinton *et al.* (1995) showed that there is an inverse relationship between mechanical advantage and the length of the major cheliped; as cheliped size increased, mechanical advantage decreased. Minor chelipeds did not show any relationship between mechanical advantage and size. There is a disparity between these results and mine, since I have shown that the major and minor chelipeds follow parallel multivariate allometric trends, while the univariate measures of mechanical advantage show different trends (see Fig. 6). The landmark-based, multivariate data appear to be detecting subtle trends that the univariate measures are unable to detect. The overall shape differences between large and small major chelipeds are the same as those between large and small minor chelipeds: as size increases, the pollex becomes slimmer and longer, leading to decreased mechanical advantage. However, the width of the manus does not show the same trend in major and minor chelipeds. The manus becomes relatively wider as size increases in major chelipeds; in minor chelipeds, the manus becomes narrower. The difference between large and small minor chelipeds is subtle and appears not to be a significant change. This may explain why the multivariate trend between the major and minor chelipeds is identical, even though the minor cheliped does not appear to show a reduction in mechanical advantage as size increases.

The similar allometric trends in the major and minor chelipeds suggest a certain amount of canalization in the development of the major cheliped. The allometric trend of shape of the major cheliped is not divergent from that of the minor cheliped, but rather is offset from it. There appears to be room for selection to act within this restricted growth regimen, since there are different mechanical trends in the major and minor chelipeds. The loss of mechanical advantage as size increases suggests that selection for gripping speed and not strength was important in the evolution of the major cheliped in *U. pugnax*. This is further supported by the observation that males of this species do not seem to damage each other during combat (Levinton *et al.*, 1995). It has been recently discovered that *Uca tetragonon* (Herbst) preys upon conspecifics and other small crabs using the major cheliped (Koga *et al.*, 1995). This new and exciting behavior should have different functional constraints than waving display and nondamaging combat and may lead to new theories about the origin of the major cheliped in the genus *Uca*.

None of this is meant to imply that display has not been important in the evolution of the major cheliped. Each species has a stereotypical complex waving display that is an inherent part of their mating system and may be important in the reproductive isolation of different species (Salmon *et al.*, 1978). Because individuals with smaller chelipeds normally retreat after encountering individuals with larger chelipeds before combat takes place, selection for size must be important. Both external morphological asymmetry (Takeda and Murai, 1993) and thoracic and cheliped muscle asymmetry (Rhodes, 1986) have been correlated with the patterns of waving displays of different species. Selection for the dual functions of display and combat has been found in other animals, such as horned beetles and deer. One of the most famous examples is the Irish Elk *Megaloceras giganteus* Blumenbach. For a long time it was thought that the immense antlers of the Irish Elk could only have been used for display (Huxley, 1932; Gould, 1974), but more recently it has been shown that they were used in combat (Kitchener, 1987).

Further investigations will allow us to compare these trends in other members of the genus and to search for correlations between the functional shape of the chelipeds and behaviors such as waving display and combat style. While this study examined the allometry of major and minor chelipeds, it would be interesting to track the ontogeny of cheliped development in a single individual, from pre-major cheliped determination through full growth. Other important comparisons for the fiddler crab include looking for differences between the shape of the minor cheliped in males and the chelipeds of females, and whether species that are predominantly right-handed show the same relationship as those that appear to choose handedness by chance. Jones and George (1982) have suggested that handedness may be a useful tool in aiding the discovery of taxonomic relationships between the species; more rigorous descriptions of cheliped shape may turn out to be equally useful. These methods could also be used to examine similar questions in other species. Smith and Palmer (1994) studied the plasticity of cheliped size and crushing force in the brachyuran crab *Cancer productus* Randall by manipulating its diet; the methods presented here could be used to determine whether there were correlated effects of diet on cheliped shape. These studies could lead to a better understanding of the evolution of asymmetry and dimorphism.

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LITERATURE CITED

Ahmed, M. 1978. Development of asymmetry in the fiddler crab *Uca cumulanta* Crane, 1943 (Decapoda Brachyura).—Crustaceana 34: 294–300.

Bookstein, F. L. 1991. Morphometric tools for landmark data.—Cambridge University Press, New York, New York. Pp. i–xvii, 1–435.

———. 1996. Standard formula for the uniform shape component in landmark data.—*In:* L. Marcus, M. Corti, A. Loy, G. Naylor, and D. Slice, eds., Advances in morphometrics. Pp. 153–168. Plenum Publishing Corporation, New York, New York.

Caravello, H. E., and G. N. Cameron. 1987. The effects of sexual selection on the foraging behaviour of the Gulf Coast fiddler crab, *Uca panacea*.—Animal Behavior 35: 1864–1874.

Christy, J. H., and M. Salmon. 1984. Ecology and evolution of mating systems of fiddler crabs (Genus *Uca*).—Biological Reviews 59: 483–509.

Crane, J. 1975. Fiddler crabs of the world.—Princeton University Press, Princeton, New Jersey. Pp. i–xxiii, 1–736.

Gould, S. J. 1974. The origin and function of 'bizarre' structures: antler size and skull size in the 'Irish Elk,' *Megaloceras giganteus*.—Evolution 28: 191–220.

Govind, C. K. 1984. Development of asymmetry in the neuromuscular system of lobster claws.—Biological Bulletin 167: 94–119.

———. 1989. Asymmetry in lobster claws.—American Scientist 77: 468–474.

Huxley, J. S. 1932. Problems of relative growth.—MacVeagh, London, England. Pp. 1–276.

Jones, D. S., and R. W. George. 1982. Handedness in fiddler crabs as an aid in taxonomic grouping of the genus *Uca* (Decapoda, Ocypodidae).—Crustaceana 43: 100–102.

Kitchener, A. 1987. Fighting behaviour of the extinct Irish Elk.—Modern Geology 11: 1–28.

Koga, T., S. Goshima, M. Murai, and S. Poovachiranon. 1995. Predation and cannibalism by the male fiddler crab *Uca tetragonon*.—Journal of Ethology 13: 181–183.

Levinton, J. S., and M. L. Judge. 1993. The relationship of closing force to body size for the major claw of *Uca pugnax* (Decapoda: Ocypodidae).—Functional Ecology 7: 339–345.

———, ———, and J.P. Kurdziel. 1995. Functional differences between the major and minor claws of fiddler crabs (*Uca*, family Ocypodidae, order Decapoda, subphylum Crustacea): a result of selection or developmental constraint?—Journal of Experimental Marine Biology and Ecology 193: 147–160.

Mellon, D. F., Jr. 1981. Nerves and transformation of claw type in snapping shrimps.—Trends in Neuroscience 4: 245–248.

———, and P. T. Stephens. 1978. Limb morphology and function are transformed by contralateral nerve section in snapping shrimps.—Nature 272: 246–248.

Miller, D. C. 1973. Growth in *Uca*, 1. Ontogeny of asymmetry in *Uca pugilator* (Bosc) (Decapoda, Ocypodidae).—Crustaceana 24: 119–131.

Morgan, T. H. 1923. The development of asymmetry in the fiddler crab.—American Naturalist 57: 269–273.

———. 1924. The artificial induction of symmetrical claws in male fiddler crabs.—American Naturalist 58: 289–295.

Rhodes, W. R. 1986. A comparative study of thoracic and cheliped muscle asymmetry in male fiddler crabs (Genus: *Uca*).—Biological Bulletin 170: 335–349.

Rohlf, F. J. 1993. Relative warp analysis and an example of its application to mosquito wings.—*In:* L. F. Marcus, E. Bello, and A. Garcia-Valdecasas, eds., Contributions to morphometrics. Pp. 131–159. Museo Nacional de Ciencias Naturales, Madrid, Spain.

———, and F. L. Bookstein, eds. 1990. Proceedings of the Michigan Morphometrics Workshop, Ann Arbor, Michigan. Pp. i–viii, 1–380.

———, and L. F. Marcus. 1993. A revolution in morphometrics.—Trends in Ecology and Evolution 8: 129–132.

———, and D. E. Slice. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks.—Systematic Zoology 39: 40–59.

Salmon, M., G. Hyatt, K. McCarthy, and J. D. Costlow, Jr. 1978. Display specificity and reproductive isolation in the fiddler crabs, *Uca panacea* and *Uca pugilator*.—Zeitschrift fuer Tierpsychologie 48: 251–276.

Smith, L. D., and A. R. Palmer. 1994. Effects of manipulated diet on size and performance of brachyuran crab claws.—Science 264: 710–712.

Sneath, P. H. A. 1967. Trend-surface analysis of transformation grids.—Journal of Zoology 151: 65–122.

Takeda, S., and M. Murai. 1993. Asymmetry in male fiddler crabs is related to the basic pattern of cheliped-waving display.—Biological Bulletin 184: 203–208.

Trinkaus-Randall, V., and C. K. Govind. 1985. Development of bilateral asymmetry in the cheliped extensor muscle of male fiddler crabs.—Journal of Crustacean Biology 5: 25–29.

Valiela, I., D. F. Babiec, W. Atherton, S. Seitzinger, and C. Krebs. 1974. Some consequences of sexual dimorphism: feeding in male and female fiddler crabs, *Uca pugnax* (Smith).—Biological Bulletin 147: 652–660.

Vernberg, F. J., and J. D. Costlow, Jr. 1966. Handedness in fiddler crabs (Genus *Uca*).—Crustaceana 11: 61–64.

Warner, G. F., and A. R. Jones. 1976. Leverage and muscle type in crab chelae (Crustacea: Brachyura).—Journal of Zoology 180: 57–68.

Yamaguchi, T. 1973. Asymmetry and dimorphism of chelipeds in the fiddler crab, *Uca lactea* De Haan.—Zoological Magazine 82: 154–158.

———. 1977. Studies on the handedness of the fiddler crab, *Uca lactea*.—Biological Bulletin 152: 424–436.

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CHAPTER 4

FIDDLER CRAB CLAW SHAPE VARIATION: A GEOMETRIC MORPHOMETRIC ANALYSIS ACROSS THE GENUS *UCA*

4.1 ABSTRACT

For decades, the extreme asymmetric chelipeds of male fiddler crabs (genus *Uca*) have been used as almost a model system for the description and discussion of allometry. Almost all previous studies, however, have concentrated on intraspecific variation and have not examined claw variation among species. Modern methods of describing shape and size, geometric morphometrics, were used to study claw variation across the genus. These analyses were also performed in a phylogenetic context using independent contrasts. Within species, major claws show allometric growth in both shape and size; minor claw growth is isometric. Across species, however, both major and minor claws show isometric trends in size and allometric trends in shape. Although the variation is much greater in major claws, the allometric pattern of shape change for both majors and minors can be characterized by a general increase in the relative length of the pollex relative to the manus, and the relative size of the propodus to that of the carpus. There is some phylogenetic clustering of claw shape and size, but there does not appear to be significant levels of phylogenetic dependence because none of the conclusions are changed when using independent contrasts.

4.2 INTRODUCTION

Interest in morphological variation has long been a driving force behind many biological studies; many careers have been jumpstarted by a fascination with the wide variety of forms found in nature. Understanding the nature and searching for an explanation of this variety is a major research focus, including fields as diverse as functional morphology, macroevolution, sexual selection, and evolutionary developmental biology. This is made more difficult when sets of morphological characters have dual functions, such as those which serve both as signals in sexual selection (ornaments) as well as weapons in direct intrasexual competition (armaments) (Berglund *et al.* 1996). A classic example of such a dichotomy can be found in the fiddler crab (Brachyura, Ocypodidae, *Uca*).

All fiddler crab species show an extreme form of sexual dimorphism and body asymmetry. Male fiddler crabs have a small minor claw used for feeding and a large major claw (four to five times longer than the minor claw and containing up to half the mass of the animal) used for display and fighting. Females have two small claws which resemble the males' minor claw. Females are usually cryptic, while males tend to be conspicuous, with flashy, gaudy colors (particularly the coloration of the major claw) easily seen from afar, especially when they are in the midst of a vigorous display of major claw waving. Most species have equal numbers of left- and right-handed males (handedness refers to the side with the major claw), except for a single clade of seven species (see Chapter 2) which is predominantly right handed (Barnwell 1982; Jones and George 1982; Shih *et al.* 1999).

Certain aspects of fiddler crab morphology have been extensively studied, especially with regard to asymmetry. Studies have ranged from how the direction of asymmetry is determined (Morgan 1923, 1924; Vernberg and Costlow 1966; Yamaguchi 1973, 1977; Ahmed 1978; Ahmed and Khan 1978) to the development of asymmetry in the chelipeds (Huxley and Callow 1933; Miller

1973) and muscles (Trinkaus-Randall and Govind 1985; Rhodes 1986), as well as description of the asymmetry in walking legs and other appendages (Tazelaar 1933; Takeda and Murai 1993). Additional morphological analyses include studies of the feeding morphology (Weissburg 1991), allometry of the abdomen (Huxley 1924b; Green and Schochet 1990) and the claws (Yerkes 1901; Huxley 1924a, 1927, 1932; Huxley and Callow 1933; Gibbs 1974; Frith and Brunemeister 1983; Rosenberg 1997), and the relationship between claw shape and closing force (Brown *et al.* 1979; Levinton and Judge 1993; Levinton *et al.* 1995). A small, multivariate analysis (principal component analysis) performed on six South American species showed a correspondence between some general measure of the shape of each species and their phylogeny (Diniz Filho 1990). Veitch (1978) and Williams *et al.* (1980) looked at simple multivariate allometry in the claws, legs, and abdomens of three species.

The study of allometry has long been connected to fiddler crabs; the original descriptions of the allometric equation (Huxley 1924a, 1927) examined the relationship between major claw mass and body mass in *Uca pugnax*. Allometry is the study of proportional changes in traits as size changes; the absence of this change is known as isometry. There are a number of fundamentally different types of allometry, depending on the scale over which it is examined (Cock 1966; Gould 1966; Levinton 1988; Klingenberg 1996). Static allometry is the study of variation among individuals of the same age class; ontogenetic allometry is the study of variation as an individual grows; evolutionary allometry is the study of variation across species. In practice, studies within populations tend to be neither static nor ontogenetic; they usually examine multiple individuals of unknown ages and often assume that size is a proxy of age. Although fiddler crabs do not grow continuously but rather in discreet molt stages, the size distribution of individuals in a population tends to be continuous (Green and Schochet 1990).

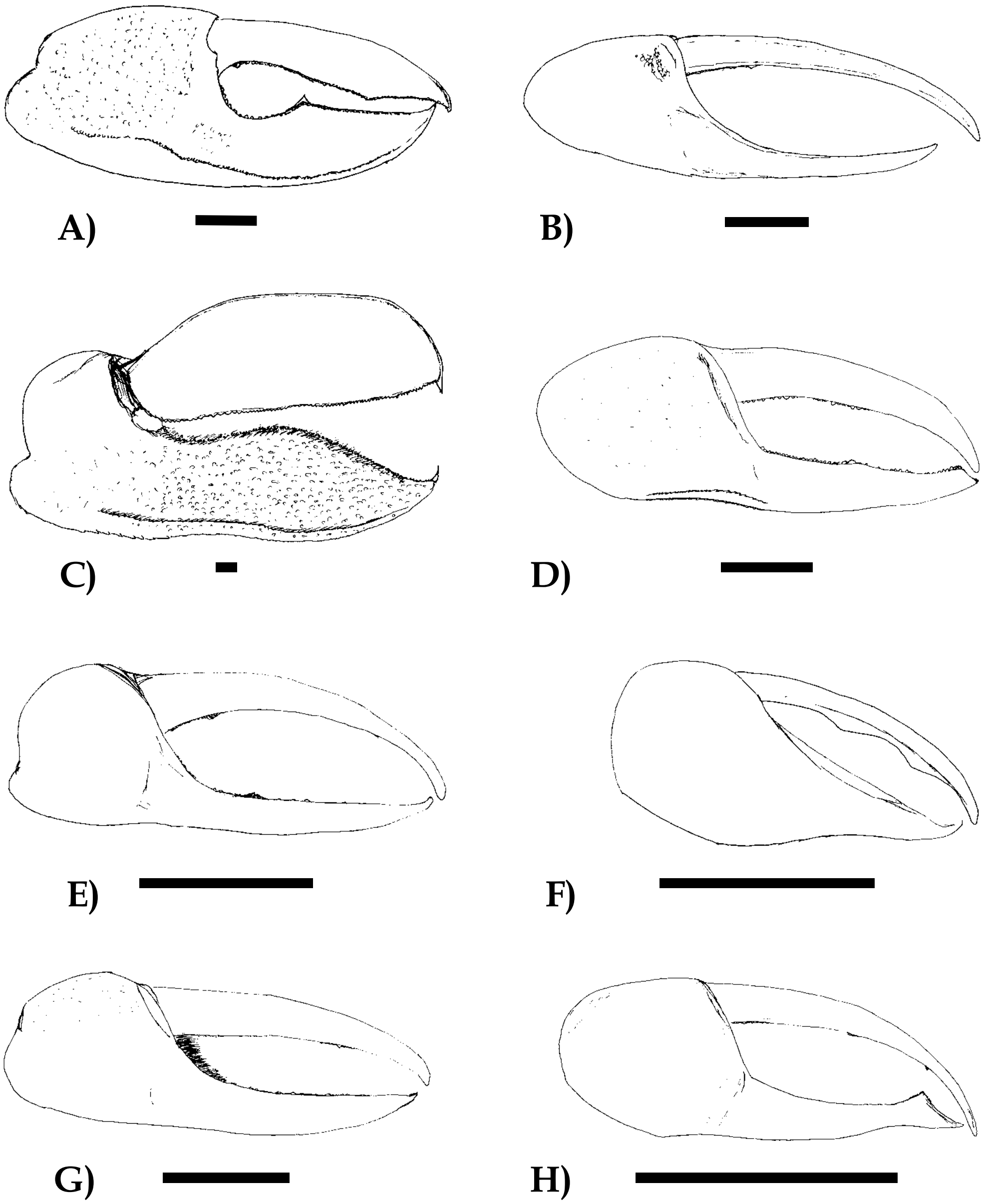

Figure 4.1. Examples of major claws from different species of *Uca*. Each illustration is of the outer surface of a right major claw; the bar under each claw represents 5 mm. A) *Uca stylifera*, B) *Uca festae*, C) *Uca ornata*, D) *Uca herradurensis*, E) *Uca terpsichores*, F) *Uca saltitanta*, G) *Uca beebei*, H) *Uca batuenta*.

Despite the large degree of interspecific variation in the major claw morphology of fiddler crabs (Figure 4.1), little work has been done to examine this variation across more than just a few species. Other than characters used in the systematic discrimination of species (e.g. Crane 1975) and a few small studies of univariate allometry (see refs. above), no large-scale comparative analysis of major claw morphology has been attempted, especially with regard to behavior. Furthermore, only Crane (1966, 1967, 1975) has proposed a functional relationship between most major claw characters and behavior, specifically to combat. Crane found that most of the discrete characters found on the major claw (e.g. the groove found on the cuff of the dactyl or the tubercles on the ventral margin of the pollex) serve as contact zones during combat. Specific characters are used during specific combat maneuvers (e.g. the groove on the cuff of the dactyl is a point of contact when two crabs interlace their claws). Crane (1975) identified 84 major claw characters in just a single subgenus, at least 60 of which were known to be used during combat.

Although apparently much more homogeneous than the major claws, there is considerable variation in the shape and structure of the minor claws as well. These differences range from gape width (the space between the dactyl and pollex), to the presence, number, and size of teeth, to the relative thickness of the chela. Minor claw variation is much less studied than that of the major claw. Crane (1975) observed that the gape width appeared to be narrower in sand-dwelling species than mud-dwelling species; this correlation was tested and confirmed by Neiman and Barnwell (1997).

The purpose of this study is to describe and explore the variation in claw shape across the genus *Uca*, and to examine the relative effects of intra- and interspecific allometry and common descent in explaining the observed variation. The role of these factors will be explored for both major and minor claws to estimate the flexibility these structures have under their differing selection pressures (e.g. sexual selection).

4.3 MATERIAL AND METHODS

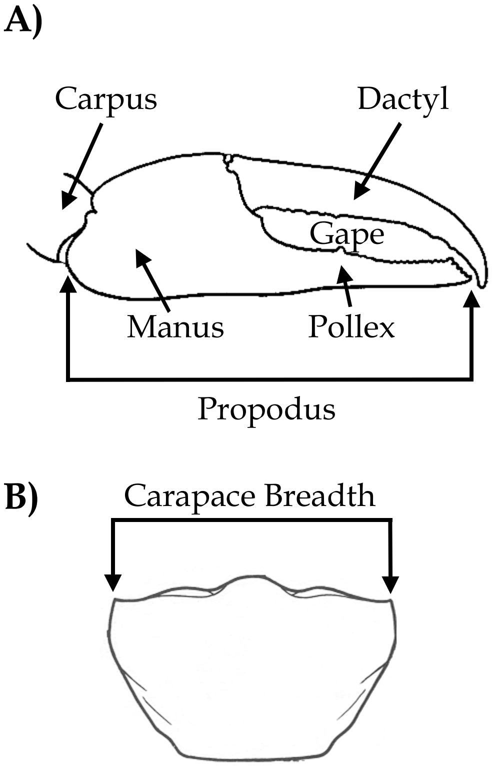

Figure 4.2. Diagrammatic representation of the morphological features of fiddler crabs described in the text. A) outside surface of a right major claw; B) dorsal view of a carapace. Figure modified from Crane (1975).

Data Acquisition

Specimens examined were obtained through personal collections by myself and others and from museum collections (Appendix I). Of the ninety-seven recognized fiddler crab species, eighty-eight were included in the analysis. The missing species are evenly spread across the genus and their exclusion should not change any overall conclusions. Major claw data was available for all eighty-eight species, minor claw data for eighty-six (the single specimens of *Uca intermedia* and *U. typhoni* were missing their minor chelipeds). Sample sizes for each species ranged from one to fifty. A total of 1652 claws were analyzed, 851 major and 801 minor.

A full, detailed, mathematical description of geometric morphometrics is beyond the scope of this paper. See Rohlf and Bookstein (1990), Bookstein (1991), Rohlf and Marcus (1993), and Marcus *et al.* (1996) as well as other specific sources referenced in this paper for specific details. A number of programs (Rohlf 1998a,b,c) were used to calculate the shape variables described below, depending specifically on the analysis being performed.

As a measure of crab size, the carapace breadth (the distance between the antero-lateral angles; Figure 4.2b) was measured with calipers and recorded to the nearest 1/20th of a millimeter for each individual crab. Previous studies (e.g. Huxley and Callow 1933; Miller 1973; Crane 1975; Frith and Brunemeister 1983) have often used carapace length, however, carapace breadth is an easier, more precise measure and has been shown to be a stronger predictor of claw length than carapace length (Frith and Brunemeister 1983).

The inner (palmar) surface of each individual claw was photographed with a digital camera. Before recording data, each photograph was reflected and rotated so that each appeared to be a left claw; this procedure was done to minimize digitizing error due to perceptual or mechanical difference in digitizing the same point in different parts of the photo (Auffray *et al.* 1996; Klingenberg and McIntyre 1998). Landmark coordinates and outlines were digitized from each photograph using tpsDig (Rohlf 1999b).

The landmarks (Figure 4.3a) used are the same as in Rosenberg (1997; Chapter 3). The six landmarks are 1) the tip of the pollex, 2) the point which marks the junction between the pollex and the manus on the ventral margin of the claw, 3,4) the lower and upper attachment points of the carpus with the manus, at the edge of the carpal cavity, and 5,6) the upper and lower points which mark the articulation of the dactyl with the manus. The six landmarks were chosen for their relative ease in identification, their apparent homology in all species, and the ability of the suite of landmarks to capture the general shape of a claw. While there were other potential landmarks that could have been used to analyze the shape of claws in specific species (e.g. the crest of the oblique ridge on the palm), only landmarks that could be found on all species were used in the analyses. No points on the dactyl were chosen for two reasons: first, because geometric morphometrics does not currently contain methods that are designed to deal with articulated structures (although see Adams 1999a,b); and second, because only a single landmark could be identified on the dactyl, the tip, and this would add little to the analyses given the strong correlation between the length of the dactyl and the length of the pollex.

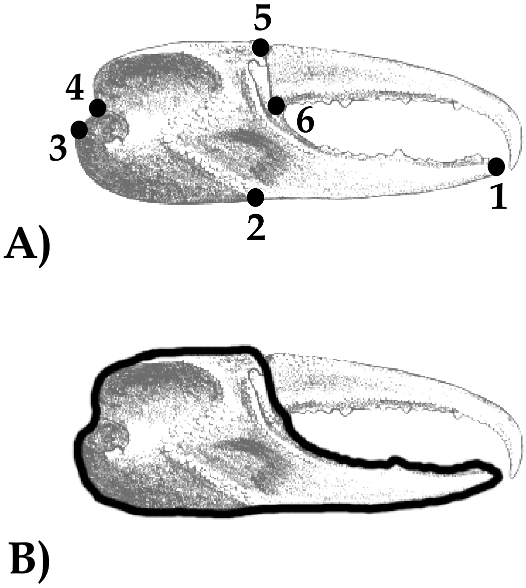

Figure 4.3. The shape data collected from each claw. A) landmarks; B) outline. Figure modified from Crane (1975).

Centroid size, which is the sum of the squared distances between each landmark and the centroid of the landmark configuration (Sneath 1967), was used as a measure of claw size. The landmark data were transformed into shape variables as follows: first, the landmarks of each specimen were optimally aligned using a Generalized Procrustes Analysis (GPA) in order to remove the non-shape effects of translation, rotation, and scale (Rohlf and Slice 1990; Rohlf 1999a). After superimposition, each landmark configuration corresponds to a single point in a non-Euclidean multi-dimensional space known as Kendall's shape space (Kendall 1981, 1984); this space has $2p - 4$ dimensions, where p is the number of two-dimensional landmarks. Because of the difficulty in performing standard multivariate statistics in non-Euclidean space, each data point is then projected into a Euclidean space (also of $2p - 4$ dimensions) tangential to a reference point (usually the mean) in the shape space (Kent 1994; Rohlf 1999a). As long as variation in shape space is small, the data in tangent space is almost a perfect approximation of the data in shape space; this was tested with the program tpsSmall (Rohlf 1998d). Multivariate descriptions of the data in tangent space (the shape variables) can be generated through a variety of methods (Rohlf 1999a); I used the thin-plate spline approach, which decomposes the data into two components of uniform shape change (Bookstein 1996) and $2p - 6$ components (known as partial warp scores, PWS) of nonuniform shape change (Bookstein 1991; Rohlf 1993). The six landmarks on the claws led to eight landmark shape variables (six PWS and two uniform scores).

The recorded outline of each claw consisted of the edge of the entire propodus (Figure 4.3b); the dactyl was not included for the same reasons it was not included with the landmark data. The outline data were transformed into shape variables by Elliptical Fourier Analysis (EFA) (Kuhl and Giardina 1982; Rohlf and Archie 1984) using Morpheus *et al.* (Slice 1998). EFA renders complex closed curves into a series of sums of sines and cosines by decomposing changes in the x- and y-coordinates of the outline independently as a function of the total chordal distance around the curve (scaled from 0 to 2π radians). This analysis generates $4h - 3$ coefficients to describe the outline, where h is the number of harmonics. The number of harmonics is somewhat arbitrary; each additional harmonic describes variation at smaller and smaller scales (Rohlf and Archie 1984). One wishes to choose enough harmonics so that the curve is being

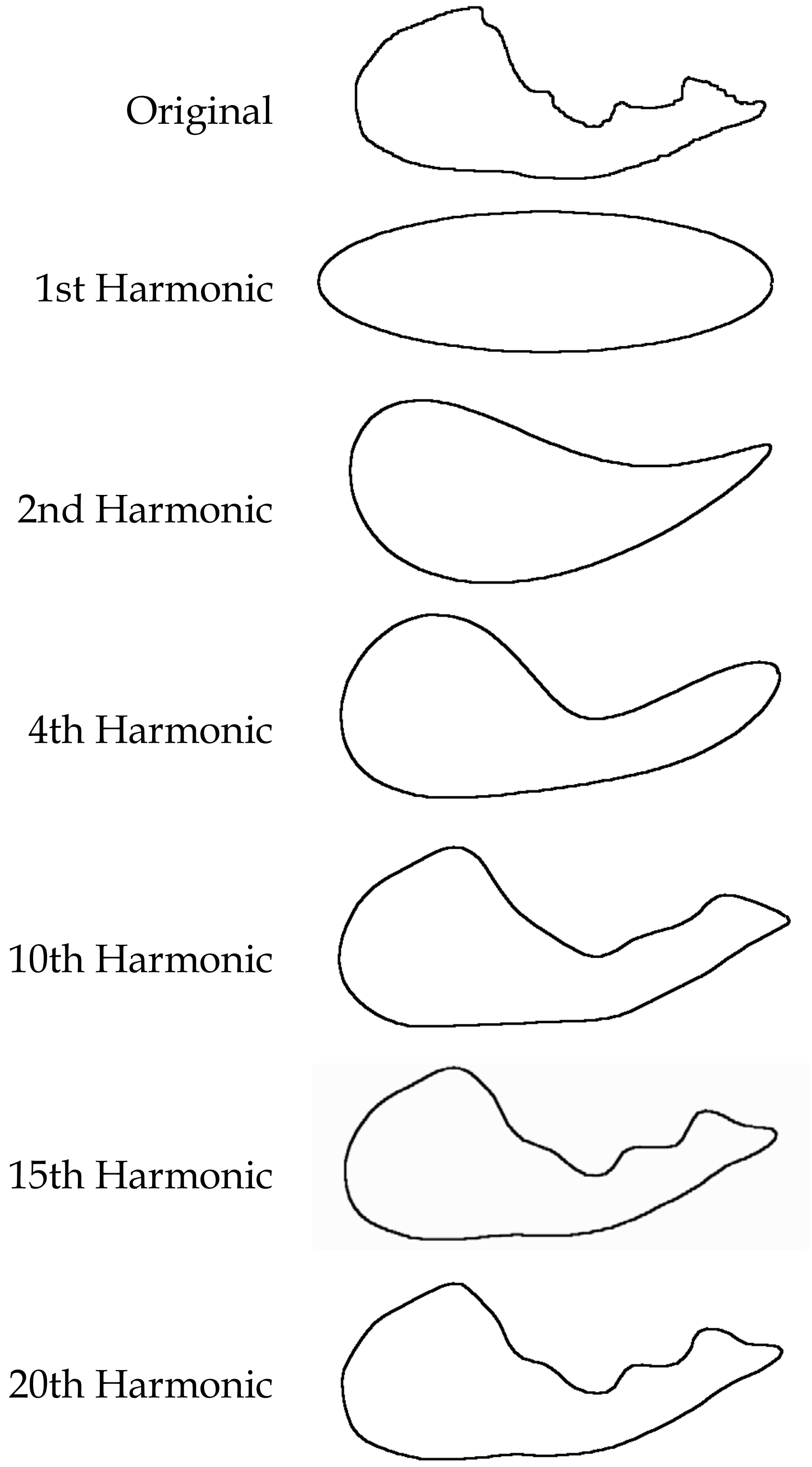

Figure 4.4. Elliptical Fourier reconstructions of an *Uca vocans* claw, illustrating how increasing the number of summed harmonics more accurately reproduces the original shape.

accurately described, but not so many that one is inflating the number of variables beyond the information content contained therein and so one does not have to deal with higher dimensional spaces than needed. Figure 4.4 illustrates the elliptical Fourier reconstruction of an *Uca vocans* claw (one of the more complicated shapes in these analyses). With only a few harmonics, the claw is poorly estimated; as the number increases, the accuracy of the reconstruction increases. Continuing to increase the number of harmonics (e.g. going from 15 to 20 in Figure 4.4) eventually adds little to the outline estimate. For these analyses I chose 12 harmonics, which was the fewest number which appeared to accurately reproduce the more complicated claw shapes, leading to 45 outline shape variables.

Analysis

Size Allometry

The intraspecific relationship of claw size to crab size (major and minor separately) was analyzed through linear regression of *ln* centroid size onto *ln* carapace breadth. The regression was calculated for each species individually (for all species with $n \geq 9$). Similar analyses have been performed previously on a number of species (Huxley and Callow 1933; Miller 1973; Gibbs 1974; Frith and Frith 1977; Frith and Brunemeister 1983; Levinton *et al.* 1995), but this is a natural starting place for this study. The previous studies used claw length, dactyl length, relative claw proportions, or claw mass.

The regression was also calculated on species means in order to examine the interspecific relationship of claw size to crab size. Because species data do not represent independent data points, it is necessary to “remove” the effect of phylogeny from comparative analyses (Felsenstein 1985; Harvey and Pagel 1991). The interspecific regression was repeated after both carapace and centroid size were standardized using Felsenstein’s method of independent contrasts

(Felsenstein 1985). Both cladograms from Chapter 2 (Figures 2.4–2.5) were used as possible phylogenies in calculating the contrasts. Although there may have been near simultaneous radiations of fiddler crab taxa, polytomies in the cladogram were assumed to be "soft" (Maddison 1989); therefore, a conservative approach was taken and contrasts were only calculated for distinct nodes; variables at polytomous nodes were estimated by averaging all of the branches of the polytomy (Rohlf 2000). Branch lengths were calculated from the phylogeny based on the number of character changes (based on the weight of the character) along each branch (Garland *et al.* 1992). These phylogenies are based on morphological characters, many of which are found on the major and minor claws. However, only a few characters referred to claw shape; therefore, there should be no concerns about circularity.

Landmark and Outline Correlation

Because all of the landmarks fall on the outline of the claw, it is quite possible that there will be a strong correlation between the two data sets. In order to examine whether the landmark and outline data are describing the same or different information, a partial least squares analysis (PLS) was performed. PLS is a technique for calculating the covariation between two multivariate data sets (Bookstein *et al.* 1996; Rohlf and Corti *In press*). This analysis calculates two sets of vectors (one for each data set) that represent linear combinations of the variables in each data set, such that the linear combinations account for as much of the covariation between the data sets as possible. Each vector in one set is only correlated with its single paired vector for the other data set. Unlike canonical correlation analysis, however, the vectors within a data set do not have to be orthogonal. The statistical significance of each correlation can be determined using a permutation test.

In order to estimate the relationship between landmark shape and outline shape, tpsPLS (Rohlf 1998a) was used to perform a PLS analysis on the landmark and outline data for major and minor claws separately. This was repeated for individual species ($n \geq 15$) and across species. All randomization tests were conducted with 999 permutations.

Shape Variation

A Relative Warps Analysis (Rohlf 1993) was performed with the landmark data using tpsRelw (Rohlf 1998c) to examine the major trends of claw shape variation; this is a principal components analysis (PCA) of the partial warp scores. It was repeated for major and minor claws separately, as well as together. The first axis of a PCA is often interpreted as representing general size (Jolicoeur and Mosimann 1960; Jolicoeur 1963); in order to see whether this holds for these data, the correlation between the scores on the first axis and centroid size was calculated.

Shape Allometry

In order to explore how shape varies with size, multivariate regression of claw shape onto centroid size was performed with tpsRegr (Rohlf 1998b). This was performed separately on major and minor claws for individual species (with $n \geq 15$) and for species means. As in some of the other analyses, it is necessary to adjust for the lack of independence due to phylogeny in the interspecific comparison. Independent contrasts for the shape variables were calculated using tpsTree (Rohlf 2000); size contrasts were calculated as above. The multivariate regression was then repeated using the contrast scores.

4.4 RESULTS

Size Allometry

Every species shows a strong relationship between carapace size and centroid size for both major and minor claws (Table 4.1). For all species, the slope of the major claw regression is greater than that of the minor claw regression. Furthermore, the slope of the minor claw regressions are all approximately equal to one, while the slopes of the major claw regressions are mostly over 1.5 and range well over 2. This indicates that within species, the size of the minor claw tends to grow with isometry, while the size of the major claw tends to grow with positive allometry.

	Majors			Minors		
Species	*n*	Slope	r^2	*n*	Slope	r^2
U. arcuata	17	2.047	0.939	15	1.146	0.979
U. batuenta	21	1.441	0.771	21	0.877	0.738
U. beebei	50	1.463	0.870	50	0.994	0.906
U. borealis	48	1.943	0.925	49	0.969	0.968
U. deichmanni	50	1.738	0.890	40	0.785	0.622
U. ecuadoriensis	13	1.743	0.894	13	1.004	0.956
U. festae	50	1.411	0.838	50	0.899	0.931
U. flammula	10	2.222	0.939	10	0.954	0.960
U. inaequalis	33	1.609	0.913	32	1.060	0.918
U. panamensis	10	1.925	0.968	10	1.110	0.908
U. pugilator	50	1.880	0.830	49	1.001	0.940
U. pugnax	50	1.348	0.434	49	0.912	0.784
U. saltitanta	50	1.729	0.749	50	1.079	0.877
U. stenodactylus	50	1.327	0.735	50	1.131	0.969
U. subcylindrica	9	1.538	0.961	13	1.020	0.918
U. tenuipedis	11	1.457†	0.486	11	1.090	0.721
U. terpsichores	50	1.096	0.726	49	0.875	0.864

Table 4.1. Results of the linear regression of *ln* centroid size onto *ln* carapace breadth for individual species ($n \geq 9$). Every regression is significant at $P \leq 0.001$, except as indicated; †$P = 0.017$.

The interspecific regressions were also significant ($P < 0.0001$). The regression line for the major claws was *ln* Centroid Size = -0.166 + 1.131 *ln* Carapace Breadth ($r^2 = 0.918$); that for the minor claws was *ln* Centroid Size = -1.010 + 0.965 *ln* Carapace Breadth ($r^2 = 0.960$). Although the slopes are quite similar (Figure 4.5a), they are significantly different from each other ($P = 0.0001$). These results indicate that there is little evolutionary allometry (Klingenberg 1996) with respect to claw size; both major and minor claw size is roughly isometric (slope = 1) across species.

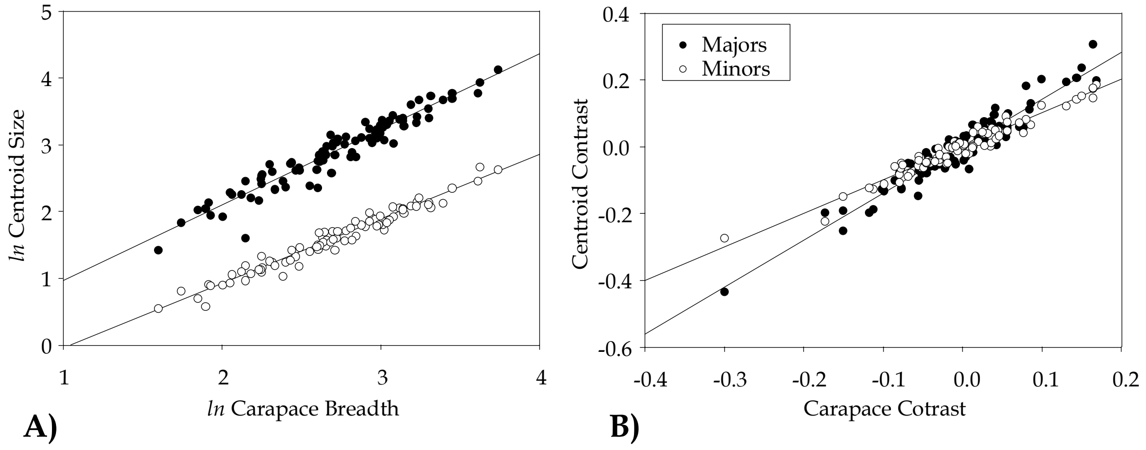

Figure 4.5. Regression of centroid size on carapace breadth for the species means. A) Regressions of *ln* centroid size on *ln* carapace breadth; B) Regressions of contrast scores of *ln* centroid size on *ln* carapace breadth.

When accounting for the lack of independence due to phylogeny, the conclusions were not dependent on the cladogram used; therefore only the results from the unconstrained analysis (Chapter 2, Figure 2.4) will be presented. The interspecific regressions (Figure 4.5b) are still both significant ($P < 0.0001$) even after the correction for phylogenetic dependence (major slope = 1.406; minor slope = 1.005); these slopes are significantly different ($P < 0.0001$). This indicates that the observed interspecific size isometry is not due to shared phylogenetic history.

Although claw size is isometric across species, the within species allometric slopes differ quite a bit among species (Table 4.1). To see whether the intraspecific allometries were themselves allometric across species (i.e. does the relationship between claw size and carapace size within species change as the mean size of the species increases), the regression between the slope of the major regression and mean carapace size was calculated. The regression was significant (F = 11.06, P = 0.005, r^2 = 0.424) with a positive slope (Figure 4.6), indicating that the larger species show stronger positive allometry than smaller species. When this analysis is corrected for phylogenetic dependence, however, the relationship becomes nonsignificant (F = 1.65, P = 0.218).

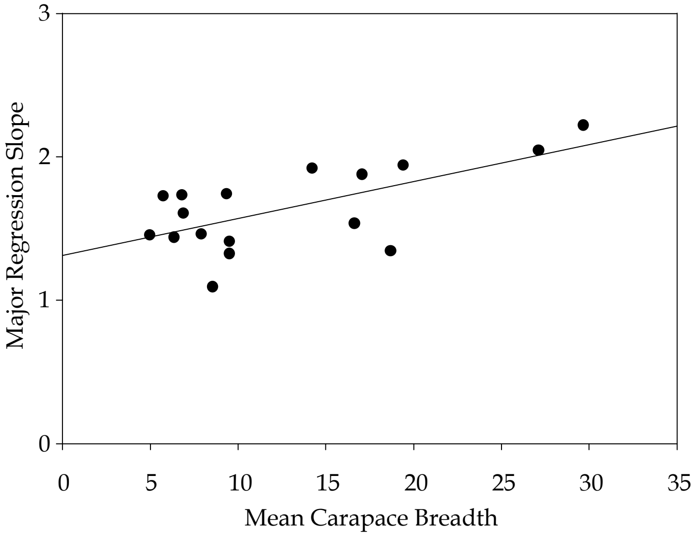

Figure 4.6. Regression of slope of major claw regression slope on mean centroid size.

Landmark and Outline Correlation

The relationship between the landmark and outline descriptions of shape varied a bit among species, although there are some general trends. Table 4.2 summarizes the from the PLS analysis for each species; only the results from the first pair of vectors is reported. For most species, the first PLS vector shows a strong, significant correlation between the landmark and outline descriptions of major claw shape; this vector explains 85-95% of the covariation between the data sets. Minor claws, on the other hand, show a weaker correlation, which is frequently not significant, and explains a much smaller percentage of the observed covariation.

	Majors				Minors			
Species	*n*	*r*	Explains	*P*	*n*	*r*	Explains	*P*
U. arcuata	17	0.952	92.6%	0.047	15	0.931	62.0%	0.101
U. batuenta	21	0.955	87.1%	0.019	21	0.954	73.7%	0.268
U. beebei	50	0.973	94.9%	0.004	50	0.886	65.1%	0.020
U. borealis	49	0.935	92.7%	0.048	50	0.894	46.2%	0.004
U. deichmanni	50	0.892	91.4%	0.023	42	0.868	59.7%	0.218
U. festae	50	0.950	97.7%	0.021	50	0.880	45.9%	0.557
U. inaequalis	33	0.900	56.5%	0.142	32	0.503	64.6%	0.372
U. pugilator	50	0.938	91.9%	0.015	49	0.891	49.8%	0.017
U. pugnax	50	0.965	91.6%	0.013	49	0.888	67.3%	0.004
U. saltitanta	50	0.922	78.5%	0.012	50	0.654	38.7%	0.640
U. stenodactylus	50	0.984	96.1%	0.015	50	0.779	59.9%	0.182
U. terpsichores	50	0.889	86.5%	0.037	49	0.832	70.4%	0.042

Table 4.2. Results of the partial least squares analysis for the relationship between the landmark and outline data for individual species ($n \geq 15$). The numbers all refer to the first PLS output vector. The percentage refers to how much of the observed covariation between the data sets is explained by the first vector; the significance refers to the correlation coefficient.

Across species, however, there was a strong correlation between outline shape and landmark configuration for both major and minor claws. For the major claws, the first PLS vector showed a correlation of 0.925 ($P = 0.030$) and explained 92.3% of the observed covariation between the landmark and outline data. For the minor claws, the first vector showed a correlation of 0.914 (P = 0.006) and explained 76.9% of the covariation; the second vector was of borderline significance (P = 0.032), with a correlation of 0.858 and explaining an additional 18.5% of the covariation. Because a majority of the observed covariation between the data sets is concentrated in the first vector, and because this vector indicates a high correlation between the two data sets, it must be considered that the outline and landmark descriptions of shape are highly redundant. The remainder of the analyses will be restricted to just the landmark data.

Shape Variation

The results of the relative warps analysis for the major claws are shown in Figures 4.7 and 4.8. The first relative warp explained 70.09% of the observed variation among species, the second 11.48%, and the third 9.81% (91.38% total). Visual inspection of the TPS warp grids allows one to make generalizations about the trends of shape variation. The first axis primarily describes variation in the relative length of the pollex relative to the manus. The second axis describes variation in the relative depth of the pollex base relative to the dactyl base, as well as the height of the carpus relative to the manus. The third axis describes variation in the relative positions of the carpus and pollex tip relative to the dactyl and pollex base. The extreme point along RW2 (the lower part of Figure 4.7) represents *Uca saltitanta*, a species with an extremely large triangular pollex. The correlation between centroid size and the scores on the first relative warp is 0.701 ($P < 0.0001$); this indicates a large degree of the variation in the first axis may be due to allometry. Although there are no distinct groupings, there is some separation of the subgenera (*sensu* Crane 1975) on these plots. In Figure 4.7, the *Deltuca* make up most of the upper part of the plot. In Figure 4.8, most of the points in the lower part are the *Celuca* and *Minuca*.

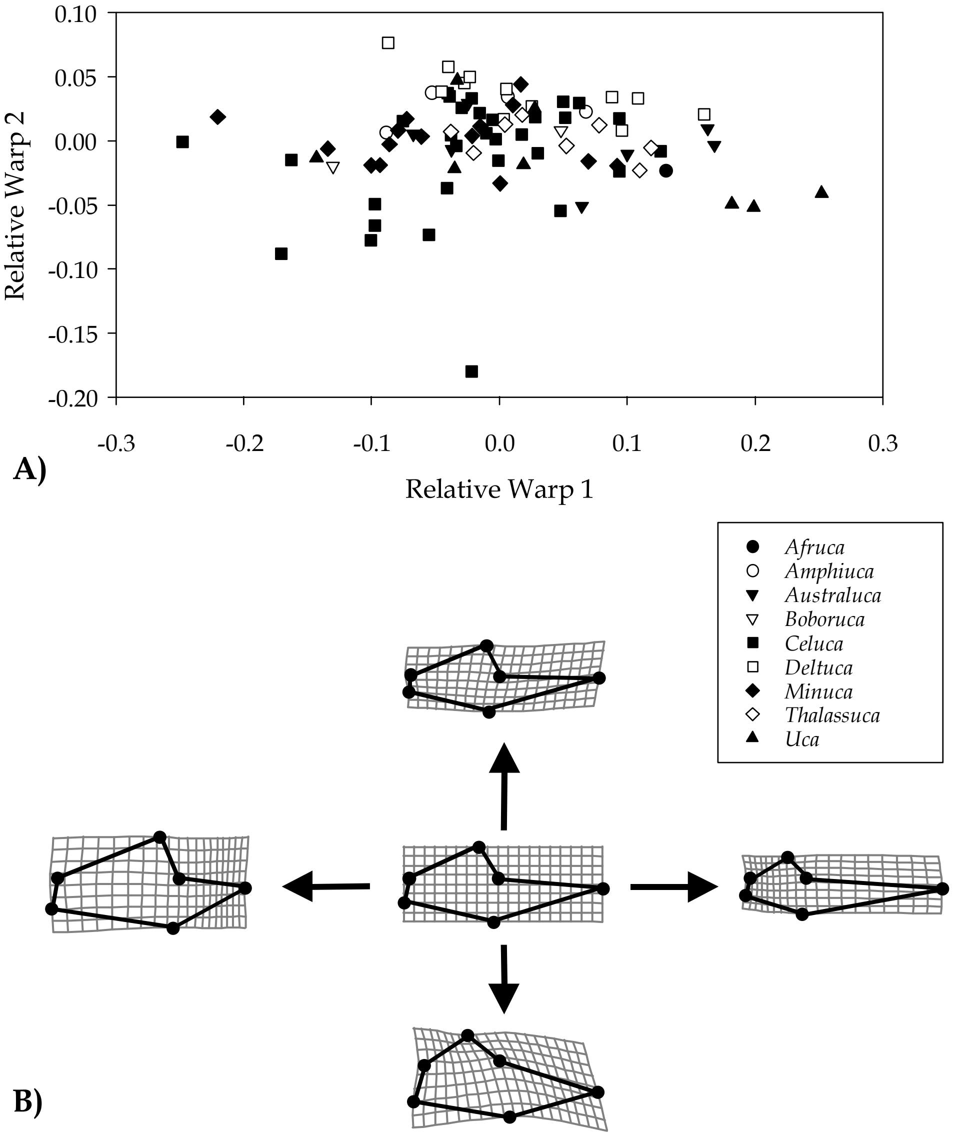

Figure 4.7. Relative warps 1 and 2 for the species means of the major claws. A) Plot of relative warp 2 vs. relative warp 1 ; B) The center landmark configuration illustrates the mean major claw shape; the other configurations illustrate the shape change represented by movement along each axis in the direction indicated by the arrows.

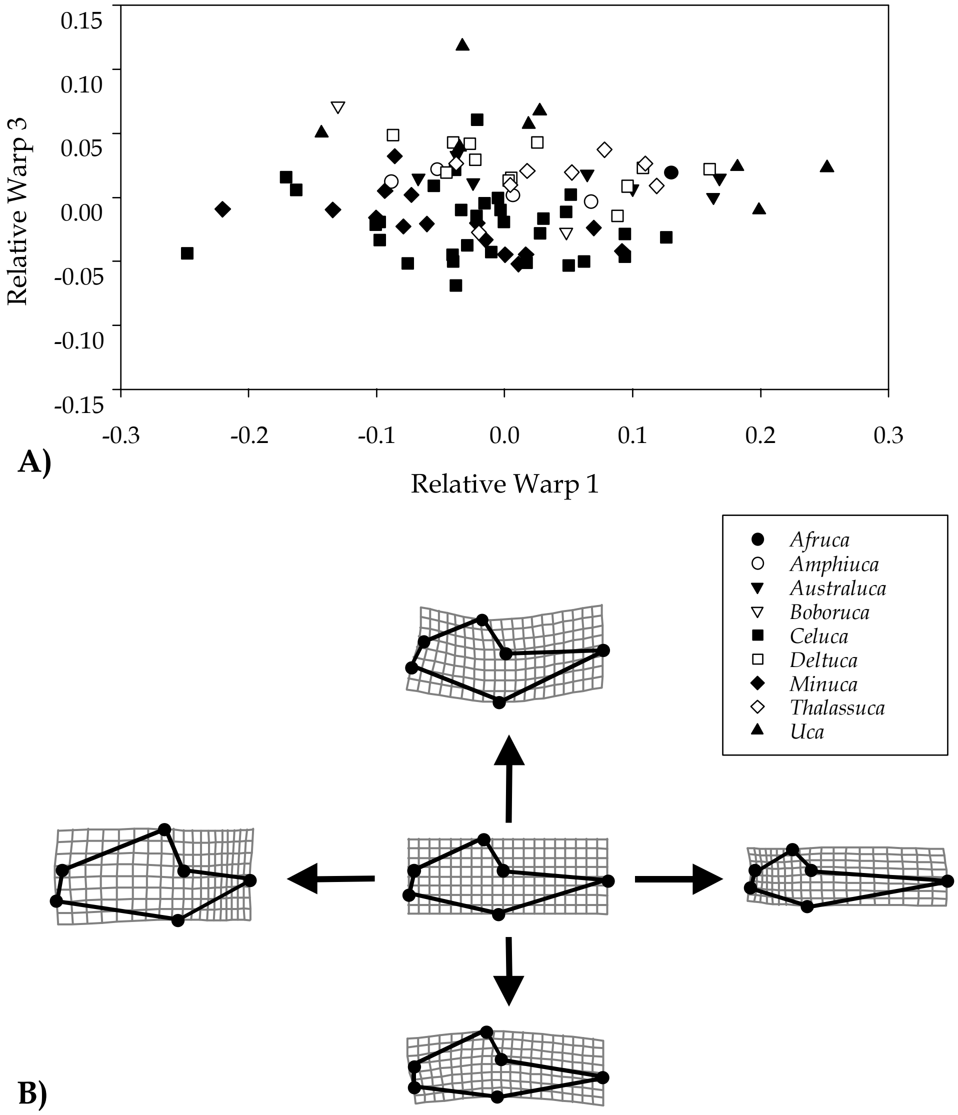

Figure 4.8. Relative Warps 1 and 3 for the species means of the major claws. A) Plot of relative warp 3 vs. relative warp 1 ; B) The center landmark configuration illustrates the mean major claw shape; the other configurations illustrate the shape change represented by movement along each axis in the direction indicated by the arrows.

The results of the relative warps analysis for the minor claws are shown in Figures 4.9 and 4.10. The first relative warp explained 47.50% of the observed variation among species, the second 24.13%, and the third 12.03% (83.66% total). The first axis primarily describes variation in the depth of the pollex relative to that of the manus and carpus; this is roughly equivalent to the second axis of the major claws. The second axis describes variation in the relative depth of the entire claw relative to its length. The third axis describes variation in the relative width of the lower manus, relative to the upper manus. The correlation between centroid size and the scores on the first relative warp is 0.136 (P = 0.210); variation in the first axis is not related to allometry. As with the major claws, there is some phylogenetic subdivision of minor claw shapes. In Figure 4.9, the *Minuca* are almost all confined to the far left part of the plot; the *Deltuca* cluster to the right and above them. On the other hand, the *Celuca* are spread evenly throughout the entire plot.

Figure 4.11 shows the results of the relative warps analysis of the species means of the 88 major and the 86 minor claws. The first relative warp explained 49.41% of the observed variation, the second 20.23%, and the third 14.73% (84.37% total). As can be observed from the spread of points along the first relative warp axis, major claw shape is more variable than minor claw shape; on the other axes the spread of major and minor claws appears to be about the same. Since major claw shape is more variable than minor claw shape, it is not surprising that the first axis represents similar shape changes as in the relative warps analysis of the major claws alone (Figure 4.7). Most of the variance reflects changes in the relative length of the pollex and height of the claw; major claws show more of this variation than do minor claws. Although there is some overlap, major and minor claw shapes are fairly distinct; the distributions of points are fairly well separated in the plot of RW2 vs RW1 and even more so in the plot of RW3 vs RW2.

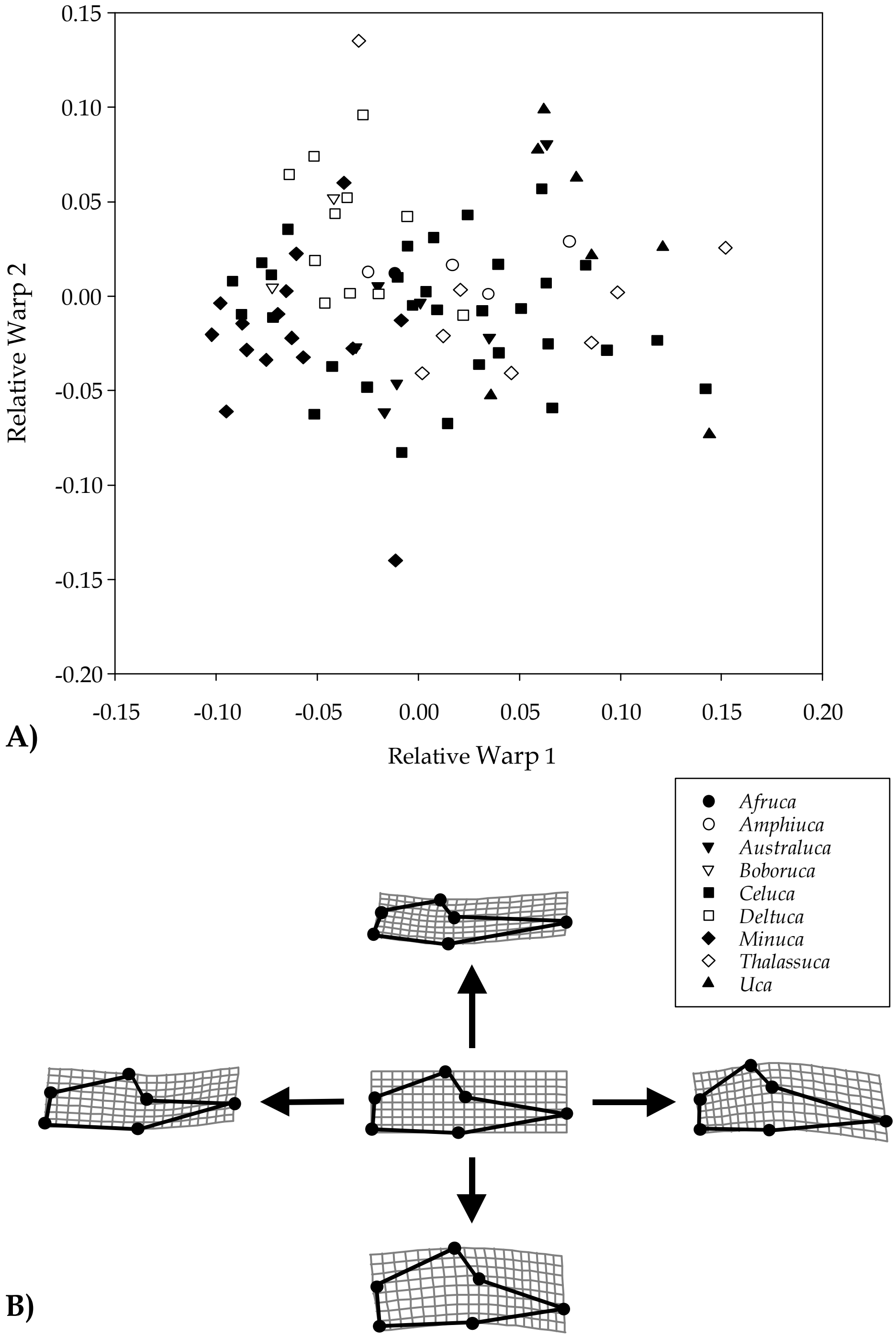

Figure 4.9. Relative Warps 1 and 2 for the species means of the minor claws. A) Plot of relative warp 2 vs. relative warp 1 ; B) The center landmark configuration illustrates the mean minor claw shape; the other configurations illustrate the shape change represented by movement along each axis in the direction indicated by the arrows.

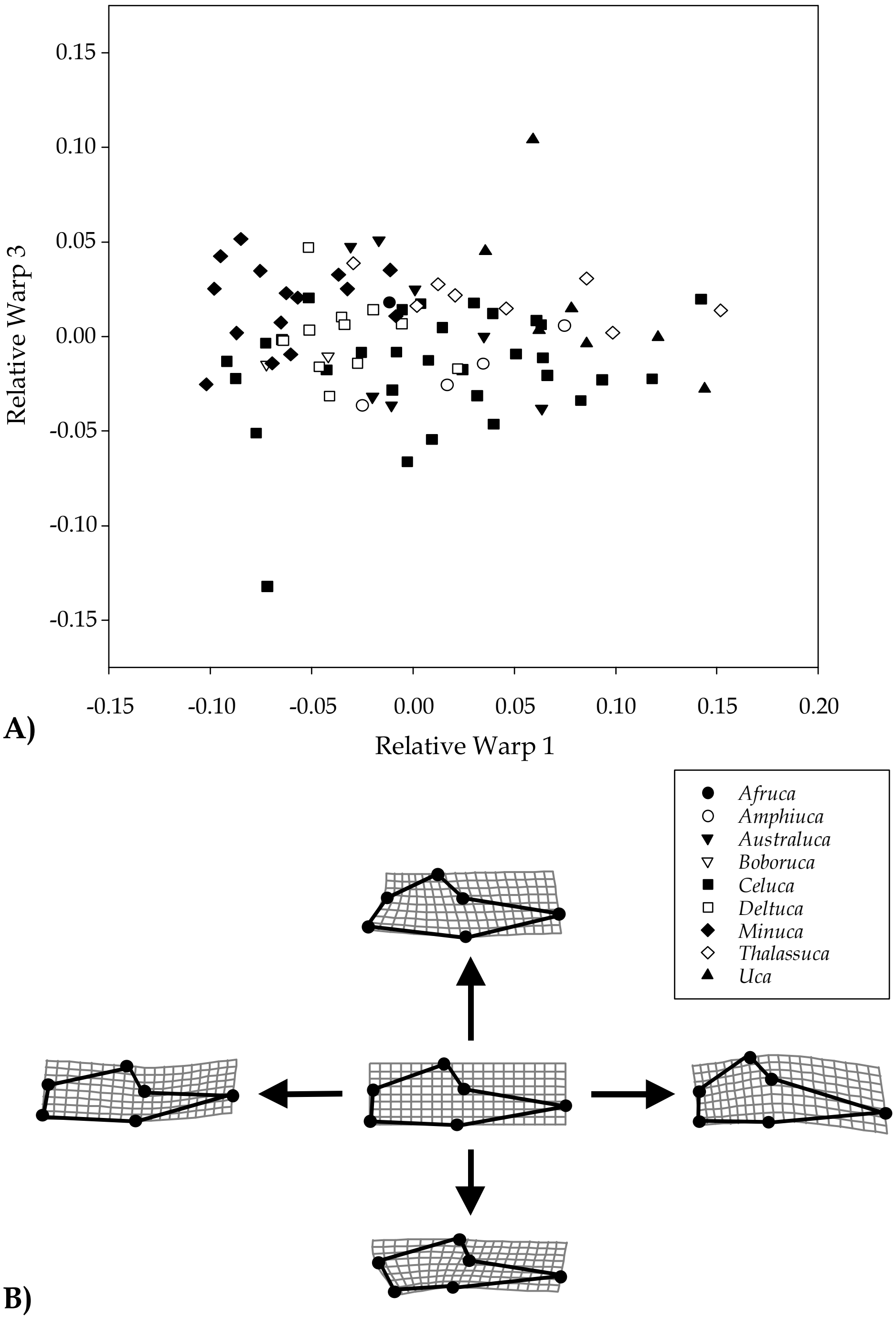

Figure 4.10. Relative Warps 1 and 3 for the species means of the minor claws. A) Plot of relative warp 3 vs. relative warp 1 ; B) The center landmark configuration illustrates the mean minor claw shape; the other configurations illustrate the shape change represented by movement along each axis in the direction indicated by the arrows.

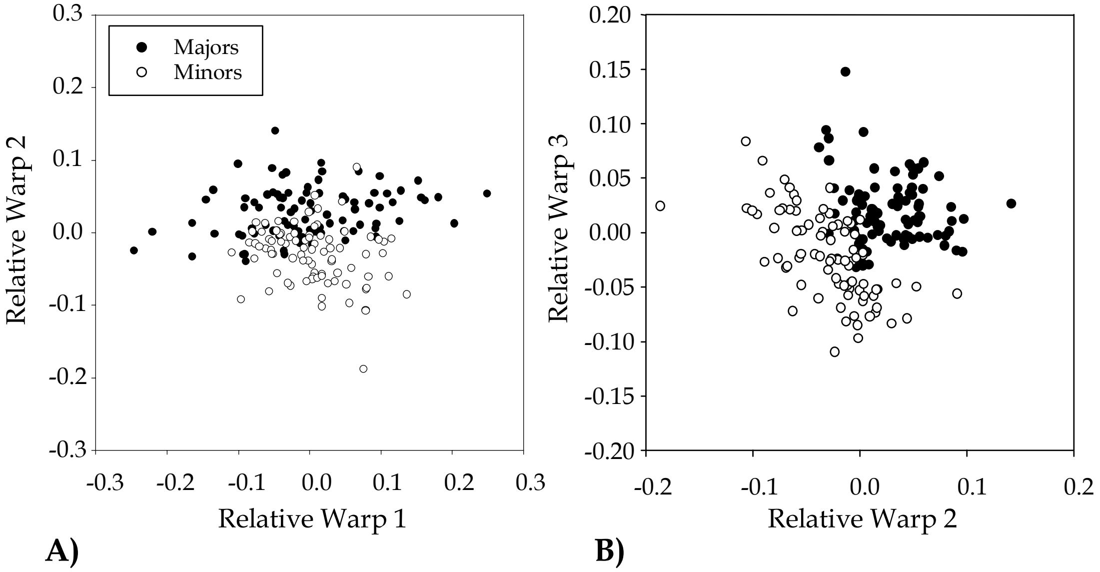

Figure 4.11. Plot of relative warps of the species means of major and minor claws. A) Relative warp 2 vs. relative warp 1; B) Relative warp 3 vs. relative warp 2. Closed circles represent major claws, open circles minor claws.

Shape Allometry

The results of the multiple regressions for shape on centroid size for each species are listed in Table 4.3. Most species shows strong shape allometry for major claws, but none for minor claws. Except for *Uca inaequalis*, the regression explains between 25 and 50% of the variation in major claw shape. In no species other than *U. saltitanta* and *U. pugilator* is there any significant allometry in minor claw shape, and even in these species the regression only explains 5% of the variation. These results parallel those of the size analysis; within species, the major claws show allometric growth and the minor claws isometric growth.

Across species, both major and minor claws show significant ($P < 0.0001$) shape allometry. The multiple regression of major claws explains 35.1% of the variation (about the same as seen within a species), minor claws 6.45%. Figure 4.12 illustrates the results of the regression. For both major and minor claws, as

	Majors			Minors		
Species	*n*	Explains	*P*	*n*	Explains	*P*
U. arcuata	17	51.3%	< 0.0001	15	6.74%	0.078
U. batuenta	21	42.8%	< 0.0001	21	2.84%	0.701
U. beebei	50	42.5%	< 0.0001	50	3.82%	0.181
U. borealis	48	23.2%	< 0.0001	49	2.85%	0.122
U. deichmanni	50	34.4%	< 0.0001	40	3.52%	0.766
U. festae	50	55.3%	< 0.0001	50	1.37%	0.264
U. inaequalis	33	5.39%	0.0121	32	1.68%	0.275
U. pugilator	50	37.7%	< 0.0001	49	4.26%	0.022
U. pugnax	50	24.2%	< 0.0001	49	3.37%	0.106
U. saltitanta	50	33.2%	< 0.0001	50	5.29%	0.015
U. stenodactylus	50	45.4%	< 0.0001	50	4.20%	0.114
U. terpsichores	50	27.4%	< 0.0001	49	5.00%	0.143

Table 4.3. Results of the multiple regression of partial warp scores (including the uniform components) onto carapace breadth for individual species ($n \geq 15$).

one moves from smaller to larger species, the pollex becomes relatively longer and the carpus relatively smaller.

After correcting for the lack of phylogenetic independence, both major and minor claws still show significant interspecific shape allometry ($P < 0.0001$). This indicates that phylogenetic relatedness alone cannot account for the observed relationship between shape and size; some of the shape variation can be explained by evolutionary allometry (Klingenberg 1996). The relationship between pollex length, propodus length, and centroid size is only a general trend; some of the species with the relatively longest chela (e.g. *Uca festae*) are among the medium to small species. However, all of the species with particularly short chela (e.g. *U. pygmaea* and *U. latimanus*) are quite tiny.

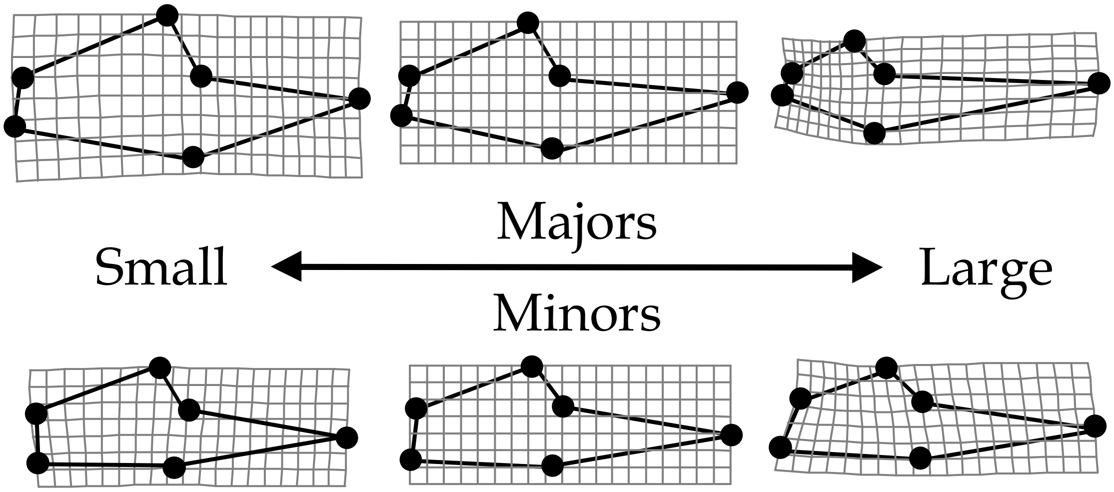

Figure 4.12. Plot of interspecific multiple regression of partial warp scores on centroid size. The center configuration illustrates the mean claw shape; the other configurations illustrate the shape change represented by increasing or decreasing centroid size.

4.5 DISCUSSION

Although most previous studies of allometry in fiddler crab claws have dealt exclusively with the major claw (Huxley 1924a, 1927; Miller 1973; Frith and Frith 1977; Veitch 1978; Williams *et al.* 1980; Frith and Brunemeister 1983; Green and Schochet 1990), a few authors (Huxley 1932; Gibbs 1974) have noted the isometric size ratio of the minor claw. All previous studies were intraspecific, except for Levinton *et al.* (1995) which examined the relationship between claw length and the Index of Force (an estimate of potential closing force based on mechanical advantage and muscle size). The present study is among the first to search for evolutionary allometry in the genus *Uca*, and the results are quite intriguing. There is a decoupling of shape and size relationships within and among species. Within species, there is strong allometric growth (of both size and shape) of major claws, while minor claws are isometric for both. Across species, however, both major and minor claws show isometry for size and allometry for shape. Allometry can account for some of the observed interspecific differences in major or minor claw shape.

There is an appreciable amount of phylogenetic clustering of major claw shape across the genus, as represented by the relative warp plots (Figures 4.7-4.8). This is more surprising than one might first guess. While there are certainly clades with distinctive claw forms, such as the large bladed claws of the American sugenus *Uca* (e.g. *Uca ornata* and *U. stylifera*, Figure 4.1a,c) or the heavily toothed claws of the *vocans* complex (Figure 4.4), these shape analyses were primarily made on landmark data which does not include information about many of these interesting claw shapes; most of the obvious variation is taking place between the landmarks, especially on the gape face of the pollex (the area between landmarks 1 and 6).

While the outline descriptions from the elliptical Fourier analysis should capture much of this variation, in practice there are a number of problems with this method. First, the scale of many of the features such as gape teeth was quite small compared to that of the main outline of the claw and required a large number of harmonics to capture (Figure 4.4), which inflated the number of variables needed to accurately describe the shape of a single claw. There was a lot of redundancy in these 45 variables as a PCA (results not shown) accounted for over 98% of the variation with just 8 variables (the same number as the landmark data). Second, EFA, as well as other landmark methods such as "eigenshape" methods, require certain arbitrary decisions that can affect the results in complicated ways (Sampson *et al.* 1996), and no method is clearly more or less correct than another. Third, EFA is poor at aligning homologous regions of the outline, unlike landmark methods which are specifically designed to align homologous landmarks (Sampson *et al.* 1996). Small variations in the position of a tooth along the outline among different individuals would cause the mean to show no tooth structure, rather than find an average position and height for the tooth. This is a serious problem with many outline methods; newer methods which propose to treat outlines as a series of landmarks or to combine landmark and outline data have been proposed (e.g. Sampson *et al.* 1996) but are still in their infancy.

As with most crustaceans, fiddler crabs are able to regenerate lost limbs. At any given time, a large proportion of individuals in a population may have regenerated major claws (e.g. Shih *et al.* 1999). Regeneration is likely to have two effects on these results, one on size allometry and one on mean shapes. Regenerating claws are smaller than would be expected for a crab of the same size with an unregenerated claw (Hopkins 1985). Because larger crabs are more likely to be regenerating a claw, because it takes longer to regenerate a larger claw than a smaller one, and because the difference in size between the original and regenerated claw is more extreme when a large claw is regenerating, in a given population, most of the variance in claw size due to regeneration is likely to be found on the larger crabs. This will have the effect of lowering the claw size/carapace breadth regression slope. This means that the observed slopes (Table 4.1) are underestimates of the slope that would be obtained through simple growth without regeneration.

The second effect of regeneration would be on shape. Some species are known to have regenerative claws (the leptochelous form) which are a different shape from the unregenerated claws (the brachychelous form) (Hagen 1962; Yamaguchi 1973; Yamaguchi and Takeda 1973; Crane 1975); other species have claws that look identical. This means that for some species, the mean is actually composed of two populations of different claw forms. Leptochelous claws tend to be simpler in structure than brachychelous claws, with fewer teeth and less armature. In some species the difference can be quite extreme; for many years the various claw forms of *Uca vocans* were the basis of separate species (Serène 1973; Crane 1975).

While the outline shape clearly differs between brachychelous and leptochelous claws, it is not clear if the landmark shape differs. In the current study, only one species, *Uca borealis* (a species from the *vocans* complex), has both a large sample size and the clear brachychelous/leptochelous dichotomoy. Of the 49 specimens, 32 were brachychelous and 17 leptochelous. The two forms are almost identical in size (brachychelous mean centroid size = 23.79; leptochelous mean centroid size = 24.87; $t_s = 0.45$; $P = 0.66$). A MANOVA revealed these claw types to be significantly different in shape (Wilk's $\Lambda = 0.1049$, $P < 0.001$). The differences are illustrated in Figure 4.13. The major shape differences between the claw forms of *U. borealis* is that the leptochelous claw is somewhat narrower and has a relatively longer pollex.

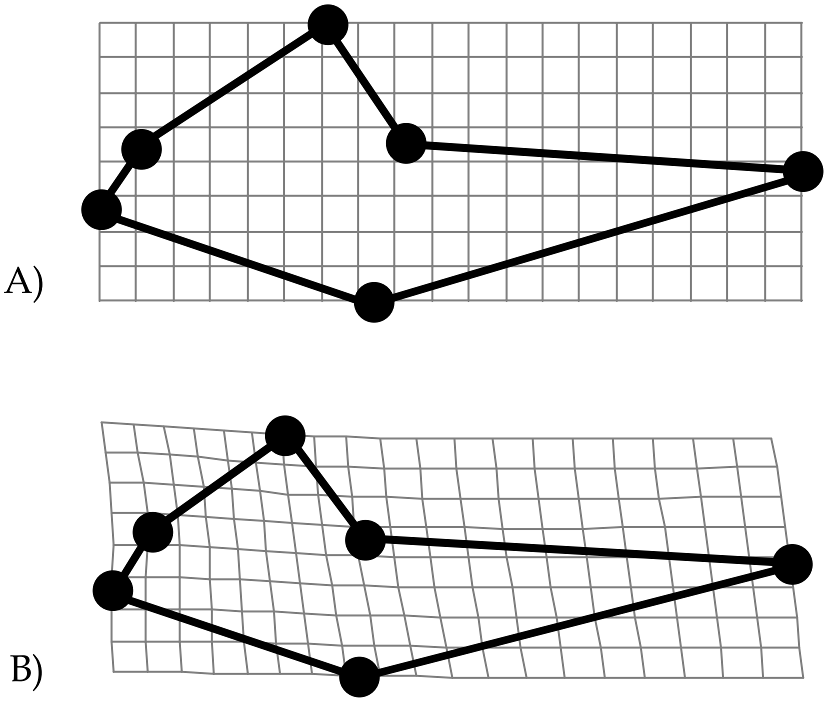

Figure 4.13. Variant claw forms of *Uca borealis*. A) Brachychelous claw; B) Leptochelous claw. The warp grid shows the transformation of the brachychelous form to the leptochelous form.

Furthermore, the slopes of both the size allometry (brachychelous slope = 1.822; leptochelous slope = 2.402; $F = 11.203$; $P = 0.0017$) and multivariate shape allometry (Wilk's $\Lambda = 0.5706$, $P = 0.0035$) significantly differ.

Taken together, these results are quite interesting. The allometric size regression slope of the regenerated claws is steeper than that of the unregenerated claws. Recall that the general allometric trend for major claw shape within species is that larger claws have relatively longer chela. Because regenerated claws are normally smaller than the original unregenerated claw (Hopkins 1985), the leptochelous form, without the complicated teeth and armature of the brachychelous form, may be an attempt to regrow a claw that is proportionally similar to a larger claw. This could have important consequences on the relationship of sexual selection and regeneration. Whether these trends hold for regenerated claws of other species cannot be determined in this study.

The description of variation is just a first step in understanding the evolution of a complex morphological structure under sexual selection. The next step is the study of how this variation specifically relates to differences in behavior moderated function. Very few structures have been subjected to a rigorous analysis of the interspecific variation as it relates to allometry, function, and behavior. One set of structures which have been rigorously analyzed and which are very comparable to the major claws of fiddler crabs with respect to their functions as ornaments and armaments are the horns and antlers of Bovidae and Cervidae (Huxley 1931; Gould 1974; Clutton-Brock *et al.* 1980; Clutton-Brock 1982; Packer 1983; Kitchener 1985, 1987a,b, 1991). Deer antlers show strong intraspecific and interspecific allometry (Huxley 1931; Gould 1974), yet they were used for more than just display, even at the largest sizes. Kitchener (1987a) showed through crystallographic and functional morphological evidence that even the extinct Irish elk, *Megaloceras giganteus*, used its immense antlers (which reached a lateral spread of up to 3.5 meters) in combat. Patterns of antlers and horns have also been examined with respect to differences in combat forms and their functional requirements (Kitchener 1985, 1991), breeding group size and structure (Clutton-Brock *et al.* 1980), and predator defense versus intrasexual competition (Packer 1983). With the greater understanding of the evolutionary patterns of claw shape in fiddler crabs, we are now better able to take the next step and study how these structures are related to their limited functions of display and combat.

4.6 CONCLUSIONS

Within species, major claw size increases allometrically, while minor claw size increases isometrically. Species vary quite a bit in the allometric slope of the major claw. Between species, both major and minor claws show isometric patterns, indicating the relationship of claw size to carapace size is constant across species.

Within species, major claw shape changes as size increases, while minor claw shape does not. These changes tend to be characterized by a general increase in the relative length of the pollex relative to the manus, and the relative size of the propodus to that of the carpus. Between species, both major and minor claws show a similar relationship between shape and size as that which is found for major claws within species. There is some phylogenetic clustering of claw shapes.

Species which regenerate claws of a different form than the original claw may be sacrificing armature in order to regrow a claw which is proportionally similar to a larger claw.

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LITERATURE CITED

Adams, D. C. 1999a. *Ecological character displacement in Plethodon and methods for shape analysis of articulated structures*. Ph.D. Thesis. Ecology and Evolution, State University of New York at Stony Brook.

Adams, D. C. 1999b. Methods for shape analysis of landmark data from articulated structures. *Evolutionary Ecology Research* 1:959-970.

Ahmed, M. 1978. Development of asymmetry in the fiddler crab *Uca cumulanta* Crane, 1943 (Decapoda Brachyura). *Crustaceana* 34:294-300.

Ahmed, M., and R. A. Khan. 1978. Development of asymmetry in the claws of the fiddler crab *Uca lactea*. *Pakistan Journal of Zoology* 10:49-54.

Auffray, J.-C., P. Alibert, S. Renaud, A. Orth, and F. Bonhomme. 1996. Fluctuating asymmetry in *Mus musculus* subspecific hybridization: Traditional and Procrustes comparative approach. Pp. 275-283 in *Advances in Morphometrics*, L. F. Marcus, M. Corti, A. Loy, G. J. P. Naylor and D. E. Slice, eds. Plenum Press: New York.

Barnwell, F. H. 1982. The prevalence of male right-handedness in the Indo-West Pacific fiddler crabs *Uca vocans* (Linnaeus) and *U. tetrogonon* (Herbst) (Decapoda: Ocypodidae). *Journal of Crustacean Biology* 2:70-83.

Berglund, A., A. Bisazza, and A. Pilastro. 1996. Armaments and ornaments: An evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society* 58:385-399.

Bookstein, F. L. 1991. *Morphometric Tools for Landmark Data.* Cambridge University Press: Cambridge.

Bookstein, F. L. 1996. Standard formula for the uniform shape component in landmark data. Pp. 153-168 in *Advances in Morphometrics*, L. F. Marcus, M. Corti, A. Loy, G. J. P. Naylor and D. E. Slice, eds. Plenum Press: New York.

Bookstein, F. L., P. D. Sampson, A. P. Streissguth, and H. M. Barr. 1996. Exploiting redundant measurement of dose and behavioral outcome: New methods from the behavioral teratology of alcohol. *Developmental Psychology* 32:404-415.

Brown, S. C., S. Cassuto, R., and R. W. Loos. 1979. Biomechanics of chelipeds in some decapod crustaceans. *Journal of Zoology* 188:143-159.

Clutton-Brock, T. H. 1982. The functions of antlers. *Behaviour* 79:108-125.

Clutton-Brock, T. H., S. D. Albon, and P. H. Harvey. 1980. Antlers, body size and breeding group size in the Cervidae. *Nature* 285:565-567.

Cock, A. G. 1966. Genetical aspects of metrical growth and form in animals. *Quarterly Review of Biology* 41:131-190.

Crane, J. 1966. Combat display and ritualization in fiddler crabs (Ocypodidae, genus *Uca*). *Philosophical Transactions of the Royal Society of London* 251B:459-472.

Crane, J. 1967. Combat and its ritualization in fiddler crabs (Ocypodidae) with special reference to *Uca rapax* (Smith). *Zoologica NY* 52:49-77.

Crane, J. 1975. *Fiddler Crabs of the World: Ocypodidae: Genus Uca.* Princeton University Press: Princeton, NJ.

Diniz Filho, J. A. F. 1990. Multivariate morphometrics and evolutionary patterns in some species of the genus *Uca* Leach, 1814 (Crustacea: Brachyura: Ocypodidae). *Revista Brasileira de Genetica* 13:687-696.

Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1-15.

Frith, D. W., and S. Brunemeister. 1983. Fiddler crab (Ocypodidae: Genus *Uca*) size, allometry and male major chela handedness and morphism on a Thailand mangrove shore. *Phuket Marine Biological Center Research Bulletin* 29:1-16.

Frith, D. W., and C. B. Frith. 1977. Observations on fiddler crabs (Ocypodidae: genus *Uca*) on Surin Island, Western Peninsular Thailand, with particular reference to *Uca tetragonon* (Herbst). *Phuket Marine Biological Center Research Bulletin* 18:1-14.

Garland, T., Jr., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* 41:18-32.

Gibbs, P. E. 1974. Notes on *Uca burgersi* Holthius (Decapoda, Ocypodidae) from Barbuda, Leeward Islands. *Crustaceana* 27:84-91.

Gould, S. J. 1966. Allometry and size in ontogeny and phylogeny. *Biological Reviews* 41:587-640.

Gould, S. J. 1974. The origin and function of "bizarre" structures: Antler size and skull size in the "Irish Elk," *Megaloceras giganteus*. *Evolution* 28:191-220.

Green, J., and J. Schochet. 1990. An analysis of growth in the fiddler crab *Uca vocans*. *Phuket Marine Biological Center Research Bulletin* 54:47-64.

Hagen, H.-O. v. 1962. Freilandstudien zur Sexual- und Fortpflanzungsbiologie von *Uca tangeri* in Andalusien. *Zeitschrift für Morphologie und Ökologie der Tiere* 51:611-725.

Harvey, P. H., and M. D. Pagel. 1991. *The Comparative Method in Evolutionary Biology*. Oxford University Press: Oxford.

Hopkins, P. M. 1985. Regeneration and relative growth in the fiddler crab. Pp. 265-275 in *Crustacean Issues 3: Factors in Adult Growth*, A. M. Wenner, ed. A. A. Balkema: Rotterdam.

Huxley, J. S. 1924a. Constant differential growth-ratios and their significance. *Nature* 114:895-896.

Huxley, J. S. 1924b. The variation in the width of the abdomen in immature fiddler crabs considered in relation to its relative growth-rate. *American Naturalist* 58:468-475.

Huxley, J. S. 1927. Further work on heterogonic growth. *Biologisches Zentralblatt* 47:151-163.

Huxley, J. S. 1931. The relative size of antlers in deer. *Proceedings of the Zoological Society of London* 1931:819-864.

Huxley, J. S. 1932. *Problems of Relative Growth*. Dial Press: London.

Huxley, J. S., and F. S. Callow. 1933. A note on the asymmetry of male fiddler-crabs (*Uca pugilator*). *Archiv für Entwicklungsmechanik der Organismen* 129:379-392.

Jolicoeur, P. 1963. Bilateral symmetry and asymmetry in limb bones of *Martes americana* and man. *Revue Canadienne de Biologie* 22:409-432.

Jolicoeur, P., and J. E. Mosimann. 1960. Size and shape variation in the painted turtle. A principal component analysis. *Growth* 24:339-354.

Jones, D. S., and R. W. George. 1982. Handedness in Fiddler Crabs as an aid in taxonomic grouping of the genus *Uca* (Decapoda, Ocypodidae). *Crustaceana* 43:100-102.

Kendall, D. G. 1981. The statistics of shape. Pp. 75-80 in *Interpreting Multivariate Data*, V. Barnett, ed. Wiley: New York.

Kendall, D. G. 1984. Shape-manifolds, Procrustean metrics and complex projective spaces. *Bulletin of the London Mathematical Society* 16:81-121.

Kent, J. T. 1994. The complex Bingham distribution and shape analysis. *Journal of the Royal Statistical Society* 56B:285-299.

Kitchener, A. C. 1985. The effect of behaviour and body weight on the mechanical design of horns. *Journal of Zoology, London* 205A:191-203.

Kitchener, A. C. 1987a. The fighting behaviour of the extinct Irish Elk. *Moden Geology* 11:1-28.

Kitchener, A. C. 1987b. Fracture toughness of horns and a reinterpretation of the horning behavior of bovids. *Journal of Zoology, London* 213:621-639.

Kitchener, A. C. 1991. The evolution and mechanical design of horns and antlers. Pp. 229-253 in *Biomechanics in Evolution*, J. M. V. Rayner and R. J. Wootton, eds., Volume 36. Cambridge University Press: Cambridge.

Klingenberg, C. P. 1996. Multivariate allometry. Pp. 23-49 in *Advances in Morphometrics*, L. F. Marcus, M. Corti, A. Loy, G. J. P. Naylor and D. E. Slice, eds. Plenum Press: New York.

Klingenberg, C. P., and G. S. McIntyre. 1998. Geometric morphometrics of developmental instability: Analyzing patterns of fluctuating asymmetry with Procrustes methods. *Evolution* 52:1363-1375.

Kuhl, F. P., and C. R. Giardina. 1982. Elliptic Fourier features of a closed contour. *Computer Graphics and Image Processing* 18:236-258.

Levinton, J. S. 1988. *Genetics, Paleontology, and Macroevolution*. Cambridge University Press: New York.

Levinton, J. S., and M. L. Judge. 1993. The relationship of closing force to body size for the major claw of *Uca pugnax* (Decapoda: Ocypodidae). *Functional Ecology* 7:339-345.

Levinton, J. S., M. L. Judge, and J. P. Kurdziel. 1995. Functional differences between the major and minor claws of fiddler crabs (*Uca*, family Ocypodidae, order Decapoda, subphylum Crustacea): A result of selection or developmental constraint? *Journal of Experimental Marine Biology and Ecology* 193:147-160.

Maddison, W. P. 1989. Reconstructing character evolution on polytomous cladograms. *Cladistics* 5:365-377.

Marcus, L. F., M. Corti, A. Loy, G. J. P. Naylor, and D. E. Slice, eds. 1996. *Advances in Morphometrics*. Plenum Press: New York.

Miller, D. C. 1973. Growth in *Uca*, 1. Ontogeny of asymmetry in *Uca pugilator* (Bosc) (Decapoda, Ocypodidae). *Crustaceana* 24:119-131.

Morgan, T. H. 1923. The development of asymmetry in the fiddler crab. *American Natualist* 57:269-273.

Morgan, T. H. 1924. The artificial induction of symmetrical claws in male fiddler crabs. *American Naturalist* 58:289-295.

Neiman, M., and F. Barnwell. 1997. Morphometric differences in small claws of the deposit-feeding fiddler crabs (*Uca* spp.). *American Zoologist* 37:47A.

Packer, C. 1983. Sexual dimorphism: The horns of African antelopes. *Science* 221:1191-1193.

Rhodes, W. R. 1986. A comparative study of thoracic and cheliped muscle asymmetry in male Fiddler Crabs (Genus: *Uca*). *Biological Bulletin* 170:335-349.

Rohlf, F. J. 1993. Relative warp analysis and an example of its application to mosquito wings. Pp. 131-158 in *Contributions to Morphometrics*, L. F. Marcus, E. Bello and A. Garcia-Valdecasas, eds. Museo Nacional de Ciencias Naturales: Madrid.

Rohlf, F. J. 1998a. *tpsPLS*. Version 1.04. Department of Ecology and Evolution, State University of New York at Stony Brook: Stony Brook, NY.

Rohlf, F. J. 1998b. *tpsRegr: Shape regression*. Version 1.19. Department of Ecology and Evolution, State University of New York at Stony Brook: Stony Brook, NY.

Rohlf, F. J. 1998c. *tpsRelw: Relative warps analysis*. Version 1.18. Department of Ecology and Evolution, State University of New York at Stony Brook: Stony Brook, NY.

Rohlf, F. J. 1998d. *tpsSmall: Is shape variation small?* Version 1.17. Department of Ecology and Evolution, State University of New York at Stony Brook: Stony Brook, NY.

Rohlf, F. J. 1999a. Shape statistics: Procrustes sumperimpositions and tangent spaces. *Journal of Classification* 16:197-223.

Rohlf, F. J. 1999b. *tpsDig*. Version 1.18. Department of Ecology and Evolution, State University of New York at Stony Brook: Stony Brook, NY.

Rohlf, F. J. 2000. *tpsTree: Fitting shapes to trees*. Version 1.14. Department of Ecology and Evolution, State University of New York at Stony Brook: Stony Brook, NY.

Rohlf, F. J., and J. W. Archie. 1984. A comparison of Fourier methods for the description of wing shape in mosquitoes (Diptera: Culicidae). *Systematic Zoology* 33:302-317.

Rohlf, F. J., and F. L. Bookstein, eds. 1990. *Proceedings of the Michigan morphometrics workshop*. University of Michigan: Ann Arbor, MI.

Rohlf, F. J., and M. Corti. *In press*. The use of two-block partial least-squares to study covariation in shape. *Systematic Biology*

Rohlf, F. J., and L. F. Marcus. 1993. A revolution in morphometrics. *Trends in Ecology and Evolution* 8:129-132.

Rohlf, F. J., and D. E. Slice. 1990. Extensions of the procrustes method for the optimal superimposition of landmarks. *Systematic Zoology* 39:40-59.

Rosenberg, M. S. 1997. Evolution of shape differences between the major and minor chelipeds of *Uca pugnax* (Decapoda: Ocypodidae). *Journal of Crustacean Biology* 17:52-59.

Sampson, P. D., F. L. Bookstein, F. H. Sheehan, and E. L. Bolson. 1996. Eigenshape analysis of left ventricular outlines from contrast ventriculograms. Pp. 211-233 in *Advances in Morphometrics*, L. F. Marcus, M. Corti, A. Loy, G. J. P. Naylor and D. E. Slice, eds. Plenum Press: New York.

Serène, R. 1973. The names of the forms of *Uca vocans* (Linnaeus) (Decapoda, Ocypodidae). *Crustaceana* 24:337-339.

Shih, H.-T., H.-K. Mok, H.-W. Chang, and S.-C. Lee. 1999. Morphology of *Uca formosensis* Rathbun, 1921 (Crustacea: Decapoda: Ocypodidae), an endemic fiddler crab from Taiwan, with notes on its ecology. *Zoological Studies* 38:164-177.

Slice, D. E. 1998. *Morpheus et al*. Version 1-31-00 Beta. Department of Ecology and Evolution, State University of New York at Stony Brook: Stony Brook, NY.

Sneath, P. H. A. 1967. Trend-surface analysis of transformation grids. *Journal of Zoology* 151:65-122.

Takeda, S., and M. Murai. 1993. Asymmetry in male fiddler crabs is related to the basic pattern of claw-waving display. *Biological Bulletin* 184:203-208.

Tazelaar, M. A. 1933. A study of relative growth in *Uca pugnax*. *Archiv für Entwicklungsmechanik der Organismen* 129:393-401.

Trinkaus-Randall, V. E., and C. K. Govind. 1985. Development of biolateral asymmetry in the cheliped extensor muscle of male Fiddler Crabs. *Journal of Crustacean Biology* 5:25-29.

Veitch, L. G. 1978. Size, shape and allometry in *Uca*; A multivariate approach. *The Mathematical Scientist* 3:35-45.

Vernberg, F. J., and J. D. Costlow, Jr. 1966. Handedness in fiddler crabs. *Crustaceana* 11:61-64.

Weissburg, M. J. 1991. Morphological correlates of male claw asymmetry in the fiddler crab *Uca pugnax* (Smith) (Decapoda, Brachyura). *Crustaceana* 61:11-20.

Williams, M. J., L. G. Veitch, and R. L. Correll. 1980. Models for describing shape and allometry, illustrated by studies of Australian species of *Uca* (Brachyura: Ocypodidae). *Australian Journal of Marine and Freshwater Research* 31:757-781.

Yamaguchi, T. 1973. Asymmetry and dimorphism of chelipeds in the fiddler crab, *Uca lactea* De Haan. *Zoological Magazine* 82:154-158.

Yamaguchi, T. 1977. Studies on the handedness of the fiddler crab, *Uca lactea*. *Biological Bulletin* 152:424-436.

Yamaguchi, T., and M. Takeda. 1973. Dimorphism of chelipeds and systematic status of a fiddler crab, *Uca marionis* (Desmarest). *Proceedings of the Japanese Society of Systematic Zoology* 9:7-12.

Yerkes, R. M. 1901. A study of variation in the fiddler crab *Gelasimus pugilator* Latr. *Proceedings of the American Academy of Arts and Sciences* 36:417-442.

CHAPTER 5

BEHAVIORAL VARIATION AND MORPHOLOGY: CLAW EVOLUTION AND SPECIALIZATION IN FIDDLER CRABS

5.1 ABSTRACT

Fiddler crabs (genus *Uca*) are among the most widely studied crustaceans with respect to many behaviors, including visual and acoustic display, mating, and sexual selection. Males of this genus have extremely dimorphic claws, which show high levels of divergence and specialization. The relationship between variation in morphology and behavior was examined within the genus, primarily concentrating on the claws and the behaviors and ecology with which they are associated. Major claws are used primarily for just two purposes, waving and combat, with a much more limited role in sound production. The relationship between waving display and major claw structure is limited to thorax muscle variation. Other than a few specific sound producing structures on the palm of the major claw, only the broadened proximal-ventral part of the manus appears to be related to acoustic display. The remaining features of the major claw appear to be used in combat; most of these features appear to play a role in defense or friction, rather than simply causing damage. Minor claw shape and structure is related to habitat type; species in habitats with large mean particle size (sandy) have broad gapes and long chela while species in habitats with small mean particle size (muddy) have narrow gapes and shorter chela.

5.2 INTRODUCTION

Attempting to understand how evolution has shaped the morphology of a structure is often confounded by the multiple functions of that structure. The difficulty in understanding all of the functions and how selection may act within this complex web has made understanding the development of most morphological characters extremely difficult. One set of characters that have often been recognized to have dual function are those which serve both as signals in sexual selection (ornaments) as well as in direct intrasexual competition (armaments) (Berglund *et al.* 1996). Sexual selection is considered to be one of the most important evolutionary forces (Andersson 1994); it can act indirectly through mate choice or directly through competition. It is invoked to explain sexual dimorphism, the evolution of extravagant morphological features, bright coloration, and complex mating behaviors. All of these are found in fiddler crabs.

Fiddler crabs (Brachyura, Ocypodidae, *Uca*) show an extreme form of sexual dimorphism and cheliped asymmetry. Male fiddler crabs have a small minor claw used for feeding and a large major claw (four to five times longer than the minor claw and containing a third to half the mass of the animal) used for display and fighting. Females have two small claws which resemble the males' minor claw. Early natural historians wondered about the use of the major claw. They speculated that it might be used to plug the burrow, as a spade for digging, a weapon in combat, a copulatory couch, or as a female attractant (Pearse 1914b; Smith and Weldon 1923). Opinions were wide and varied. Calman (1911) felt the claw was too large and unwieldy for fighting. Alcock (1892, 1900, 1902) saw it used as a weapon and as an attractant for females; he felt the latter was particularly important. He speculated that combat was undoubtedly the original force behind the evolution of the claw, but that later the attractant to females caused the evolution of the bright, gaudy coloration. Pearse

(1912, 1914a,b) believed the primary function of the claw was as a weapon. Since these early studies it has become increasing clear that the claw is used for both visual display and combat, although the importance of each is still debated. Because these functions have predictable constraints, it should be possible to study male fiddler crab behavior as a means of understanding how evolution has shaped the major claw. In general fiddler crabs are excellent organisms upon which to study behavior because all species are primarily diurnal, they have a varied and high degree of ritualized behavior, they are quite willing to ignore motionless researchers, and they are easy to mark and manipulate in the field.

Many forms of fiddler crab behavior have been systematically and extensively described, including reproductive behavior (Pearse 1914a; Crane 1958, 1975; Christy 1978, 1983; Salmon *et al.* 1978; Greenspan 1980, 1982; Zucker 1983; Christy and Salmon 1984, 1991; Murai *et al.* 1987, 1995, 1996; Murai 1992; Nakasone and Murai 1998), visual and acoustic display (Crane 1957, 1975; Gordon 1958; Salmon and Stout 1962; Salmon 1965, 1967; Salmon and Atsaides 1968; Hyatt 1977a,b; Salmon *et al.* 1978; Hagen 1983, 1984, 1993; Christy 1988a,b), and feeding (Miller 1961; Valiela *et al.* 1974; Murai *et al.* 1983; Caravello and Cameron 1987a,b; Weissburg 1990, 1992, 1993). In comparison, combat behavior has been understudied (Crane 1967; Powers 1975; Hyatt and Salmon 1978, 1979; Jennions and Backwell 1996).

The purpose of this work is to examine the relationship of interspecific variation in the shape and structure of the claws of male fiddler crabs to differences in their ecology and behavior. The structure of the major claw is examined with respect to its dual functions of display and combat. The structure of the minor claw is examined with respect to feeding and habitat choice.

5.3 MATERIAL AND METHODS

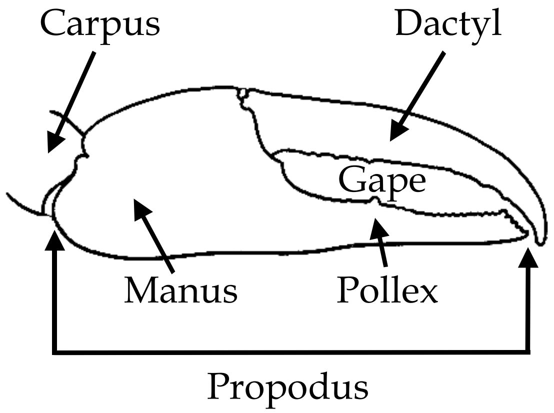

Figure 5.1. Diagrammatic representation of claw morphology. Figure modified from Crane (1975).

Specimens examined came from my collections and others and from museum collections (Appendix I). Of the ninety-seven recognized fiddler crab species, eighty-eight were examined. The missing species are evenly spread across the genus and their omission should not change any conclusions. Major claws were available for all eighty-eight species, minor claws for eighty-six (the single specimens of *Uca intermedia* and *U. typhoni* were missing their minor chelipeds). Sample sizes for each species ranged from one to fifty. A total of 1652 claws were examined, 851 major and 801 minor.

Details of crab morphology, including discrete descriptions of claw morphology were originally examined with respect to phyogenetic inference (Chapter 2). Geometric morphometric shape descriptions of the claws were used in studies of allometry within and across species (Rosenberg 1997; Chapter 4). A detailed description is provided there, so only a brief summary follows: the palmar surface of each individual claw was digitally photographed and the coordinates of six landmarks were recorded for each specimen (Figure 5.2). These landmarks were transformed into eight shape variables through the thin-plate spline (TPS) decomposition (Rohlf and Bookstein 1990; Bookstein 1991; Rohlf and Marcus 1993). These eight variables completely capture the shape information contained within the landmarks and can be used in standard multivariate statistical tests.

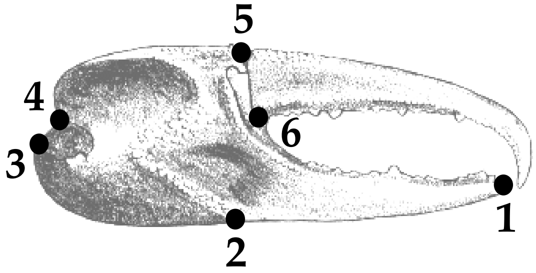

Figure 5.2. The landmark data collected from each claw. The landmarks are 1) the tip of the pollex, 2) the point which marks the junction between the pollex and the manus on the ventral margin of the claw, 3,4) the lower and upper attachment points of the carpus with the manus, at the edge of the carpal cavity, and 5,6) the upper and lower points which mark the articulation of the dactyl with the manus. Figure modified from Crane (1975).

The behavioral data for all species comes first and foremost from published descriptions and studies (see below). These descriptions have been complemented by my own field observations and video of twenty-two species. Two species, *Uca pugnax* and *U. pugilator*, were observed at Flax Pond, Long Island, NY, over multiple summers from 1995 through 1999. The other twenty (Table 5.1) were observed at five field sites in and around the Pacific entrance of the Panama canal, from September through December of 1997. Fiddler crabs were videotaped in the field with a Canon ES6000 Hi8 camcorder. Filming was non-intrusive and captured typical behaviors such as feeding, waving, fighting, and surface breeding.

Rodman Mudflat	Diablo Mangrove	Naos Sand Beach
U. batuenta	*U. argillicola*	*U. deichmanni*
U. beebei	*U. herradurensis*	*U. terpsichores*
U. deichmanni	*U. oerstedi*	
U. heteropleura	*U. ecuadoriensis*	
U. inaequalis		
U. intermedia		
U. terpsichores		
U. oerstedi	Diablo Stream Inlet	Naos Rocky Inlet
U. ornata	*U. beebei*	*U. panamensis*
U. princeps	*U. festae*	
U. saltitanta	*U. umbratila*	
U. stenodactylus		
U. stylifera		
U. tenuipedis		

Table 5.1. Fiddler crab species studied at each of five field sites in and around the Pacific entrance of the Panama canal.

After briefly reviewing mating patterns and female choice in fiddler crabs, four sets of behaviors will be examined in succession: visual display, acoustic display, combat, and feeding. Each will be examined with respect to interspecific variation and morphological specialization.

5.4 BEHAVIORS

Historically, fiddler crabs have been split into two large categories based on morphology, geography, and behavior (Chapter 2; Bott 1954; Crane 1975; Christy and Salmon 1984). The narrow-front group consists of the Indo-West Pacific species, characterized by simple waving displays and surface mating

(Salmon 1984); the broad-front group consists of the American species, characterized by complex visual and acoustic displays, where males court females and entice them to enter the male's burrow for underground mating. Males then guard the burrow against intruders until the female has ovulated and the eggs have been fertilized (Christy 1982; Goshima and Murai 1988; Goshima *et al.* 1996). A few species did not fit the pattern. The four Indo-West Pacific species of the subgenus *Amphiuca* (*sensu* Crane, 1975) have broad-fronts but behavioral patterns like the narrow-fronts. The American subgenera *Boboruca* (broad-fronts) and *Uca* (narrow-fronts) have some behaviors like broad-front species and some like narrow-front species (Crane 1975; Salmon 1987).

It has become increasingly clear that the underground/above ground mating distinction is an oversimplification. A number of species in both geographic regions perform both underground and surface mating (Murai *et al.* 1987, 1996; Salmon 1987; Koga *et al.* 1998, 1999). One of these species, *Uca paradussumieri*, has underground mating in the female's burrow, rather than that of the male (Koga *et al.* 1999). In a number of species, the male is known to attempt to startle, scare, or even herd the female into his burrow (Salmon 1967; Crane 1975; Zucker 1983). Mating behavior has only been rigorously studied in a few species; as more detailed studies are performed on a wider variety of species even greater variation is likely to emerge.

It is almost a paradigm of sexual selection in general (as well as for fiddler crabs specifically) that females choose mates based on the size of greatly enlarged structures, yet the evidence for female choice based on major claw size in fiddler crabs is weak. A number of studies have found no evidence for females choosing males based on claw size (Greenspan 1980; Christy 1983, 1987; Salmon 1984; Koga *et al.* 1999), while others have found strong evidence (Hyatt 1977a; Yparreguirre 1981; Backwell and Passmore 1996; Oliveira and Custódio 1998; Latruffe *et al.* 1999); some of these studies looked at the same species (e.g. Yparreguirre 1981 vs. Salmon 1984; Hyatt 1977a vs. Christy 1983). A number of factors may explain the conflicting results, including temporal variation in female choosiness (Backwell and Passmore 1996) and experimental design. In some species, females preferentially approach larger males, but final mate choice is based on burrow quality, which is independent of male size (Backwell and Passmore 1996). Apparent size-assortative mating may be due to females not being able to fit into the burrow of a smaller male (Christy 1983).

Visual Display

Next to the extreme asymmetry, fiddler crabs are best known for their visual display; in fact, the German name for these crabs, *Winkerkrabbe*, means "waving crabs." Waving is probably the most studied behavior in fiddler crabs (Müller 1869; Darwin 1874; Alcock 1892, 1902; Pearse 1912, 1914a,b; Verwey 1930; Hediger 1933, 1934; Gray 1942; Crane 1957, 1975; Gordon 1958; Salmon 1965, 1967; Salmon and Atsaides 1968; Aspey 1971; Altevogt 1972, 1978; Hyatt 1977a,b; Doherty 1978, 1982; Salmon *et al.* 1978, 1979; Hagen 1983, 1993; Salmon and Kettler 1987; Schinca 1992; Takeda and Murai 1993; Pope 1997; Backwell *et al.* 1998, 1999; Jennions and Backwell 1998; Oliveira and Custódio 1998; Latruffe *et al.* 1999). Other ocypodid crabs are known to have simplistic waving (Wright 1968; Altevogt 1978), but none come close to the complexity seen in *Uca*.

First described over 300 years ago (Salmon 1983b), it was not until the 1940's that Crane (1941) first recognized that male waving was species specific in terms of its spatial and temporal patterns. Because species specificity of waving display is so strong, Crane (1957) stated in no uncertain terms that an observer should be able to tell species apart solely by watching their display. "In spite of group similarities, the display of each species is so distinct that, if seen in moderate intensity and advanced stages, none could ever be confused in the field with that of any other species, even from other parts of the world" (Crane 1957:74). For the most part this is true: after a month in the field, this author could easily distinguish and identify males of any of the twenty Panamanian species in Table 5.1 without a direct morphological examination, but rather by a combination of their visual display and color. However, it turns out there are exceptions: the closely related species *Uca burgersi* and *U. mordax*, for example, have virtually indistinguishable waving display (Crane 1975; Hagen 1983).

Types of Waving

Fiddler crabs have often been classified by their wave pattern (Crane 1957, 1975). Waves have roughly been divided into two forms: vertical (Figure 5.3) and lateral (Figure 5.4).

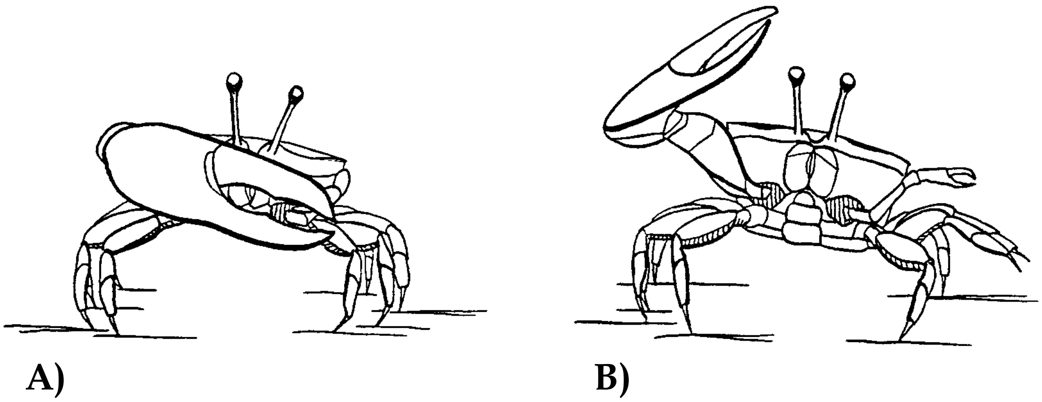

Figure 5.3. Basic vertical wave. A wave of *Uca demani* is pictured. The claw is raised and lowered within a single plane. A) Resting position; B) Maximum elevation of claw. Figure modified from Crane (1957).

In vertical waving, the male raises and lowers the claw in a plane in front of the body. In lateral waving, the male moves the claw laterally, away from the body. Vertical waving was thought to be used by "primitive" narrow-front crabs of the Indo-West Pacific and lateral waving by "advanced" broad-font crabs of the Americas (Crane 1957). The rough waving designations are perfectly correlated with phylogenetic divisions within the genus (Chapter 2). This has

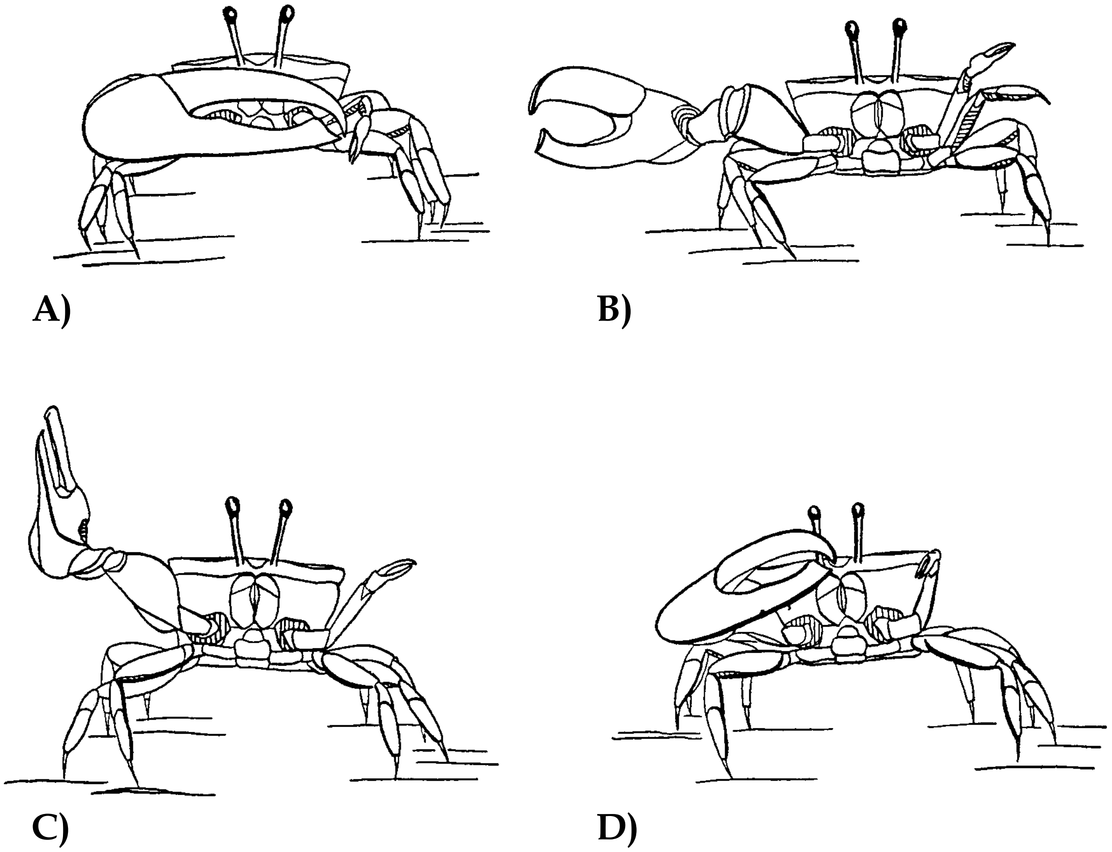

Figure 5.4. Basic lateral wave. A wave of *Uca perplexa* is pictured. The claw is moved in a lateral circle in the following order: A) Resting position; B) Flexed outward; C) Raised; D) Lowered. Figure modified from Crane (1957).

turned out to be an oversimplification (Crane 1975) and possibly a misinterpretation of the direction of evolution within the genus (Salmon and Zucker 1988; Levinton *et al.* 1996; Sturmbauer *et al.* 1996). Waves can be vertical, lateral, or in between; they can be a smooth motion or punctuated by jerks and pauses (Figure 5.5). Some species' waves are circular, others are more linear. Some species wave quickly, while others are slower and more deliberate.

Although the speed and timing of waves are also species specific, comparing these factors is complicated because they are dependent on the breeding activity of the crab, the time relative to low tide, the presence of both

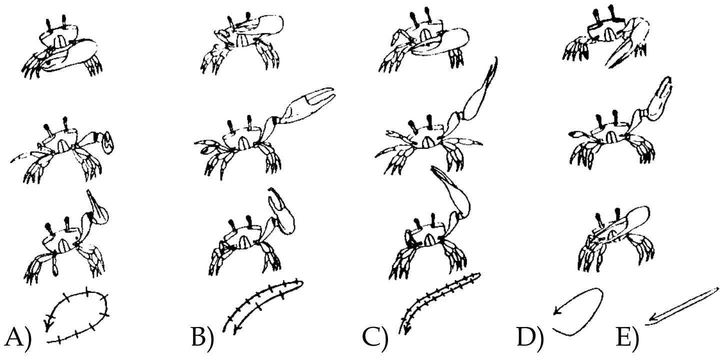

Figure 5.5. Variations on basic waving patterns. From top to bottom, the sketches illustrate three stages of a wave. Arrows indicate the path of the tip of the major claw during the wave; tick marks indicate pauses or jerks. A) *Uca mordax*; B) *Uca rapax*; C) *Uca pugnax*; D,E) *Uca speciosa*. *Uca speciosa* shows different waves to females (D) and intruding males (E). Figure modified from Salmon (1967).

other males or females, the size of the crab, and temperature (Hyatt 1977a,b; Doherty 1978, 1982; Jennions and Backwell 1998). In general, the timing of an individual's waving is thought to be independent of the waving of other individuals, although males of *Uca annulipes* and *U. perplexa* will sometimes wave synchronously (Gordon 1958; Backwell *et al.* 1998, 1999).

The visual display of most species is not restricted to motion of the major cheliped. Virtually every part of the body may be involved in display. While some species will hold the rest of their body motionless while waving, many others raise or lower their body during the wave. *Uca heteropleura* rises up on the tips of its legs during its wave; *U. intermedia* has an almost identical motion, except it doesn't rise quite as high and does it at double the speed. Other species show lateral movement as they wave; *U. stylifera* takes slow steady steps, while *U. stenodactylus* quickly dashes from side to side. Many species have associated movements of the ambulatories or the minor claw. An individual of *U. ornata* missing its major cheliped was filmed "waving" despite the missing limb; it performed all of the other display motions including the final punctuation involving a delicate raise of the minor claw. Species with very similar major cheliped wave patterns can often be distinguished by the motions of their other appendages (Salmon and Kettler 1987).

Waving and Morphology

A number of morphological features are correlated with variation in waving display (Rhodes 1986; Takeda and Murai 1993). Because the major cheliped contains a third to half of the crab's mass, it is not surprising that muscle characteristics would be correlated with display. Rhodes (1986) found that thoracic muscle sarcomere length is correlated with the speed and duration of waving. The thoracic muscles move the major cheliped during a wave; longer sarcomeres provide more strength, but contract slower. Species with slower, longer waves have longer sarcomeres than those with quicker, shorter waves. Asymmetry in males is not localized to just the chelipeds, but extends to other appendages such as the eyestalks and ambulatories. Takeda and Murai (1993) found that the degree of asymmetry in the ambulatories was related to waving pattern. In vertical waving, the major cheliped is lifted directly above the crab; the weight of the claw is distributed fairly evenly among the legs on both sides of the animal. In lateral waving, the claw is held out to the side of the crab; the weight of the claw must be supported much more by the legs on the major side. Species with lateral waving have the greatest asymmetry between the ambulatories on the major and minor sides; species with vertical waving have little to no asymmetry between their ambulatories (Takeda and Murai 1993). Species with waves intermediate between lateral and vertical have intermediate asymmetry.

There are no known morphological correlates between the major claw and waving display. Because of its extreme size, one would expect selection for waving display to have reduced the mass of the major claw; it should become a weak, flimsy, gaudy structure, used to get attention but not much else. Although major claws tend to be extremely gaudy and colorful, they are neither weak nor flimsy. In the one species studied, the major claw retains functionality at all sizes (Levinton and Judge 1993; Levinton *et al.* 1995). The extensive armature on the claws of most species precludes the claim that major claws are flimsy or weak.

A MANOVA was performed to see if there were differences in the shape of the major claws of lateral, semi-lateral, and vertical waving species. Wave form was categorized after Crane (1975). Claw shape was significantly different (Wilk's $\Lambda = 0.4777$, $P < 0.001$) among these groups, but there are additional complications. First, the average claw size among the groups was also significantly different ($F = 4.45$, $P = 0.014$), with vertical waving species being about 40% larger than lateral waving species. Since claw shape is allometric (Chapter 4), the observed differences may be due to differences in size. To account for the size difference, a MANCOVA was performed to see if shape differed once size was taken into account. The multivariate slopes were not significantly different (Wilk's $\Lambda = 0.8214$, $P = 0.493$), indicating similar allometric trends within the groups. This is equivalent to a homogeneity of slopes test in an ANCOVA (Sokal and Rohlf 1995). The MANCOVA was significant (Wilk's $\Lambda = 0.5247$, $P < 0.001$), indicating significant claw shape differences among the different waving forms. However, because phylogenetic structure is correlated with wave type, the analysis is really comparing claw shape in the Indo-West Pacific narrow-front species to the American broad-front species.

Functions of Waving

The function of the waving has been widely debated in the literature. Many authors (Müller 1869; Darwin 1874; Alcock 1892, 1902; Pearse 1914a,b) believed male waving is used to attract females. Others (Verwey 1930; Hediger 1933, 1934; Gray 1942) felt the visual display has no courtship function, but rather plays a role in territoriality and male-male interactions. It has become increasing clear that visual display plays a major role in both (Crane 1975).

The species specificity of waving is a crucial component of premating isolation. Species recognition and sexual selection in fiddler crabs seems largely driven by female choice. Males will actively court objects that are only vaguely female-like (Hagen 1962a; Salmon and Stout 1962; Aspey 1971). On the other hand, females will only respond to males displaying the correct wave form (Aspey 1971; Salmon *et al.* 1978). However, waving is also clearly used as a threat gesture to ward away other males. This is particularly apparent in the Indo-West Pacific species where breeding occurs on the surface and females are not attracted to male burrows (Crane 1975; Salmon 1987). Using video play back experiments in the lab, Pope (1997) showed that males of *Uca pugilator* waved more often when females were present than when they were absent, regardless of whether or not other males were present. However, males would also start waving when presented with the visual image of another male waving, even when females were absent.

Waving display has always been considered part of the sexual dimorphism in *Uca*; therefore, it was quite surprising when female waving was discovered in a number of Australian species. In an unpublished thesis, Zann (1979) reported female waving in two species; this observation has since been confirmed and expanded to include four more species (Salmon 1984; Hagen 1993). The role of female waving is far from clear. Although it primarily appears to be used in agonistic interactions, the few waving females in a population show signs of special sexual excitement (Hagen 1993). Zann (1979) and Hagen (1993) both thought female waving represented an ancestral condition in the genus because it is spread among three different subgenera (*Deltuca*, *Australuca*, and *Thalassuca*) and is known in at least one other member of the family Ocypodidae, *Heloecius cordiformis* (Haddon 1976). However, these subgenera do not reside in basal positions in the phylogeny (Chapter 2; Levinton *et al.* 1996; Sturmbauer *et* *al.* 1996) as previously thought (Crane 1975), the three subgenera are closely related to each other within the Indo-West Pacific clade, and *Heloecius* is not closely related to *Uca* (Levinton *et al.* 1996). While female waving may be a shared-derived character in the Indo-West Pacific clade, it cannot be considered an ancestral character of the genus. Females of two American sibling species, *Uca musica* and *U. terpsichores*, have a rejection display in which the female quickly bobs her body and raises both chelipeds (personal observation; Zucker and Denny 1979), but this can hardly be considered waving and is contextually very different from the female waving seen in the Australian species.

Acoustic Display

Although not as well studied, acoustic display serves many of the same roles as visual display and is a key component of both courtship and agonistic interactions for many species. Also like visual display, acoustic signals are species specific (Salmon and Atsaides 1968; Crane 1975; Salmon *et al.* 1978, 1979; Salmon and Kettler 1987); in some cases species that are virtually indistinguishable through morphology or visual display produce completely different acoustic signals (Hagen 1984). The sounds fiddler crabs create have often been subdivided into categories based on the acoustic impression of the observer, such as *rapping* or *honking*, or by the way they were produced such as stridulation or drumming (Hagen 1975); the latter seems to be a less arbitrary way of classifying sound. Fiddler crabs do not “hear” airborne sounds; rather, they detect vibrations in the substrate through a vibration receptor (Barth’s organ) on their ambulatories (Horch and Salmon 1969; Salmon *et al.* 1977).

Types of Acoustic Signals

Every species of fiddler crab probably produces sounds through stridulation (Crane 1975). Stridulation is an action where one body part is rubbed against another to form a sound; these body parts often have specialized sound producing structures such as tubercles and ridges. For many years, sound production in *Uca* was assumed through morphological analysis rather than observation; tape recordings of sounds have been rigorously analyzed since 1962 (Altevogt 1962; Hagen 1962b; Salmon and Stout 1962). Stridulation can occur between a number of appendages such as either the major or minor merus and the carapace or a pair of ambulatory legs. The only parts of the major claw that may be involved in stridulation are structures on the lower inner part of the palm, such as the distinct series of ridges of *Uca musica* and *U. terpsichores*, which are rubbed against tubercles on the front of the first ambulatory to produce sound (Figure 5.6).

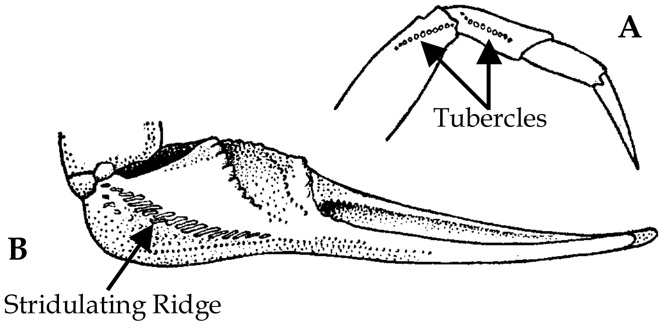

Figure 5.6. Acoustic specializations of *Uca musica* and *Uca terpsichores*. A) Anterior view of first ambulatory on major side; B) Ventral view of major claw. Figure modified from Rathbun (1914).

The other use of the major claw in sound production is drumming. Some species produce sounds by banging the proximal-ventral part of the major manus against the substrate. The behavior is found in a wide variety of species across the genus (Crane 1975). The only morphological specialization that might be associated with this behavior is an enlargement of the proximal-ventral part of the manus; however, many species with an apparent enlargement are not known to drum. In a few species, drumming has become a direct part of the waving display. The most distinctive of these is *Uca saltitanta*, which also has one of the most extreme claw shapes (Chapter 4). This species has an extremely broad, triangular pollex with a greatly enlarged manus (Figure 5.7).

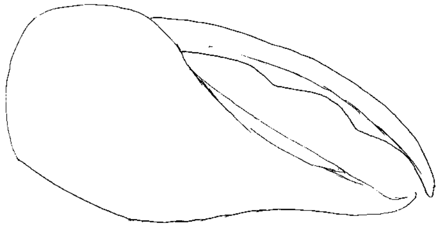

Figure 5.7. Outer view of right major claw of *Uca saltitanta*.

This species has a lateral wave, where the claw is lifted straight up above its carapace, then brought rapidly downwards to strike the ground in front of it. Occasionally, the species adds what appears to be a drum roll; the major claw becomes a blur as it rapidly vibrates in front of the crab, presumably striking the ground. How many strikes cannot be determined from standard video; even at 30 frames a second the claw is a blur on individual frames. It is thought that the extreme shape of the lower manus is an adaptation for this drumming (J. Christy, personal communication). Some species, e.g. *Uca terpsichores*, also rap the ground with the tip of the pollex as part of their visual display; this motion is probably more visual than acoustic, because the claw does not strike the surface with every motion (Zucker 1974).

A MANOVA was performed to see if there were differences in the shape of the major claws of drumming and non-drumming species. Drumming species were identified from Crane (1975) and personal observation and videotape. When there was uncertainty due to lack of observation, species were designated as non-drumming. Claw shape was significantly different (Wilk's $\Lambda = 0.8195$, $P = 0.038$) among drummers and non-drummers. The average claw size among the groups was not significantly different (F = 2.24, P = 0.138), although the non-drumming species were 25% larger than drumming species. A MANCOVA was performed to see if shape differed once size was taken into account. The multivariate slopes were not significantly different (Wilk's Λ = 0.9123, P = 0.501), indicating similar allometric trends within the groups. The MANCOVA was significant (Wilk's Λ = 0.8053, P = 0.025), indicating that drummers and non-drummers have different shaped claws, even after size is taken into account (Figure 5.8).

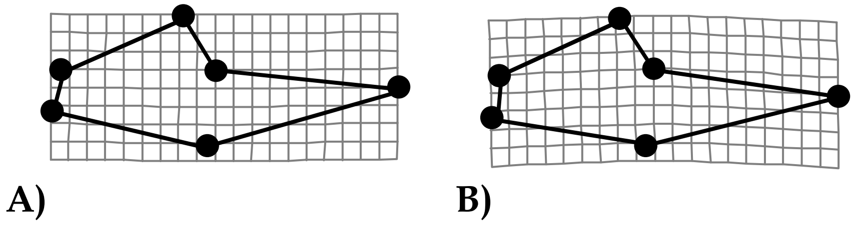

Figure 5.8. The shape of the major claw of drumming and non-drumming species. A) Average shape of major claw of non-drumming species; B) Average shape of major claw of drumming species.

Despite the statistical significance, the claw shapes are very similar and differences subtle. The difference is that in drumming species (Figure 5.8b), the distal landmarks (the tip of the pollex and the edges of the carpal cavity) are slightly lower and closer to the base of the claw, relative to the interior landmarks (the bases of the dactyl and pollex). This leads to a flatter base of the propodus (landmarks 1 to 3, Figure 5.2).

Most of the seventeen drumming species are among the *Celuca* (both American and Indo-West Pacific), with a few additional species from the *Minuca*, *Afruca*, and *Deltuca*. Because of the phyletic distance of these subgenera, as well as the polyphyletic nature of the *Celuca* (Chapter 2), there should not be too much concern about phylogenetic dependence in these analyses.

Functions of Acoustic Signals

Sound production in fiddler crabs has been extensively studied in a number of species in the Americas and West Africa (Burkenroad 1947; Altevogt 1962, 1964; Hagen 1962b, 1975, 1984; Salmon 1962, 1965, 1967, 1971; Salmon and Stout 1962; Salmon and Atsaides 1968; Horch and Salmon 1969; Salmon and Horch 1972, 1976; Crane 1975; Salmon and Hyatt 1979; Horch *et al.* 1980; Pawlik *et al.* 1980; Salmon 1983a; Müller 1989); much less is known about sounds production for species of the Indo-West Pacific (Crane 1975). Acoustic display is a critical component of courtship; males of many species shift from visual to acoustic display as a female approaches, in order to entice her into his burrow (Altevogt 1962; Hagen 1962a,b; Salmon 1965). Acoustic display is the primary courtship signal when species court at night or in dense mangroves with reduced visual fields (Burkenroad 1947; Hagen 1961; Salmon and Stout 1962; Salmon 1967). The West African fiddler crab, *Uca tangeri*, which lives in one of the most complicated habitats in terms of dense mangroves and visual obstruction, appears to have the most complicated acoustic signals of any fiddler crab, producing two very distinct types of signals; other species appear to produce only a single sound (Hagen 1962a; Salmon and Atsaides 1968).

Little is known about acoustic signaling and agonistic display, but as with visual display, it can be extremely difficult to distinguish between the influence of courtship and agonistic interactions in a natural setting (Hagen 1984; Pope 1997). There are reasons to believe that the acoustic specializations in *Uca terpsichores* (Figure 5.6) play a role in agonistic interactions. While watching male-male combat, *U. terpsichores* was observed to perform a unique, but extremely common motion as part of its male-male interactions. This motion consists of an individual male facing its opponent and moving its major claw horizontally back and forth in front of its body four or five times, with the pollex possibly scraping the substrate. A pair of combatants will alternate this maneuver as much as ten times each, with an individual occasionally approaching or withdrawing in response to its opponent's motion. Even when the combat proceeds to contact and more forceful maneuvers, they often return to this face-off position and alternation of pollex scraping. Although the sounds that can be heard on the videotape are inconclusive, I believe the combatants are producing sounds with this motion through stridulation between the ridges on the palm and the tubercles on the first ambulatory. A similar sort of motion is not found as part of the courting behavior of this species.

Combat

Even though intermale combat is a dominant feature of the genus *Uca* that had been recognized by naturalists for decades (e.g. Alcock 1892; Pearse 1912, 1914a), it has been studied very little in comparison to other behaviors. It had been proposed that combat between male fiddler crabs was completely ritualized and injury occurred only in rare instances (Huxley 1932; Crane 1967). Crane (1967) first attempted to describe in detail the various components and maneuvers involved in the combat of a single species, *Uca rapax*. She suggested that many previously unexplained morphological features of the major claw were primarily used in combat. Figure 5.9 illustrates just a few of the morphological features of the major claw, found in a single subgenus, which have been proposed to play a role in combat as grip points and contact surfaces for grappling.

Although she did provide frequency tables of each recognized combat maneuver, no quantitative attempt was made to describe the interrelationship, order, or importance of each move. She noted that combat tended to take place between two possible sets of opponents: burrow resident versus wanderer or burrow resident versus neighboring burrow resident. Aggressive wandering males will move through the population, challenging burrow residents to combat. When burrow neighbors fight, the are usually both in display phase.

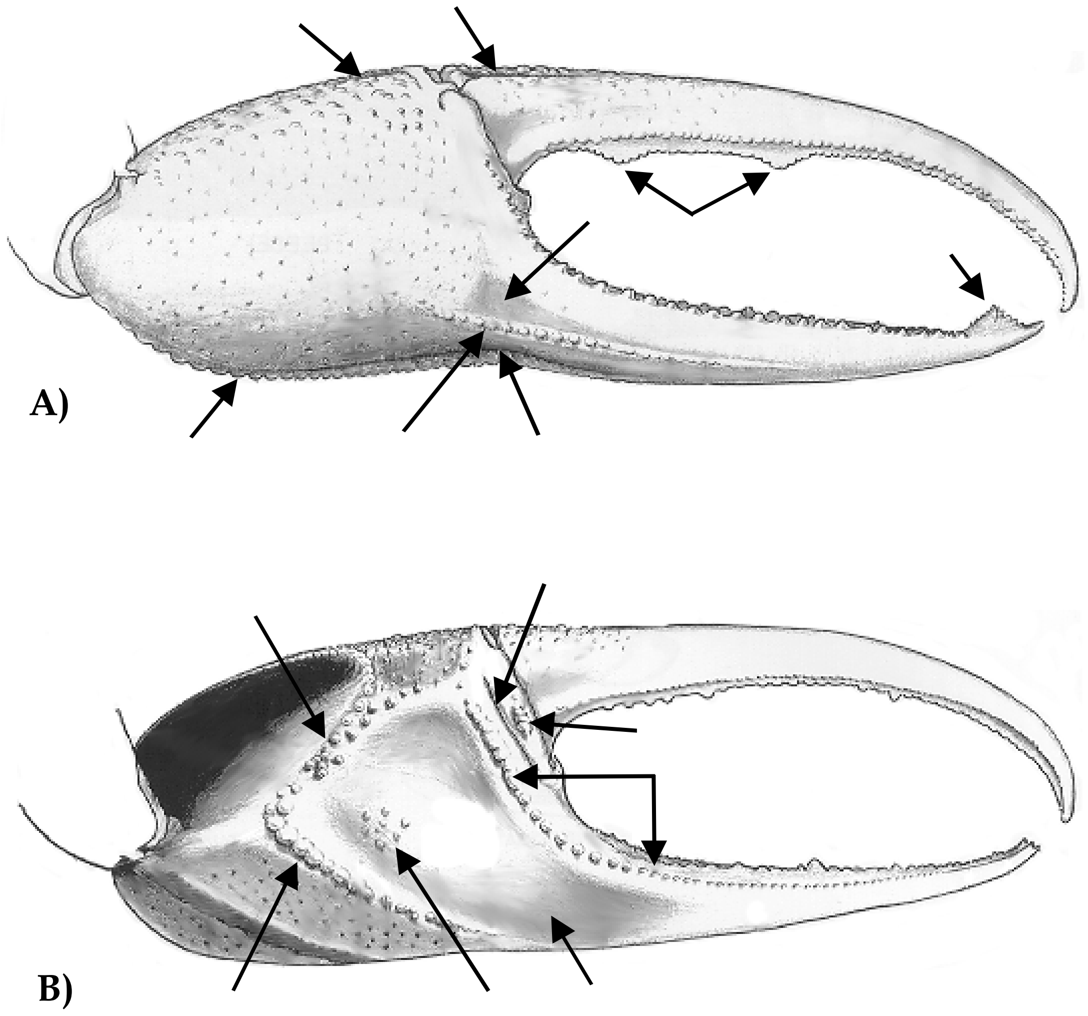

Figure 5.9. Major claw morphology as it relates to combat. The arrows point to just some of the many morphological structures on the major claw that are suspected to play a role in combat. A) Outer surface; B) Palmar (inner) surface. Figure modified from Crane (1975).

Powers (1975) described the situations under which combat occurs in *Uca panacea* and the general outcomes of each situation. Fighting usually occurred between wanderers and residents; fighting between neighbors was rarer and lasted for a much shorter time. He did observe a number of occasions where fighting led to the autonomy of a major claw. Size appeared to be the major factor in determining a winner, although there was an effect of burrow residency. He was unable to describe the specific combat maneuvers in the manner of Crane (1967).

Quantification of combat maneuvers, as well as the only direct comparison of combat between two species (*Uca pugnax* and *U. pugilator*), was studied by Hyatt and Salmon (1978, 1979). They characterized the combat of both species, including the quantitative relationship between different combat maneuvers; correlated combat success with physical and behavioral characters of the combatants; and discussed how the observed differences between the two species might be related to differences in their preferred habitat (Hyatt and Salmon 1978). They found differences between the species in the frequency and sequences of different combat maneuvers, as well as the tempo and length of fights. For both species, size and burrow residency were critical factors in determining the winner of a fight. In a second study, they analyzed the data with regard to the degree of ritualization and the potential information being passed on at each step of combat between the two species (Hyatt and Salmon 1979). They found that the amount of information being transmitted between the combatants (the "efficiency" of the communication system) was about the same for both species. They did not examine morphology with respect to combat. The same data was also used to propose and test game theory models for fiddler crab combat (Hyatt *et al.* 1979).

Jennions and Backwell (1996) performed a manipulation experiment on a fifth species, *Uca annulipes*, by removing males from burrows and releasing them far from their own burrows but in close proximity to other burrow-holding males, hoping the displaced males would initiate combat. Displaced males tended to pick fights with burrow residents that were smaller than themselves. Although they did not examine specific combat maneuvers *a la* Crane (1967) or Hyatt and Salmon (1978, 1979), they did provide solid support for the importance of both size and burrow residency on the outcome and duration of combat encounters. Fights lasted longer when the opponents (or their claws) were more similar in size. The importance of size and burrow residency on the outcome of combat has also been confirmed for *U. tangeri* (Latruffe *et al.* 1999).

All of these studies have concentrated on just one or two species and no research has been done to look at combat in the genus as a whole. Only Crane (1967, 1975) has discussed how morphological features of the major claw may be related to combat. Some general trends do emerge. First, both size and burrow residency play a large role in determining the outcome of a fight. Second, combatants that are more similar in size will tend to fight longer than combatants that are unequal. Third, wanderers tend to pick fights with residents that are smaller than themselves. Finally, all of the five species studied seem to show noticeable differences from each other in the frequency and types of combat maneuvers used during fights.

One theme of the above studies has been the role of ritualization in preventing injury. The large degree of morphological specialization, the fact that major claws retains functionality at all sizes (Levinton and Judge 1993; Levinton *et al.* 1995), and frequently signs of injury due to intraspecific interactions (P. Backwell, J. Christy, personal communication; Powers 1975; Jones 1980), all suggest that combat behavior must have played an important role in maintaining the structure of the claw. Game theory also suggests that selection would support honest signaling in structures which function as both ornaments and armaments (Berglund *et al.* 1996). However, it should be remembered that fighting is not necessarily equivalent to inflicting damage.

My own observations indicate that the fighting varies tremendously among species with respect to the manner in which individuals engage in combat, the frequency of certain maneuvers, and, to a lesser extent, the situations under which they fight. Unfortunately, these differences are hard to describe and harder to quantify. Data collection can be very difficult. Previous studies (Hyatt and Salmon 1978, 1979) were made by researchers with binoculars describing what they observed into tape recorders; using videotape one quickly realizes that what one sees with the naked eye is not the same as what one sees in slow motion or frame by frame. Potential statistical analyses (e.g. information analysis Estabrook 1967; Dingle 1972; Steinberg 1977; Hyatt and Salmon 1979) require large sample sizes that can be difficult to obtain given the scattered and unpredictable nature of fighting. Hyatt and Salmon (1978, 1979) observed over 400 fights for both of the species they studied; in three months of observation, I only was able to videotape a couple dozen fights across seven species (out of twenty taped).

Types of Combat

The combat maneuvers described by Crane (1967, 1975) and Hyatt and Salmon (1978, 1979) appear to be generally applicable to most species, although the frequency of each maneuver varies tremendously among each species I observed fighting. Certain maneuvers may never be performed by some species (this study; Hyatt and Salmon 1978, 1979). Although normally classified in terms of low-intensity and high-intensity acts, from a morphological standpoint it makes more sense to classify the maneuvers with respect to the functional requirements. The first set of maneuvers do not involve contact, but rather consist of threatening gestures at the opponent (e.g. the extension of the claw towards the opponent); these are often tightly linked to aspects of the visual display.

The second set involve contact of the outside surfaces of the claws; these include maneuvers such as the manus push or manus rub (Figure 5.10). The primary feature associated with these maneuvers would be the tuberculation on the outside of the manus of most species (Crane 1975). Another possible feature that might be associated with these maneuvers are the large, pile-filled pits on the outside of the pollex of three closely related species (*Uca ornata*, *U. maracoani*, and *U. insignis*). Stimulation of this pile (as would happen during a manus rub) appears to have a calming influence on the crab (personal observation).

Figure 5.10. Illustration of the manus rub during male-male combat. Figure modified from Crane (1967).

The third set involve contact between a chela of one combatant and the claw of the other, without either combatant attempting to grip the claw of the other (Figure 5.11). These maneuvers can be characterized as one crab sliding its or tapping its chela on the claw of the opponent, and appear to involve small tubercle teeth on the inner surface of the chela or grooves on various parts of the claw (Crane 1975).

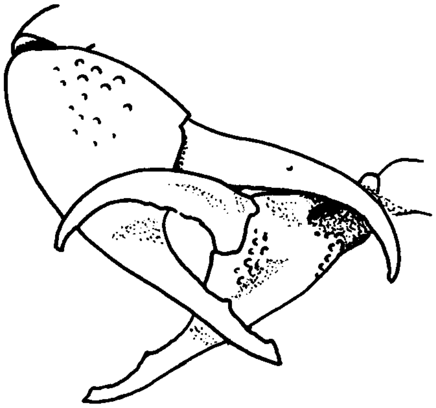

Figure 5.11. Illustration of the dactyl slide during male-male combat. Figure modified from Crane (1967).

The fourth set is similar to the third, except that one or both combatants are attempting to grip the claw of the other; maneuvers of the third and fourth set can be hard to distinguish because they often grade into each other. Most of the morphological features of the claw may be related to these more forceful maneuvers; grooves and ridges are probably grip points for teeth or the tips of the chela (Crane 1975). The goal and frequency of these types of maneuvers vary tremendously among species, which may explain the extreme morphological variation. Some species have large teeth that might be used to puncture the opposing claw; these species tend to have large ridges or tubercles that may serve as protection against damage.

A common maneuver is for two crabs to interlock their claws with a solid grip (Figure 5.12); they then appear to try to pull or push the other off balance. Many features appear specifically to aid in maintaining this grip. For example, this type of maneuver is the most common form of fighting in *Uca stylifera* (this study). The claw of this species has a large pollex with a distinctive tooth and notch at the proximal part of the gape (Figure 5.12a). The palm ridges of this species (the oblique turberculate ridge and the predactyl ridge) are quite large, creating a deep valley between them (Figure 5.12b). When two claws of about the same size are interlocked in the grip position used during this combat maneuver, the notch sits directly on top of the predactyl ridge, with the tooth in the valley, locked up against the ridge. This causes a tight contact surface and allows the crabs to test their strength or leverage without the claws sliding. The winning crab is often able to upend or throw its opponent (see below). These ridges may also help protect a crab from damage by preventing an opponent's tooth from pushing downward against the palm and possibly puncturing it.

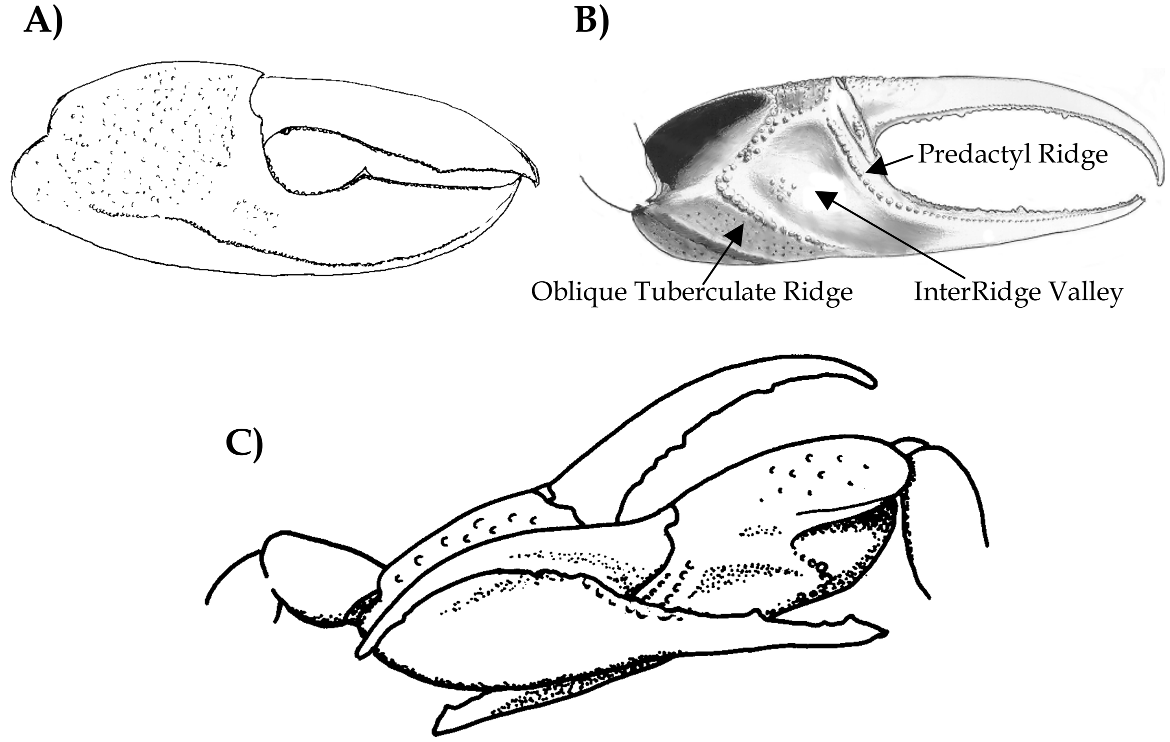

Figure 5.12. Illustration of interlocking claws and some related morphological features. A) Outer view of *Uca stylifera* claw; B) Palmar view of major claw (modified from Crane 1975); C) Interlocked claws (modified from Crane 1967).

It should be noted that parts of the crab other than the major claw become involved in combat. A combatant will often grip his opponent on the merus, carpus, or carapace with their major claw, often leading to flings or upsets. Many species will kick or step on opponents with their ambulatories (Crane 1975). Females have also been observed to fight, usually by kicking or pushing at each other (Powers 1975; Salmon 1984, 1987).

The shape of the major claw may also play an important role in combat. Claw biomechanics have been studied for a wide variety of crabs, including *Uca* (Warner and Jones 1976; Brown *et al.* 1979; Seed and Hughes 1997). Studies of the closing force of the major and minor claws of *Uca pugnax* (Levinton and Judge 1993; Levinton *et al.* 1995) found that major claws are functional at all sizes.

Closing force was strongly correlated with claw length. They also found that closing force scaled as predicted from calculations of muscle cross-sectional area and mechanical advantage. The index of mechanical advantage (IMA) can be calculated as claw height divided by pollex length (Levinton and Judge 1993). By assuming the muscle mass within the manus to be ellipsoid, the length, width, and height of the manus can be used to estimate the index of muscle cross-section area (IXA) as

$$\left[\frac{4}{3}\pi\left(\frac{M}{2}\right)\left(\frac{W}{2}\right)\left(\frac{H}{2}\right)\right]^{2/3}$$

The index of force (IF) is simply the product of IMA and IXA. A number of simple relationships can be generated from these formula. Within species, as size increases, minor claws do not change shape (isometry), while major claws do change shape (allometry) (Chapter 4). Specifically, the primary shape change is that larger major claws have a longer pollex relative to their height. This means that major claws will show a decline in mechanical advantage as they grow, while minor claws will show no change. Large major claws should produce *relatively* less force than small major claws because of the decline in IMA; there should be no change for minor claws. These predictions were confirmed for *Uca pugnax* (Levinton *et al.* 1995). Other than size, there is surprisingly little difference in the composition of the closer muscle in major and minor claws, both consisting primarily of slow muscle fibers (Govind *et al.* 1986).

One assumption is that the force is being produced at the tip of the claw. If the occlusion surface is not at the tip, but rather somewhere along the length of the chela (e.g. at a large tooth), the distance to this point should be used in the calculation instead of the length of the entire pollex. Therefore, the presence of a subdistal tooth will increase the closing force by decreasing the practical lever arm. Furthermore, the presence of a tooth increases the amount of pressure that is generated by reducing the surface area through which the force is being applied (pressure is simply the quotient of force and surface area). In order to use these formulae across species, one must also assume that the composition of the closer muscle within the manus does not vary amongst species. Thoracic muscles do vary among species (Rhodes 1986), but interspecific variation in the closer muscle of the claw has not been studied. Some species certainly seem to pinch much harder than others of similar size collected at the same time and place, although this may have more to do with aggressiveness than potential closing force (personal observation).

The importance of closing force in combat is far from clear. If the goal of a fight was to damage the opponent, closing force and pressure would play a critical role. Although claws do frequently become damaged during fighting (P. Backwell, J. Christy, personal communication; Powers 1975; Jones 1980), none of the previously published studied (covering five species in two subgenera) reported damage frequency, except for Powers (1975) who reported a small number of fights ending in the autonomy of a claw. I have never seen combat clearly result in damage in any of the nine species (in three subgenera) for which I have observed fighting. This does not mean combat is completely ritualized and never leads to damage, as has been previously suggested (e.g. Huxley 1932). The defensive morphology is highly derived and appears to effectively minimize damage, but for some species and situations the danger in fighting has clearly not been eliminated. *Uca festae* has the longest relative chela in the genus (Crane 1975); a cost of these long, thin chela is fragility. Casual field observations revealed much higher rates of broken chela in the field than in any other species examined (this study). Whether these were damaged during a fight in unknown, since only five fights were witnessed for this species.

Flings, flips, and upsets appear to be much more common than has been previously reported (Crane 1967; Hyatt and Salmon 1978, 1979). Part of the reason is that they can occur extremely quickly and may easily be missed by the naked eye. On videotape, flings that are seen in slow motion are often missed when played at normal speed; the entire sequence occurs in a third of a second or less (present study; Hyatt and Salmon 1978). A number of forces are at play during a fling. First, the flinger usually must have a solid grip on the flung crab. As discussed above, there are specialized grip points and structures which allow claws to lock together without sliding or extreme closing force. Second, the flinger must produce enough force to pull his opponent away from the ground and into the air. As crabs begin to fight they often dig in with their ambulatories, hold their bodies close to the surface, and appear to hang onto the ground with all of their legs (personal observation). Occasionally crabs are upset or flipped without the opponent having a grip; the flipper puts the tip of his claw under the opponent and simply lifts him off his feet with a quick, solid push. The strength used to flip or fling an opponent does not come from the muscles within the claw, but rather from the thoracic muscles that move the cheliped.

Functions of Combat

Combat in fiddler crabs is thought to have a function in territoriality and breeding. Combat is much more frequent at the height of the breeding season for some species (Hyatt and Salmon 1978), although not for others (Powers 1975). In many species, one of the main factors by which females choose males is burrow quality (Christy 1983; Backwell and Passmore 1996). Males defend high quality burrows in order to attract females. In no species does combat appear to have a direct role in mate choice; females do not judge males on their prowess. Neighboring males will often fight, even when both already possess burrows. Because the fights often end with one crab retreating into its burrow, these combats may be an attempt by one crab to suppress the signaling of a neighbor. In some species, the loser will be driven from its burrow, which the winner will then destroy (Zucker 1977). Combat also plays a role in post-copulatory mate guarding (Christy and Schober 1994). In species with below ground mating, males will defend a burrow containing a recently mated female until she ovulates in order to prevent another male from mating with her (Koga *et al.*

1999). This is important because studies suggest a last male mating advantage in fiddler crabs (Murai *et al.* 1987). There is no mate guarding after surface mating.

Combat in fiddler crabs is restricted to intraspecific encounters (Powers 1975; present study). Although highly territorial species (e.g. *Uca stenodactylus*) will chase or threaten males from other species away from their burrows, these encounters almost never result in contact between the two crabs and certainly never escalate to grappling.

Feeding

Fiddler crabs are specialized deposit feeders. They scoop sediment off of the ground (with the minor claw if male, with both claws if female) and use their mouth parts to scrape organic matter (e.g. algae or diatoms) away from the sand or mud. The remaining inorganic sediment is then dropped as a tiny pellet; these pellets often litter the area around burrows and in some species can be used to determine feeding activity or the gender of the crab. Because they only have one claw with which to feed, male crabs feed longer and scoop faster than do females (Valiela *et al.* 1974; Caravello and Cameron 1987a; Weissburg 1990, 1992, 1993); once the major claw reaches a certain size, it is an ineffective feeding tool (Merz *et al.* 1999). On very rare occasions male fiddler crabs in a few species have been seen to hunt smaller crabs with the major claw (Koga *et al.* 1995), but this cannot be considered a major or normal component of feeding.

Fiddler crabs are found in a variety of habitats usually ranging from pure sand to deep mud, although one species (*Uca panamensis*) lives on rocks. Most species of fiddler crab have a strong preference for habitat type, often restricting their distribution to specific intertidal zones and substrates with specific mud/sand ratios (Ono 1965; Crane 1975; Frith and Frith 1978; Icely and Jones 1978; Jaramillo and Lunecke 1988). These preferences are what allow the spatial overlap of so many species. For example, in the fall of 1997, I found sixteen species of *Uca* living side by side on a large mudflat adjacent to Rodman Naval Base at the Pacific entrance of the Panama Canal. The species were not randomly distributed across the mudflat, but rather inhabited specific zones, such as a sand bar, the sand/mud interface next to the bar, the mangroves at the edge of the flat, or the deep soft mud in the center of the flat (although there was plenty of overlap among species in neighboring zones).

The feeding and sorting mechanisms of fiddler crabs have been described and compared in detail by a number of authors (Altevogt 1957; Miller 1961; Crane 1975). Morphological variation in some of these structures has also been examined with respect to habitat type (Ono 1965; Icely and Jones 1978). Because of the way fiddler crabs feed, much of the variation has been described with respect to the average particle size in the sediment. Fiddler crab substrates range from clean sands (largest mean particle size) to those dominated by silt and clay (smallest mean particle size), with a continuous range of intermediates. The major feeding structures and their relationship to habitat will be described in detail below. The external feeding structures fall into two categories, those on the mouth (or buccal cavity) used for the processing of sediment, and those on the minor cheliped used for the collection and transport of sediment from the ground to the mouth. Although there is also variation in the internal feeding structures, e.g. the proventriculus (Icely and Jones 1978), they will not be discussed here.

Mouthparts

The mouths of fiddler crabs include six separate paired appendages layered one after the other (Miller 1961; Ono 1965); from inside to outside, these include a mandible, two maxillae, and three maxillipeds (Figure 5.13).

The feeding mechanism works as follows (Miller 1961; Crane 1975): a scoop of substrate is placed in the buccal cavity by the minor cheliped and stuck against the setae of the first maxilliped. The digestible organic matter is usually

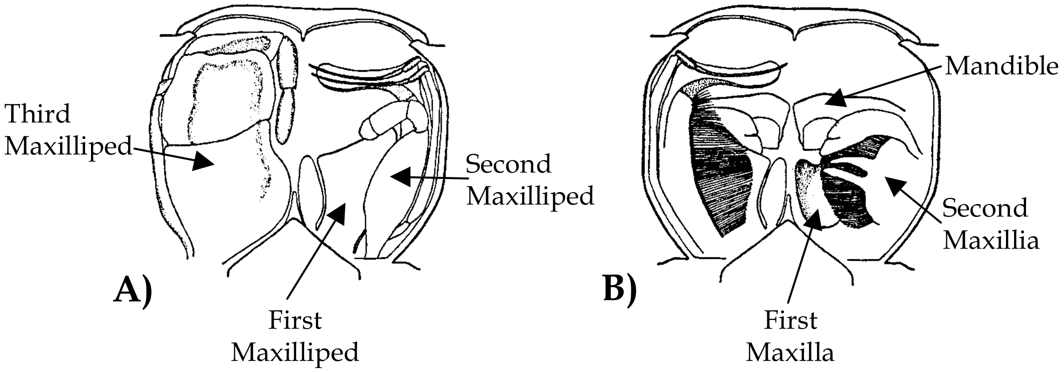

Figure 5.13. Buccal cavity of *Uca*. A) The maxillipeds, with left third maxilliped removed; B) Right first maxilliped and left maxillae and mandible. Figure modified from Miller (1961).

lighter than the coarse, inorganic particles. The setae of the second maxilliped are then vibrated across the matter trapped in the first maxilliped, while water is simultaneously flooded into the mouth. The setae of the second maxilliped sweep the coarser, heavier particles free from the first maxilliped; during the motion, specialized setae on the second maxilliped scour organic material off of the inorganic particles. The setae of the maxillae sweep the organic material clear of the first and second maxillipeds and deeper into the mouth, onto the mandibles where it is then ingested. As the second maxillipeds finish their sweep, the inorganic matter is flushed back to the third maxilliped, where it is gathered into a small pellet which will eventually fall or be removed by the small cheliped.

Two features of the mouthparts have been studied with respect to habitat and feeding: the general size and shape of the merus of the third maxilliped relative to the carapace and the shape, distribution, and number of specialized spoon-tipped setae on the inner edge of the merus of the second maxilliped. There is evidence to suggest that there may be a large degree of additional variation in the setae on both the first and the remainder of the second maxilliped (Ono 1965), but this has not been widely studied across the genus.

The third (or outer) maxilliped seems to serve two functions in feeding (Ono 1965). First, it serves as a cover for the sediment that has been placed in the buccal cavity. Second, it acts as a roller plate to collect the inorganic matter where it is made into the discarded pellet. While looking at a number of species from the family Ocypodidae (including two *Uca*), Ono (1965) found that species living on sandier beaches had a relatively broader third maxilliped than those living on muddier beaches. He proposed that a broad maxilliped is an adaptation to larger particle size. Similar studies on additional *Uca* species have supported the correlation between the relative size of the third maxilliped and average preferred sediment particle size (Hagen 1970, 1987; Thurman 1982, 1984, 1987), although there are outliers such as *Uca subcylindrica* (Thurman 1984).

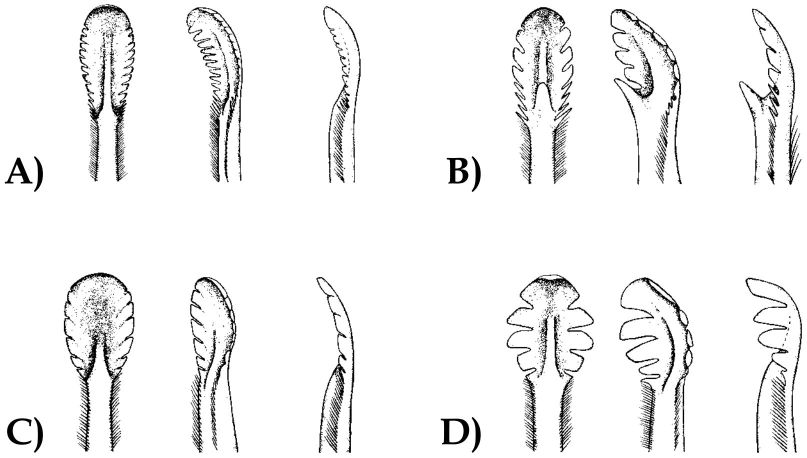

Figure 5.14. Examples of spoon-tipped setae found on the second maxilliped of *Uca*. A) *Uca tetragonon*; B) *Uca maracoani*; C) *Uca chlorophthalmus*; D) *Uca lactea*. Figure modified from Crane (1975).

First mentioned by Matthews (1930), the spoon-tipped setae of the second maxilliped were described in detail by Crane (1941). These setae, located on the inner edge of the anterior half of the manus, end with concave, pectinate tips (Figure 5.14). Some species virtually lack these specialized setae, while others have hundreds. In general, species in muddier habitats tend to have few spoon-tipped setae, while those in sandy habitats have the most (Miller 1961; Ono 1965; Crane 1975; Icely and Jones 1978), although there are exceptions (Thurman 1984). The setae appear to hold large particles (e.g. sand) in place while softer bristles scrape organic matter from them (Miller 1961). The shape and structure of the spoon-tips varies considerably among species (Crane 1975); how these differences relate to habitat type has never been reported.

Beyond the interspecific differences described above, many of these features show sexual dimorphism due to differences in male and female feeding behaviors (Weissburg 1991), as well as interpopulation differences in widespread species (Hagen 1987). Females have more setae than males, which allows them to more efficiently separate food from the sediment; this is necessary due to the faster feeding rate gained from feeding with both claws (Weissburg 1991).

Minor Claws

The main function of the minor cheliped is to scoop a small amount of material from the substrate and transport it to the mouth. The primary morphological features of the minor claws that aid in the collection and transport of sediment from the ground to the mouth are the spoon-shaped tip of the chela and specialized setae at the margins and tips of the gape (Figure 5.15). Species vary in the degree of the spoon-shaped tip and in the number and thickness of the setae. In many species, the setae form a thick basket at the end of the chela (Crane 1975). The relative height of the claw gape (the space between the pollex and dactyl when the latter is closed, Figure 5.1) and the presence of small serrations or teeth may also contribute to the ability of a claw to collect food.

Crane (1975) reported, in general, that narrow gapes with serration tended to be associated with muddy habitats, while wider gapes without serration were associated with sandy habitats. In a study of four east African species, Icely and Jones (1978) found that the sand dwelling species had the longest chela, the

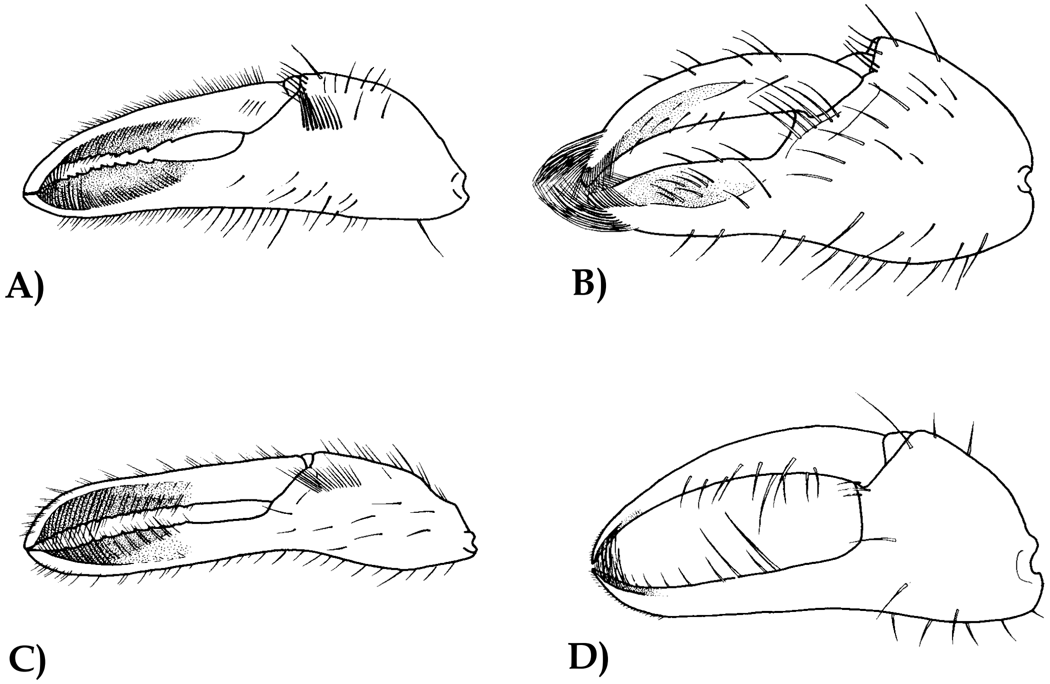

Figure 5.15. Minor claws of four species, representing some of the variation in specialized feeding structures. A) *Uca flammua*; B) *Uca panamensis*; C) *Uca thayeri*; D) *Uca terpsichores*. Figure modified from Crane (1975).

widest gape, and the least degree of spoonation at the tips. They concluded these were adaptations to large particle size. As one moves to species living in muddier habitats and smaller particle size, they found that the spoonation of the tip became more distinct, the chela became shorter, and the gape narrower. They did not find a pattern to the setae. The general correlation of the mud/sand gradient with gape width was confirmed by Neiman and Barnwell (1997).

Uca panamensis, the sole species which lives on rocks and tide pools, has relatively short chela with extremely thick, stiff setae on their tips (Figure 5.15b). These setae appear specialized for scraping algae and organic matter off of the rocks upon which they live (Crane 1975; Prahl and Guhl 1981).

The relationship between minor claw shape and habitat type was examined using the geometric morphometric data collected previously (Chapter

4). Habitats were ranked on a five point mud-sand scale, with 1 indicating a pure sand beach and 5 soft, pure mud. Intermediate values indicated relative mud/sand admixtures. Habitat designations were made initially for the 20 species studied in Panama; they ranged over the entire mud-sand scale. Habitats for the remainder of the species were then determined by comparing published descriptions (Crane 1975; Icely and Jones 1978; George and Jones 1982; Thurman 1982, 1984, 1987; Shih *et al.* 1999) of their habitat type with those of the species already included. Species with wide habitat ranges (e.g. *Uca beebei* or *U. tangeri*) were given intermediate values. This analysis included 85 species. *U. intermedia* and *U. typhoni* were not included because no data on their claw shape was available; *U. panamensis* was not included because its unique habitat could not be readily ranked on the mud-sand scale.

The relationship between minor claw shape and habitat was evaluated with a two block Partial Least Squares analysis (PLS). PLS is a technique for calculating the covariation between two multivariate data sets (Bookstein *et al.* 1996; Rohlf and Corti *In press*). This analysis calculates two sets of vectors (one for each data set) which represent linear combinations of the variables in each data set, such that the linear combinations account for as much of the covariation between the data sets as possible. Because one of these data sets (habitat) consisted of a single variable, the analysis is really just calculating the covariance between one variable and the others. The significance of the correlation was estimated by permuting the relationship between the shapes and the habitats (999 permutations).

There was a significant correlation between minor claw shape and habitat ($r = 0.4382$; $P = 0.001$). Figure 5.16 illustrates the shape differences at the extreme habitat types. Sand dwelling species have relatively shorter manus and longer chela than mud dwelling species. The distance between landmarks 2 and 6 is also much broader in sand dwelling species. This distance represents both the width of the pollex and the width of the gape; these cannot be clearly distinguished from these data. Because minor pollex width appears fairly uniform among species (the major exception being a few of the *Australuca* which have a relatively thick minor pollex), this difference may represent the difference in gape width previously noted by Crane (1975) and Neiman and Barnwell (1997).

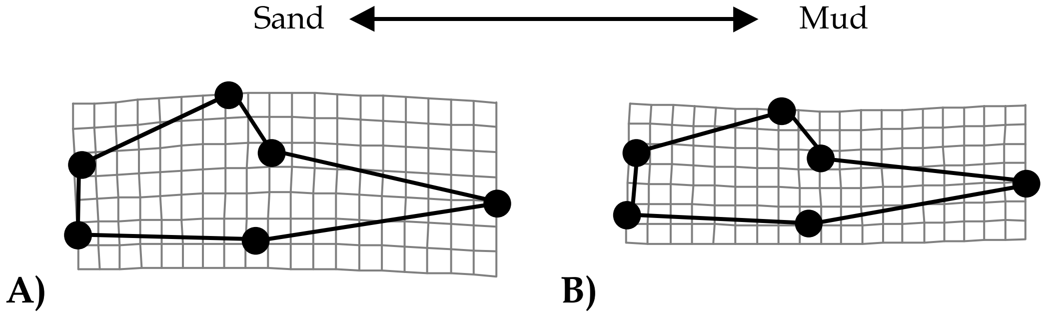

Figure 5.16. The relationship between minor claw variation and habitat. A) Shape of minor claw in pure sand habitat (type 1); B) Shape of minor claw in pure mud habitat (type 5).

Because the habitat designations are fairly coarse and are only approximate, it was necessary to test the robustness of these results. A fixed proportion of the habitat values were randomly changed by one step and the analysis was repeated to see if the result was still significant. This procedure was repeated multiple times for each proportion to be tested to see how many of the habitat designations had to be incorrect for the conclusions to be overturned. The results turned out to be surprisingly robust; between 50 and 60% of the values had to be changed before any of the analyses began to become nonsignificant ($P > 0.05$).

The minor cheliped is used for other functions than feeding (Crane 1975). In many species (e.g. *Uca ornata*) it is waved in tandem with the major claw during visual displays; males use it to pat and pluck at the female during copulation; it can be an important sound producing mechanism by rubbing the merus against the carapace; it is also occasionally used to clean other appendages or the eyestalks.

5.5 CONCLUSIONS

There is strong integration between claw morphology and behavior in fiddler crabs. Variation in both major and minor claws can be explained by specific differences in function and use across species.

Major claws are used primarily for just two purposes, waving and combat, with a much more limited role in sound production. The relationship between waving display and major claw structure is limited to thorax muscle variation. Other than a few specific sound producing structures on the palm of the major claw, only the broadened proximal-ventral part of the manus appears to be related to acoustic display. The remaining features of the major claw appear to be used in combat; most of these features appear to play a role in defense or friction, rather than for causing damage.

Minor claw shape and structure is related to habitat type; species in habitats with large mean particle size (sandy) have broad gapes and long chela while species in habitats with small mean particle size (muddy) have narrow gapes and shorter chela.

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LITERATURE CITED

Alcock, A. 1892. On the habits of *Gelasimus annulipes*, Edw. *Annals and Magazine of Natural History, Series XI* 10:415-416.

Alcock, A. 1900. Materials for a carcinological fauna of India No. 6. The Brachyura Catometopa, or Grapsoidea. *Journal of the Asiatic Society of Bengal* 64:279-486.

Alcock, A. 1902. *A Naturalist in Indian Seas*. London.

Altevogt, R. 1957. Untersuchungen zur Biologie, Ökologie und Physiologie Indischer Winkerkrabben. *Zeitschrift für Morphologie und Ökologie der Tiere* 46:1-110.

Altevogt, R. 1962. Akustische Epiphänomene im Sozialverhalten von *Uca tangeri* in Südspanien. *Verhandlungen der Deutschen Zoologischen Gesellschaft* 26:309-315.

Altevogt, R. 1964. Ein antiphoner Klopfkode und eine neue Winkfunktion bei *Uca tangeri*. *Naturwissenschaften* 51:644-645.

Altevogt, R. 1972. Physiological inter-relations of display and locomotion in fiddler crabs: An evolutionary aspect. *Journal of the Marine Biological Association of India* 14:456-467.

Altevogt, R. 1978. Proto-fiddlers and fiddlers: Pathways to waving in Indian Brachyuran crabs. *Journal of the Bombay Natural History Society* 75:800-809.

Andersson, M. 1994. *Sexual Selection*. Princeton University Press: Princeton, NJ.

Aspey, W. P. 1971. Inter-species sexual discrimination and approach-avoidance confict in two species of fiddler crabs, *Uca pugnax* and *Uca pugilator*. *Animal Behaviour* 19:669-676.

Backwell, P., M. Jennions, N. Passmore, and J. H. Christy. 1998. Synchronized courtship in fiddler crabs. *Nature* 391:31-32.

Backwell, P. R. Y., M. D. Jennions, J. H. Christy, and N. I. Passmore. 1999. Female choice in the synchronously waving fiddler crab *Uca annulipes*. *Ethology* 105:415-421.

Backwell, P. R. Y., and N. I. Passmore. 1996. Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, *Uca annulipes*. *Behavioral Ecology and Sociobiology* 38:407-416.

Berglund, A., A. Bisazza, and A. Pilastro. 1996. Armaments and ornaments: An evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society* 58:385-399.

Bookstein, F. L. 1991. *Morphometric Tools for Landmark Data*. Cambridge University Press: Cambridge.

Bookstein, F. L., P. D. Sampson, A. P. Streissguth, and H. M. Barr. 1996. Exploiting redundant measurement of dose and behavioral outcome: New methods from the behavioral teratology of alcohol. *Developmental Psychology* 32:404-415.

Bott, R. 1954. Dekapoden (Crustacea) aus El Salvador. 1. Winkerkrabben (*Uca*). *Senckenbergiana biologica* 35:155-180.

Brown, S. C., S. Cassuto, R., and R. W. Loos. 1979. Biomechanics of chelipeds in some decapod crustaceans. *Journal of Zoology* 188:143-159.

Burkenroad, M. D. 1947. Production of sound by the fiddler crab, *Uca pugilator* Bosc, with remarks on its nocturnal mating behaviour. *Ecology* 28:458-462.

Calman, W. T. 1911. *The Life of Crustacea*. Methuen & Co. Ltd.: London.

Caravello, H. E., and G. N. Cameron. 1987a. The effects of sexual selection on the foraging behaviour of the gulf coast fiddler crab, *Uca panacea*. *Animal Behaviour* 35:1864-1874.

Caravello, H. E., and G. N. Cameron. 1987b. Foraging time allocation in relation to sex by the gulf coast fiddler crab (*Uca panacea*). *Oecologia* 72:123-126.

Christy, J. H. 1978. Adaptive significance of reproductive cycles in the fiddler crab *Uca pugilator*: A hypothesis. *Science* 199:453-455.

Christy, J. H. 1982. Burrow structure and use in the sand fiddler crab *Uca pugilator* (Bosc). *Animal Behaviour* 30:687-694.

Christy, J. H. 1983. Female choice in the resource-defense mating system of the sand fiddler crab, *Uca pugilator*. *Behavioral Ecology and Sociobiology* 12:169-180.

Christy, J. H. 1987. Female choice and breeding behavior of the fiddler crab *Uca beebei*. *Journal of Crustacean Biology* 70:624-635.

Christy, J. H. 1988a. Pillar function in the fiddler crab *Uca beebei* (I): Effects on male spacing and aggression. *Ethology* 78:53-71.

Christy, J. H. 1988b. Pillar function in the fiddler crab *Uca beebei* (II): Competitive courtship signaling. *Ethology* 78:113-128.

Christy, J. H., and M. Salmon. 1984. Ecology and evolution of mating systems of fiddler crabs (genus *Uca*). *Biological Reviews* 59:483-509.

Christy, J. H., and M. Salmon. 1991. Comparative studies of reproductive behavior in mantis shrimps and fiddler crabs. *American Zoologist* 31:329-337.

Christy, J. H., and U. M. Schober. 1994. A test for resource-defence mating in the fiddler crab *Uca beebei*. *Animal Behaviour* 48:795-802.

Crane, J. 1941. Crabs of the genus *Uca* from the west coast of Central America. *Zoologica NY* 26:145-208.

Crane, J. 1957. Basic patterns of display in fiddler crabs (Ocypodidae, Genus *Uca*). *Zoologica NY* 42:69-82.

Crane, J. 1958. Aspects of social behavior in fiddler crabs, with special reference to *Uca maracoani* (Latreille). *Zoologica NY* 43:113-130.

Crane, J. 1967. Combat and its ritualization in fiddler crabs (Ocypodidae) with special reference to *Uca rapax* (Smith). *Zoologica NY* 52:49-77.

Crane, J. 1975. *Fiddler Crabs of the World: Ocypodidae: Genus Uca*. Princeton University Press: Princeton, NJ.

Darwin, C. 1874. *The Descent of Man and Selection in Relation to Sex*. 2nd Edition. A. L. Burt Company: New York.

Dingle, H. 1972. Aggressive behavior in stomatopods and the use of information theory in the analysis of animal communication. Pp. 126-156 in *Behavior of Marine Animals. Volume 1: Invertebrates*, H. E. Winn and B. L. Olla, eds. Plenum Press: New York.

Doherty, J. A. 1978. *The effects of temperature on the timing, form and variability of the wave display in the fiddler crabs Uca minax (Le Conte) and Uca pugnax (Smith)*. M.S. Thesis. University of Wisconsin.

Doherty, J. A. 1982. Stereotypy and the effects of temperature on some spatio-temporal subcomponents of the 'courtship wave' in the fiddler crabs *Uca minax* (Le Conte) and *Uca pugnax* (Smith) (Brachyura, Ocypodidae). *Animal Behaviour* 30:352-363.

Estabrook, G. F. 1967. An information theory model for character analysis. *Taxon* 16:86-97.

Frith, D. W., and C. B. Frith. 1978. Notes on the ecology of fiddler crab populations (Ocypodidae: genus *Uca*) on Phuket, Surin Nua and Yao Yai Islands, Western Peninsular Thailand. *Phuket Marine Biological Center Research Bulletin* 25:1-13.

George, R. W., and D. S. Jones. 1982. A revision of the fiddler crabs of Australia (Ocypodinae: *Uca*). *Record of the Western Australian Museum* Supplement:1-99.

Gordon, H. R. S. 1958. Synchronous claw-waving of fiddler crabs. *Animal Behaviour* 6:238-241.

Goshima, S., T. Koga, and M. Murai. 1996. Mate acceptance and guarding by male fiddler crabs *Uca tetragonon* (Herbst). *Journal of Experimental Marine Biology and Ecology* 196:131-143.

Goshima, S., and M. Murai. 1988. Mating investment of male fiddler crabs, *Uca lactea*. *Animal Behaviour* 36:1249-1251.

Govind, C. K., M. M. Quigley, and K. M. Mearow. 1986. The closer muscle in the dimorphic claws of male fiddler crabs. *Biological Bulletin* 170:481-493.

Gray, E. H. 1942. Ecological and life history aspects of the red-jointed fiddler crab, *Uca minax* (Le Conte), region of Solomons Island, Maryland. *Chesapeake Biological Laboratory Publication* 51:3-20.

Greenspan, B. N. 1980. Male size and reproductive success in the communal courtship system of the fiddler crab *Uca rapax*. *Animal Behaviour* 28:387-392.

Greenspan, B. N. 1982. Semi-monthly reproductive cycles in male and female fiddler crabs, *Uca pugnax*. *Animal Behaviour* 30:1084-1092.

Haddon, F. W. 1976. *The behaviour and seasonal distribution of the semaphore crab, Heloecius cordiformis (H. Milne Edwards) (Ocypodidae: Crustacea)*. Bachelor of Letters Thesis. University of New England.

Hagen, H.-O. v. 1961. Nächtliche Aktivität von *Uca tangeri* in Südspanien. *Naturwissenschaften* 48:140.

Hagen, H.-O. v. 1962a. Experimentelle studien zum Winken von *Uca tangeri* in Südspanien. *Verhandlungen der Deutschen Zoologischen Gesellschaft* 25:424-432.

Hagen, H.-O. v. 1962b. Freilandstudien zur Sexual- und Fortpflanzungsbiologie von *Uca tangeri* in Andalusien. *Zeitschrift für Morphologie und Ökologie der Tiere* 51:611-725.

Hagen, H.-O. v. 1970. Anpassungen an das spezielle Gezeitenzonen-Niveau bei Ocypodiden (Decapoda, Brachyura). *forma et functio* 2:361-413.

Hagen, H.-O. v. 1975. Klassification und phylogenetische Einordnung der Lautäußerungen von Ocypodiden und Grapsiden (Crustacea, Brachyura). *Zeitschrift für Zoologische systematik und Evolutionsforschung* 13:300-316.

Hagen, H.-O. v. 1983. Visual and acoustic display in *Uca mordax* and *U. burgersi*, sibling species of neotropical fiddler crabs. I. Waving display. *Behaviour* 83:229-250.

Hagen, H.-O. v. 1984. Visual and acoustic display in *Uca mordax* and *U. burgersi*, sibling species of neotropical fiddler crabs. II. Vibration signals. *Behaviour* 91:204-228.

Hagen, H.-O. v. 1987. Allometric growth in two populations of *Uca tangeri* from the Guadalquivir estuary (Andalusia). *Investigacíon Pesquera (Barcelona)* 51:443-452.

Hagen, H.-O. v. 1993. Waving display in females of *Uca polita* and of other Australian fiddler crabs. *Ethology* 93:3-20.

Hediger, H. 1933. Beobachtungen an der Marokkonischen Winkerkrabbe, *Uca tangeri* (Eydoux). *Verhandlungen der Schweizerischen naturforschenden Gesselschaft* 114:388-389.

Hediger, H. 1934. Notes sur la biologie d'un crabe de l'embouchure de l'oued Bou Regreg *Uca tangeri* (Eydoux). *Bulletin de la Société des Sciences Naturelles du Maroc* 13:254-259.

Horch, K. W., and M. Salmon. 1969. Production, perception and reception of acoustic stimuli by semiterrestrial crabs (Genus *Ocypode* and *Uca*, family Ocypodidae). *forma et functio* 1:1-25.

Horch, K. W., M. Salmon, and N. Coonrod. 1980. Response of acoustic interneurons in ghost and fiddler crabs to sounds of conspecifics and sympatric heterospecifics. *Marine Biology Letters* 1:167-173.

Huxley, J. S. 1932. *Problems of Relative Growth*. Dial Press: London.

Hyatt, G. W. 1977a. Field studies of size-dependent changes in waving display and other behaviour in the fiddler crab, *Uca pugilator* (Brachyura, Ocypodidae). *Marine Behaviour and Physiology* 4:283-292.

Hyatt, G. W. 1977b. Quantitative analysis of size-dependent variation in the fiddler crab wave display (*Uca pugilator*, Brachyura, Ocypodidae). *Marine Behaviour and Physiology* 5:19-36.

Hyatt, G. W., and M. Salmon. 1978. Combat in the fiddler crabs *Uca pugilator* and *U. pugnax*: A quantitative analysis. *Behaviour* 65:182-211.

Hyatt, G. W., and M. Salmon. 1979. Comparative statistical and information analysis of combat in fiddler crabs, *Uca pugilator* and *U. pugnax*. *Behaviour* 68:1-23.

Hyatt, G. W., S. D. Smith, and T. E. S. Raghavan. 1979. Game theory models of intermale combat in fiddler crabs (Genus *Uca*). Pp. 414-429 in *Applied Game Theory*, S. J. Brams, A. Schotter and G. Schwödiauer, eds. Physica-Verlag: Würzburg-Wien.

Icely, J. D., and D. A. Jones. 1978. Factors affecting the distribution of the genus *Uca* (Crustacea: Ocypodidae) on an East African shore. *Estuarine and Coastal Marine Science* 6:315-325.

Jaramillo, E., and K. Lunecke. 1988. The role of sediments in the distribution of *Uca pugilator* (Bosc) and *Uca pugnax* (Smith) (Crustacea, Brachyura) in a salt marsh of Cape Cod. *Meeresforschung* 32:46-52.

Jennions, M. D., and P. R. Y. Backwell. 1996. Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. *Biological Journal of the Linnean Society* 57:293-306.

Jennions, M. D., and P. R. Y. Backwell. 1998. Variation in courtship rate in the fiddler crab *Uca annulipes*: Is it related to male attractiveness? *Behavioral Ecology* 9:605-611.

Jones, A. R. 1980. Chela injuries in the fiddler crab, *Uca burgersi* Holthius. *Marine Behavior and Physiology* 7:47-56.

Koga, T., P. R. Y. Backwell, M. D. Jennions, and J. D. Christy. 1998. Elevated predation risk changes mating behaviour and courtship in a fiddler crab. *Proceedings of the Royal Society of London* 265B:1385-1390.

Koga, T., S. Goshima, M. Murai, and S. Poovachiranon. 1995. Predation and cannibalism by the male fiddler crab *Uca tetragonon*. *Journal of Ethology* 13:181-183.

Koga, T., M. Murai, and H.-S. Yong. 1999. Male-male competition and intersexual interactions in underground mating of the fiddler crab *Uca paradussumieri*. *Behaviour* 136:651-667.

Latruffe, C., P. K. McGregor, and R. F. Oliveira. 1999. Visual signalling and sexual selection in male fiddler crabs *Uca tangeri*. *Marine Ecology Progress Series* 189:233-240.

Levinton, J., C. Sturmbauer, and J. H. Christy. 1996. Molecular data and biogeography: Resolution of a controversy over evolutionary history of a pan-tropical group of invertebrates. *Journal of Experimental Marine Biology and Ecology* 203:117-131.

Levinton, J. S., and M. L. Judge. 1993. The relationship of closing force to body size for the major claw of *Uca pugnax* (Decapoda: Ocypodidae). *Functional Ecology* 7:339-345.

Levinton, J. S., M. L. Judge, and J. P. Kurdziel. 1995. Functional differences between the major and minor claws of fiddler crabs (*Uca*, family Ocypodidae, order Decapoda, subphylum Crustacea): A result of selection or developmental constraint? *Journal of Experimental Marine Biology and Ecology* 193:147-160.

Matthews, L. H. 1930. Notes on the fiddler-crab, *Uca leptodactyla*, Rathbun. *Annals and Magazine of Natural History, Series X* 5:659-663.

Merz, R. A., S. B. Altsculer, and K. C. Hauser. 1999. Growing ploughshares into swords: The morphological and functional transition of feeding to display claws in maturing male fiddler crabs. *American Zoologist* 39:40A.

Miller, D. C. 1961. The feeding mechanism of fiddler crabs, with ecological considerations of feeding adaptations. *Zoologica NY* 46:89-100.

Müller, F. 1869. *Facts and arguments for Darwin*. John Murray: London.

Müller, W. 1989. Untersuchungen zuer akustisch-vibratorischen Kommunikation und Ökologie tropischer und subtropischer Winkerkrabben. *Zoologische Jahrbücher. Abteilung für Systematik, Ökologie und Geographie der Tiere* 116:47-114.

Murai, M. 1992. Courtship activity of wandering and burrow-holding male *Uca arcuata*. *Ethology* 92:124-134.

Murai, M., S. Goshima, and Y. Henmi. 1987. Analysis of the mating system of the fiddler crab, *Uca lactea*. *Animal Behaviour* 35:1334-1342.

Murai, M., S. Goshima, K. Kawai, and H.-S. Yong. 1996. Pair formation in the burrows of the fiddler crab *Uca rosea* (Decapoda: Ocypodidae). *Journal of Crustacean Biology* 16:522-528.

Murai, M., S. Goshima, and Y. Nakasone. 1983. Adaptive droving behavior observed in the fiddler crab *Uca vocans vocans*. *Marine Biology* 76:159-164.

Murai, M., T. Koga, S. Goshima, and S. Poovachiranon. 1995. Courtship and the evolution of underground mating in *Uca tetragonon* (Decapoda: Ocypodidae). *Journal of Crustacean Biology* 15:655-658.

Nakasone, Y., and M. Murai. 1998. Mating behavior of *Uca lactea perplexa* (Decapoda: Ocypodidae). *Journal of Crustacean Biology* 18:70-77.

Neiman, M., and F. Barnwell. 1997. Morphometric differences in small claws of the deposit-feeding fiddler crabs (*Uca* spp.). *American Zoologist* 37:47A.

Oliveira, R. F., and M. R. Custódio. 1998. Claw size, waving display and female choice in the European fiddler crab, *Uca tangeri*. *Ethology, Ecology & Evolution* 10:241-251.

Ono, Y. 1965. On the ecological distribution of ocypoid crabs in the estuary. *Memoirs of the Faculty of Science, Kyushu University. Series E (Biology)* 4E:1-60.

Pawlik, J., R. Lewis, and F. H. Barnwell. 1980. Different mechanisms of sound production in two closely related species of fiddler crabs. *American Zoologist* 20:957.

Pearse, A. S. 1912. The habits of fiddler-crabs. *Philippine Journal of Science* 7D:113-133.

Pearse, A. S. 1914a. Habits of fiddler crabs. *Annual Report of the Smithsonial Institution* 1913:415-428.

Pearse, A. S. 1914b. On the habits of *Uca pugnax* (Smith) and *U. pugilator* (Bosc). *Transactions of the Wisconsin Academy of Sciences, Arts, and Letters* 17:791-802.

Pope, D. S. 1997. Fiddler crab claw waving: A signal to males, females, or both? *American Zoologist* 37:95A.

Powers, L. W. 1975. *The Fiddler Crab Burrow: A Study in Behavioral Ecology*. Ph.D Thesis. University of Texas at Austin.

Prahl, H. v., and F. Guhl. 1981. Notas sobre la biologia de *Uca* (*Minuca*) *panamensis* (Stimpson, 1859) (Crustacea, Ocipoidade) y su distribucion en Colombia. *Anales del Instituto de Investigaciones Marinas de Punta de Betin* 11:147-152.

Rathbun, M. J. 1914. New genera and species of American Brachyrhynchous crabs. *Proceedings of the United States National Museum* 47:117-129.

Rhodes, W. R. 1986. A comparative study of thoracic and cheliped muscle asymmetry in male Fiddler Crabs (Genus: *Uca*). *Biological Bulletin* 170:335-349.

Rohlf, F. J., and F. L. Bookstein, eds. 1990. *Proceedings of the Michigan morphometrics workshop*. University of Michigan: Ann Arbor, MI.

Rohlf, F. J., and M. Corti. *In press*. The use of two-block partial least-squares to study covariation in shape. *Systematic Biology*

Rohlf, F. J., and L. F. Marcus. 1993. A revolution in morphometrics. *Trends in Ecology and Evolution* 8:129-132.

Rosenberg, M. S. 1997. Evolution of shape differences between the major and minor chelipeds of *Uca pugnax* (Decapoda: Ocypodidae). *Journal of Crustacean Biology* 17:52-59.

Salmon, M. 1962. Courtship and sound production in the sand fiddler, *Uca pugilator*. *American Zoologist* 2:553.

Salmon, M. 1965. Waving display and sound production in the courtship behavior of *Uca pugilator*, with comparison to *U. minax* and *U. pugnax*. *Zoologica NY* 50:123-150.

Salmon, M. 1967. Coastal distribution, display and sound production by Florida fiddler crabs (genus *Uca*). *Animal Behaviour* 15:449-459.

Salmon, M. 1971. Signal characteristics and acoustic detection by the fiddler crabs, *Uca rapax* and *Uca pugilator*. *Physiological Zoölogy* 44:210-224.

Salmon, M. 1983a. Acoustic “calling” by fiddler and ghost crabs. *Australian Museum Memoir* 18:63-76.

Salmon, M. 1983b. Courtship, mating systems, and sexual selection in Decapods. Pp. 143-169 in *Studies in Adaptation: The Behavior of Higher Crustacea*, S. Rebach and D. W. Dunham, eds. John Wiley & Sons: New York.

Salmon, M. 1984. The courtship, aggression and mating system of a “primitive” fiddler crab (*Uca vocans*: Ocypodidae). *Transactions of the Zoological Society of London* 37:1-50.

Salmon, M. 1987. On the reproductive behavior of the fiddler crab *Uca thayeri*, with comparisons to *U. pugilator* and *U. vocans*: Evidence for behavioral convergence. *Journal of Crustacean Biology* 7:25-44.

Salmon, M., and S. P. Atsaides. 1968. Visual and acoustical signalling during courtship by fiddler crabs (genus *Uca*). *American Zoologist* 8:623-639.

Salmon, M., S. D. Ferris, D. Johnston, G. W. Hyatt, and G. S. Whitt. 1979. Behavioral and biochemical evidence for species distinctiveness in the fiddler crabs, *Uca speciosa* and *U. spinicarpa*. *Evolution* 33:182-191.

Salmon, M., and K. W. Horch. 1972. Acoustic signalling and detection by semiterrestrial crabs of the family Ocypodidae. Pp. 60-96 in *Behavior of Marine Animals. Volume 1: Invertebrates*, H. E. Winn and B. L. Olla, eds. Plenum Press: New York.

Salmon, M., and K. W. Horch. 1976. Acoustic interneurons of fiddler and ghost crabs. *Physiological Zoology* 49:214-226.

Salmon, M., K. W. Horch, and G. W. Hyatt. 1977. Barth's myochordotonal organ as a receptor for auditory and vibrational stimuli in fiddler crabs (*Uca pugilator* and *U. minax*). *Marine Behaviour and Physiology* 4:187-194.

Salmon, M., and G. W. Hyatt. 1979. The development of acoustic display in the fiddler crab *Uca pugilator*, and its hybrids with *U. panacea*. *Marine Behaviour and Physiology* 6:197-209.

Salmon, M., G. W. Hyatt, K. McCarthy, and J. D. Costlow, Jr. 1978. Display specificity and reproductive isolation in the fiddler crabs, *Uca panacea* and *U. pugilator*. *Zeitschrift für Tierpsychologie* 48:251-276.

Salmon, M., and M. K. Kettler. 1987. The importance of behavioral and biochemical differences between fiddler crab taxa, with special reference to *Uca rapax* (Smith) and *U. virens* (Salmon & Atsaides). *Contributions in Marine Science* 30:63-76.

Salmon, M., and J. F. Stout. 1962. Sexual discrimination and sound production in *Uca pugilator* Bosc. *Zoologica NY* 47:15-20.

Salmon, M., and N. Zucker. 1988. Interpreting differences in the reproductive behavior of fiddler crabs (genus *Uca*). Pp. 387-407 in *Behavioral Adaptation to Intertidal Life*, G. Chelazzi and M. Vannini, eds. Plenum Press: New York.

Schinca, A. 1992. Le exhibicion de ondeo (waving display) en *Uca uruguayensis* (Decapoda, Brachyura). *Boletin de la Sociedad Zoologica del Uruguay. Segunda Epoca* 7:37-38.

Seed, R., and R. N. Hughes. 1997. Chelal characteristics and foraging behaviour of the blue crab *Callinectes sapidus* Rathbun. *Estuarine, Coastal and Shelf Science* 44:221-229.

Shih, H.-T., H.-K. Mok, H.-W. Chang, and S.-C. Lee. 1999. Morphology of *Uca formosensis* Rathbun, 1921 (Crustacea: Decapoda: Ocypodidae), an endemic fiddler crab from Taiwan, with notes on its ecology. *Zoological Studies* 38:164-177.

Smith, G., and W. F. R. Weldon. 1923. Crustacea. Pp. 1-217 in *The Cambridge Natural History*, S. F. Harmer and A. E. Shipley, eds., Volume 4. Macmillan and Co., Ltd.: London.

Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*. Third Edition. W. H. Freeman and Company: New York.

Steinberg, J. B. 1977. Information theory as an ethological tool. Pp. 47-74 in *Quantitative Methods in the Study of Animal Behavior*, B. A. Hazlett, ed. Academic Press: New York.

Sturmbauer, C., J. S. Levinton, and J. H. Christy. 1996. Molecular phylogeny analysis of fiddler crabs: Test of the hypothesis of increasing behavioral complexity in evolution. *Proceedings of the National Academy of Sciences USA* 93:10855-10857.

Takeda, S., and M. Murai. 1993. Asymmetry in male fiddler crabs is related to the basic pattern of claw-waving display. *Biological Bulletin* 184:203-208.

Thurman, C. L., II. 1982. On the distinctness of the fiddler crabs *Uca minax* (LeConte) and *Uca longsignalis* Salmon & Atsaides in their region of sympatry (Decapoda Brachyura, Ocypodidae). *Crustaceana* 43:37-50.

Thurman, C. L., II. 1984. Ecological notes on fiddler crabs of south Texas, with special reference to *Uca subcylindrica*. *Journal of Crustacean Biology* 4:665-681.

Thurman, C. L., II. 1987. Fiddler crabs (genus *Uca*) of eastern Mexico (Decapoda, Brachyura, Ocypodidae). *Crustaceana* 53:94-105.

Valiela, I., D. F. Babiec, W. Atherton, S. Seitzinger, and C. T. Krebs. 1974. Some consequences of sexual dimorphism: Feeding in male and female Fiddler Crabs, *Uca pugnax* (Smith). *Biological Bulletin* 147:652-660.

Verwey, J. 1930. Einges über die Biologie Ost-Indischer Mangrovekrabben. *Treubia* 12:167-261.

Warner, G. F., and A. R. Jones. 1976. Leverage and muscle type in crab chelae (Crustacea: Brachyura). *Journal of Zoology* 180:57-68.

Weissburg, M. J. 1990. *The Foraging Biology of Uca pugnax: Mechanics, Functional Morphology and Feeding Strategies*. Ph.D. Thesis. Department of Ecology and Evolution, State University of New York at Stony Brook.

Weissburg, M. J. 1991. Morphological correlates of male claw asymmetry in the fiddler crab *Uca pugnax* (Smith) (Decapoda, Brachyura). *Crustaceana* 61:11-20.

Weissburg, M. J. 1992. Functional analysis of fiddler crab foraging: Sex-specific mechanics and constraints in *Uca pugnax* (Smith). *Journal of Experimental Marine Biology and Ecology* 156:105-124.

Weissburg, M. J. 1993. Sex and the single forager: Gender-specific energy maximization strategies in fiddler crabs. *Ecology* 74:279-291.

Wright, H. O. 1968. Visual displays in brachyuran crabs: Field and laboratory studies. *American Zoologist* 8:655-665.

Yparreguirre, C. A. 1981. *Sexual selection in the fiddler crab, Uca vocans (Linnaeus)*. Ph.D. Thesis. Department of Ecology and Evolution, State University of New York at Stony Brook.

Zann, M. C. 1979. *The spatial distribution and socioecological factors influencing spacing in five ocypodid crab species (Decapoda: Brachyura) on the eastern Australian coast*. Honours Thesis. University of Queensland.

Zucker, N. 1974. Shelter building as a means of reducing territory size in the fiddler crab, *Uca terpsichores*(Crustacea: Ocypodidae). *American Midland Naturalist* 91:224-236.

Zucker, N. 1977. Neighbor dislodgement and burrow filling activities by male *Uca musica terpsichores*: A spacing mechanism. *Marine Biology* 41:281-286.

Zucker, N. 1983. Courtship variation in the neo-tropical fiddler crab *Uca deichmanni*: Another example of female incitation to male competition? *Marine Behavior and Physiology* 10:57-79.

Zucker, N., and R. Denny. 1979. Interspecific communication in fiddler crabs: Preliminary report of a female rejection display directed toward courting heterospecific males. *Zeitschrift für Tierpsychologie* 50:9-17.

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, CA
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

Species	Collection
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, NC, 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, FL, 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, NY, July 1998
Uca pugnax	MSR – Flax Pond, Long Island, NY, 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, TX, 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, FL, 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

Species	Collection
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 or 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 postero-ventral 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/equal (0) or longer (1) than 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; 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 (>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. Antero-ventral margin of major merus is without (0) or with (1) tuberculation.
28. Antero-dorsal margin of major merus is without (0) or with (1) tuberculation (Crane 1975).
29. Antero-dorsal margin of major merus without (0) or with (1) a distal tooth (Jones and Morton 1994).
30. Antero-dorsal margin of major merus without (0) or with (1) a large convex flange (Crane 1975).
31. Antero-dorsal 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 antero-dorsal margin of major carpus (possible variation = 3 tubercles vs 1 tubercle).
36. Vertical row of tubercles absent (0) or present (1) from anterior surface of major carpus.
37. Antero-dorsal 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; Hagen 1980).
60. Major palm has one (0) or two (1) predactyl ridges (Crane 1975).
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/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) forcep-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 margin 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. Ambulatories are short (0) or long (1) (Crane 1975).
103. Merus of the 1st ambulatory is slender (0) or broad (1).
104. Merus of the 2nd ambulatory is slender (0) or broad (1).
105. Merus of the 3rd ambulatory is slender (0) or broad (1).
106. Merus of the 4th ambulatory is slender (0) or broad (1).
107. Dorsal margin curvature of the merus of the 2nd ambulatory is straight (0) or convex (1).
108. Dorsal margin curvature of the merus of the 3rd ambulatory is straight (0) or convex (1).

109. Dorsal margin curvature of the merus of the 4th ambulatory is straight (0) or convex (1).
110. Posterior surface of 1st ambulatory 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.
112. Ambulatory meri without (0) or with (1) tubercles on striae.
113. Anterior tubercles on the manus of the 1st ambulatory are absent (0) or present (1).
114. Anterior tubercles on the merus of the 1st ambulatory are absent (0) or present (1).
115. Anterior tubercles on the carpus of the 1st ambulatory are absent (0) or present (1).
116. Pile absent (0) or present (1) on the manus of the 1st ambulatory.
117. Pile absent (0) or present (1) on the carpus of the 1st ambulatory.
118. Pile absent (0) or present (1) on the merus of the 1st ambulatory.
119. Pile absent (0) or present (1) on the carpus of the 2nd ambulatory.
120. Pile absent (0) or present (1) on the manus of the 2nd ambulatory.
121. Pile absent (0) or present (1) on the merus of the 2nd ambulatory.
122. Pile absent (0) or present (1) on the carpus of the 3rd ambulatory.
123. Pile absent (0) or present (1) on the manus of the 3rd ambulatory.
124. Pile absent (0) or present (1) on the merus of the 3rd ambulatory.
125. Pile absent (0) or present (1) on the carpus of the 4th ambulatory.
126. Pile absent (0) or present (1) on the merus of the 4th ambulatory.
127. Large teeth absent (0) or present (1) on postero-ventral margin of the merus of the 1st ambulatory.
128. Large teeth absent (0) or present (1) on postero-ventral margin of the merus of the 2nd ambulatory.
129. Large teeth absent (0) or present (1) on postero-ventral margin of the merus of the 3rd ambulatory.
130. Large teeth absent (0) or present (1) on postero-ventral margin of the merus of the 4th ambulatory.
131. Antero-ventral margin serration absent (0) or present (1) distally on the merus of the 1st ambulatory.
132. Antero-ventral margin serration absent (0) or present (1) proximally on the merus of the 1st ambulatory.
133. Postero-ventral margin serration absent (0) or present (1) on the merus of the 1st ambulatory.
134. Dorsal margin serration absent (0) or present (1) on the merus of the 1st ambulatory.
135. Antero-ventral margin serration absent (0) or present (1) distally on the merus of the 2nd ambulatory.

136. Antero-ventral margin serration absent (0) or present (1) proximally on the merus of the 2nd ambulatory.
137. Postero-ventral margin serration absent (0) or present (1) on the merus of the 2nd ambulatory.
138. Dorsal margin serration absent (0) or present (1) on the merus of the 2nd ambulatory.
139. Antero-ventral margin serration absent (0) or present (1) distally on the merus of the 3rd ambulatory.
140. Antero-ventral margin serration absent (0) or present (1) proximally on the merus of the 3rd ambulatory.
141. Postero-ventral margin serration absent (0) or present (1) on the merus of the 3rd ambulatory.
142. Dorsal margin serration absent (0) or present (1) on the merus of the 3rd ambulatory.
143. Antero-ventral margin serration absent (0) or present (1) distally on the merus of the 4th ambulatory.
144. Antero-ventral margin serration absent (0) or present (1) proximally on the merus of the 4th ambulatory.
145. Postero-ventral margin serration absent (0) or present (1) on the merus of the 4th ambulatory.
146. Dorsal margin serration absent (0) or present (1) on the merus of the 4th ambulatory.
147. Setae absent (0) or present (1) on ventral margin of the merus of the ambulatories.
148. Setae absent (0) or present (1) on dorsal margin of the merus of the ambulatories.
149. Setae on ventral margin of 1st ambulatory merus are sparse (0) or numerous (1).
150. Setae on ventral margin of 1st ambulatory merus are short (0) or long (1).
151. Setae on dorsal margin of 1st ambulatory merus are sparse (0) or numerous (1).
152. Setae on dorsal margin of 1st ambulatory merus are short (0) or long (1).
153. Setae on ventral margin of 2nd ambulatory merus are sparse (0) or numerous (1).
154. Setae on ventral margin of 2nd ambulatory merus are short (0) or long (1).
155. Setae on dorsal margin of 2nd ambulatory merus are sparse (0) or numerous (1).
156. Setae on dorsal margin of 2nd ambulatory merus are short (0) or long (1).
157. Setae on ventral margin of 3rd ambulatory merus are sparse (0) or numerous (1).
158. Setae on ventral margin of 3rd ambulatory merus are short (0) or long (1).
159. Setae on dorsal margin of 3rd ambulatory merus are sparse (0) or numerous (1).

160. Setae on dorsal margin of 3rd ambulatory merus are short (0) or long (1).
161. Setae on ventral margin of 4th ambulatory merus are sparse (0) or numerous (1).
162. Setae on ventral margin of 4th ambulatory merus are short (0) or long (1).
163. Setae on dorsal margin of 4th ambulatory merus are sparse (0) or numerous (1).
164. Setae on dorsal margin of 4th ambulatory merus are short (0) or long (1).
165. Ambulatories 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 1900; 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 (0) or greater (1) than the width of the eyestalk (Crane 1975).
173. Eyestalk is thin (0) or thick (1) (Rathbun 1900; Dai and Young 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 crenellations are evenly sized (0) or largest at outer margin (1).
178. Suborbital crenellations are small (0) or large (1) (Crane 1975).
179. Suborbital crenellations 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 crenellations.
181. Floor of orbit without (0) or with (1) a line of accessory granules behind crenellations (George and Jones 1982; 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) lots of setae.
185. Frontal margin is thin (0) or thick (1).
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 antero-lateral angle.

190. Outer corner or suborbital margin is not (0) or is (1) a 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. Antero-lateral margins of carapace are absent (0) or present (1).
199. Antero-lateral margins of carapace are convergent (0), parallel (1), or divergent (2).
200. Antero-lateral margins of carapace are short (0) or long (1).
201. Antero-lateral angles of carapace shape is acute (0) or square (1) (Bairagi and Misra 1988).
202. Antero-lateral angles point towards the front (0), at an angle (1), or to the side (2).
203. Antero-lateral/dorso-lateral junction of carapace is curved (0) or sharply angled (1).
204. Dorso-lateral margins of carapace are absent (0) or present (1) (George and Jones 1982).
205. Dorso-lateral margins of carapace are short (0) or long (1).
206. Dorso-lateral margins of carapace are curved (0) or straight (1) (Thurman 1979).
207. Dorso-lateral margins converge slightly (0) or strongly (1) (Thurman 1979).
208. Dorso-lateral margin spines are absent (0) or present (1) (Crane 1975).
209. Dorso-lateral margins of carapace consist of a microscopically beaded line of tubercles (0) or large, widely spaced tubercles (1) (Hagen and Jones 1989).
210. Postero-lateral stria are absent (0), 1 pair (1), or 2 pair (2) (George and Jones 1982; Hagen 1984).
211. Postero-lateral stria are without (0) or with (1) hairs (Hagen 1980).
212. Postero-lateral stria 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 antero-lateral and vertical-lateral margins.
216. Large tubercle absent (0) or present (1) at antero-lateral—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
	0000000001	1111111112	2222222223	3333333334	4444444445
	1234567890	1234567890	1234567890	1234567890	1234567890
Uca annulipes	0100011100	0000120010	0N10001100	0000001110	0001100010
Uca arcuata	0110011100	0000100000	1110011100	0000001110	0111101111
Uca argillicola	1110011100	0000110010	1010001100	0000001110	0111101011
Uca batuenta	0100011100	0000110011	1110001000	0000010110	00110NN010
Uca beebei	0110011100	0000111111	1110001100	0000001111	00010NN010
Uca bellator	1100011100	0000111110	1110011100	1010001111	0001101011
Uca bengali	0110011100	0011110011	1010001100	0010001111	0111100010
Uca borealis	00N0011000	0000110011	0N11011110	0000101110	11110NN111
Uca brevifrons	1110011100	0000100011	1110000100	0000001110	01110NN011
Uca burgersi	0110011100	0000100011	1010001100	0100010111	0111100011
Uca capricornis	1110011100	0000100010	1110011100	0000001110	0111101111
Uca chlorophthalmus	0110011000	0000110010	1010001010	0000001110	1011101010
Uca coarctata	0110011100	0000100010	1010011110	0010001001	0111101111
Uca coloradensis	0110011100	0000110011	1010001100	0000001110	00110NN010
Uca crassipes	0110011000	0000110010	1010001010	0000001110	1011101010
Uca crenulata	0100011100	0000110011	1010001100	0000001110	00110NN010
Uca cumulanta	1110011100	0000110010	1010001100	0000000110	00110NN010
Uca dampieri	0100011000	0000120011	0N11011010	0000101110	11110NN111
Uca deichmanni	0100011100	0000120011	0N10001100	0000000110	00010NN011
Uca demani	0110011100	0000120010	1110011100	0000001111	0111101111
Uca dorotheae	0100011100	0000120011	1010001100	0000001111	00010NN010
Uca dussumieri	1110011100	0000110011	1010011100	0000001111	0111110111
Uca ecuadoriensis	1110011100	0000100011	1010001100	0100001110	0011100010
Uca elegans	1100011100	0000120010	1010011100	1000001011	0111110011
Uca festae	0110011100	0000110011	1010001100	0100001111	00010NN010
Uca flammula	0110011100	0000110010	1010011110	0000001110	0111101111
Uca forcipata	1110011100	0000110011	1110011100	0000001111	0111101111
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Uca galapagensis	1110011100	0000100011	1010001100	0100011110	0111100011
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Uca hesperiae	0100011000	0000120011	0N11001110	0000101110	11110NN111
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Uca intermedia	0100011010	0000110011	1110011101	0100001111	01000NN111
Uca inversa	0110011000	0000120010	0N10001100	1000001110	10110NN010
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Uca leptodactyla	0100011100	0000120010	0N10001100	0010000111	00010NN010
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Uca panacea	0110011100	0000110010	1010001100	0000001110	0011100011
Uca panamensis	1100011100	0000000011	0N10001100	0000000010	00000NN00N
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Uca seismella	0100011100	0000101110	1110011100	1010001111	0101101011
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Uca subcylindrica	0110011100	0000100011	1110001100	0000101111	1111100111
Uca tallanica	0100111100	0000110011	1110001100	0110001111	0111101110
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Uca vocator	1110011100	0000100011	1010001100	0100001110	0011100010
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Uca beebei	0011001000	0N01100000	0000001011	01110NN00N	0000001000
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Uca oerstedi	1011101001	0N00100000	1000001011	11110NN00N	0000000000
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Uca urvillei	1011000001	1100100000	1001000110	1002100110	0000000000
Uca virens	0011010101	0N01101000	0000011111	11110NN00N	0010000000
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Uca longidigitum	N011101100	0000000000	0000000000	0011001100	1100111101
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Uca vomeris	N000001100	1000000000	0000000000	0011001101	1101111101
Uca zacae	N000000001	0100001010	0100100000	0001000100	0100011101

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Uca argillicola	0001000100	0100000011	0011011011	0000111010	0101101100
Uca batuenta	0001000100	0000000011	0011011000	0000111100	0100100111
Uca beebei	0001100110	0100000011	1011011111	0000111010	0100100120
Uca bellator	00NN00NN00	NN00000000	0101010000	1100111010	0100000101
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Uca burgersi	0001000100	0100100011	1011011111	0001111010	0101100121
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Uca elegans	1001100100	0000000000	0101010000	0000111010	0100000101
Uca festae	0001100110	0000000011	1011011110	0000101110	0101100121
Uca flammula	1001100110	0000000001	1100010000	0000110011	0100000100
Uca forcipata	0001000100	0000000001	0100010011	0000110011	0100001100
Uca formosensis	00NN00NN00	NN00000001	0101010100	0000110110	0101000111
Uca galapagensis	0001000100	0100100011	1011010111	0000111010	0101100121
Uca herradurensis	0001000100	0100100011	1011010111	0000101000	0101100121
Uca hesperiae	1100110011	0011000001	0101010110	0000110110	0101000100
Uca heteropleura	00NN00NN00	NN0001*PP*00	0100010110	0000110110	0100000100
Uca hirsutimanus	0001000100	0000000001	0101010000	1100111010	0100000100
Uca inaequalis	0001000100	0000000011	0011010000	0000111000	0111101101
Uca insignis	00NN00NN00	NN00010?00	1100010110	0000110110	0101010110
Uca intermedia	00NN00NN00	NN00010*P*00	0100010110	0000110110	0101000110
Uca inversa	0001000100	0000000011	0101010000	0000111110	1100100100
Uca lactea	0001000100	0000000011	0111011110	0000101110	0101120100
Uca latimanus	0001000100	0100000011	1011011111	0000111010	0101100120
Uca leptodactyla	0101010101	0101000011	0011011111	0000111100	0101120120
Uca limicola	1101110111	0101000011	0011011111	0000111110	0101100111
Uca longidigitum	0001000100	0000000000	0101010000	0100111010	0100000101
Uca major	00NN00NN00	NN00010000	0100010110	0000110110	0101000100
Uca maracoani	10NN10NN10	NN10010*P*00	1100010110	0000110110	0101010110

	1111111111 5555555556 1234567890	1111111111 6666666667 1234567890	1111111111 7777777778 1234567890	1111111111 8888888889 1234567890	1111111112 9999999990 1234567890
Uca marguerita	0001000100	0100100011	1011011111	0001111010	0101100121
Uca minax	1111111111	1111100011	1011010111	0000101010	0101100121
Uca mjoebergi	0001000100	0000000011	0111011110	0000101110	0101120100
Uca mordax	0001000100	0000100011	1011011111	0001111010	0111100121
Uca neocultrimana	11NN11NN11	NN00000001	0101010010	0000110110	0100000100
Uca oerstedi	0001000100	0000100011	0011011110	0000111010	0111100121
Uca ornata	00NN00NN00	NN00010000	1100010100	0000110110	0100010100
Uca panacea	1101110111	0111100011	1011010111	0000111010	0101100121
Uca panamensis	0000000000	0000000011	1011011111	0000101100	0101110111
Uca paradussumieri	1000100010	0000000001	0100011000	0000110010	0100000100
Uca perplexa	0001000100	0000000011	0111011110	0000101110	0101120100
Uca polita	1000100010	0000000000	0101010000	0100111010	0100000101
Uca princeps	00NN00NN00	NN00010*P*00	1100010110	0000110110	0101000100
Uca pugilator	1101110111	0111100011	1011010111	0000111010	0101100121
Uca pugnax	1001100110	0100100011	0011011111	0000111010	0101100121
Uca rapax	1001100110	0100100011	1011010111	0000111010	0101100121
Uca rhizophorae	1001100110	0000000001	0100011000	0000100011	0100000100
Uca rosea	0000000000	0000000001	0100011000	0000110011	01000010NN
Uca saltitanta	0001000100	0100000011	0011011000	0000111000	0101100121
Uca seismella	0000000000	0000000000	0101010000	0100111010	0100000101
Uca signata	0001000100	0000000001	0101010000	1100111010	0100000101
Uca sindensis	0001000100	0000000011	0101010010	0000111110	0100100100
Uca speciosa	1001100110	0000100011	0011011111	0000111110	0111100111
Uca spinicarpa	1001100110	0000100011	0011011111	0000111110	0111100111
Uca stenodactylus	0001000100	0100000011	1011011110	0000101010	0101100111
Uca stylifera	00NN00NN00	NN00011100	0100010110	0000110110	0100000100
Uca subcylindrica	1111111111	0100100011	0011010111	0000111010	0101120121
Uca tallanica	0001000100	0000100011	0011011110	0000111100	0111100100
Uca tangeri	00NN00NN00	NN00010000	1101010110	0010111100	0101100120
Uca tenuipedis	0001000100	0000000011	0011011100	0000111000	0101100111
Uca terpsichores	0001000100	0100000011	1011011111	0000111000	0101100100
Uca tetragonon	1101110000	0000000001	0101010110	0000110110	0101000100
Uca thayeri	1100110011	0011000011	1111011111	0000111110	0111100111
Uca tomentosa	??01000100	0000000011	0011011110	0000111000	0111100111
Uca triangularis	0001000100	0100000011	0011011110	1110101110	0100101100
Uca typhoni	1101110111	0100000001	0100010001	1010110011	0100000100
Uca umbratila	1001100110	0110000011	1111011111	0000111110	0111100111
Uca uruguayensis	0110011001	0001100011	0011011111	0000111000	0101100110
Uca urvillei	1101110010	0000000001	0100010000	1010110011	0101000101
Uca virens	1011101110	0110100011	1011011111	0000111010	0101100121
Uca vocans	1100110011	0000000001	0101010110	0000110110	0100000100
Uca vocator	10NN10NN10	NN10100011	0011010011	0000101110	0111100121
Uca vomeris	1101110011	0010000001	0101010110	0000110110	0101000100
Uca zacae	0001000100	0000100011	1011011111	0000101010	0111101100

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Uca annulipes	0001110001	0010000000	1011111110	002000
Uca arcuata	0101101000	NN10000000	0011101000	000000
Uca argillicola	0101111002	0010000000	1011111110	112000
Uca batuenta	1101101001	0010000000	1010100110	112000
Uca beebei	1211100001	0010000111	10100NNNN0	112000
Uca bellator	0101101001	0110000000	00120NNNN0	110000
Uca bengali	0101101000	NN10000000	1012100110	112000
Uca borealis	0001010000	NN10000000	0012111000	001000
Uca brevifrons	1011100001	0010000000	1012110000	001000
Uca burgersi	1001111002	0010000000	1011111100	001000
Uca capricornis	0101101000	NN10000000	0012110000	001000
Uca chlorophthalmus	0001101001	0110000000	10110NNNN0	112000
Uca coarctata	0101101000	NN10000000	00120NNNN0	110000
Uca coloradensis	0011111001	0010100000	1011111110	112000
Uca crassipes	0001101001	0110000000	10110NNNN0	112000
Uca crenulata	0011101001	0010100000	1012111110	112000
Uca cumulanta	1011111001	0010100000	10110NNNN0	112001
Uca dampieri	0001010000	NN10000000	0111100000	001000
Uca deichmanni	1201111002	0010000111	1011111110	002000
Uca demani	0101101000	NN10000000	0011111100	001000
Uca dorotheae	1211010001	0010000111	10100NNNN0	112000
Uca dussumieri	0101101000	NN10000000	0012110000	001000
Uca ecuadoriensis	1001111001	0010000000	1012111000	001010
Uca elegans	0101101000	NN10000000	0011?????0	110000
Uca festae	1111101001	0110100000	10110NNNN0	112000
Uca flammula	0101101000	NN10000000	00120NNNN0	110000
Uca forcipata	0101101000	NN10000000	0012100000	010000
Uca formosensis	0001101000	NN10100000	0011101000	001000
Uca galapagensis	1001111002	0010000000	1012111010	001000
Uca herradurensis	1001111002	1010000000	1012111100	001000
Uca hesperiae	0001010000	NN10000000	0111101000	001000
Uca heteropleura	1101100000	NN10000000	000N100000	01N100
Uca hirsutimanus	0101101001	0010000000	00110NNNN0	110000
Uca inaequalis	1111111001	0110000000	10100NNNN0	112001
Uca insignis	0101100000	NN11011000	000N11N1N0	001000
Uca intermedia	1111100000	NN10000000	010N100000	01N000
Uca inversa	0001001000	NN10000000	100N111000	112000
Uca lactea	0101110001	0010100000	1012111110	002000
Uca latimanus	1001110001	0010000111	1011111000	002000
Uca leptodactyla	1101100001	0010000111	1011111110	002000
Uca limicola	1211110001	0010100111	10110NNNN0	112000
Uca longidigitum	0101001000	NN10000000	00100NNNN0	110000
Uca major	0101100000	NN10100000	010N100010	01N000
Uca maracoani	0101100010	NN11001000	000N11N1N0	001000

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	0000000001	1111111112	2222222223	333333
	1234567890	1234567890	1234567890	123456
Uca marguerita	1001111002	0010000000	1011111000	001000
Uca minax	1001111001	1010000000	1011111010	002000
Uca mjoebergi	0101110001	0010000000	1010111110	002000
Uca mordax	1001101001	0010000000	1011111000	002000
Uca neocultrimana	0001010000	NN10000000	0012111000	001000
Uca oerstedi	1011101001	0110100000	10100NNNN0	112000
Uca ornata	0101100010	NN11001000	000N100000	010000
Uca panacea	1001111001	0110100000	1011?????0	01?000
Uca panamensis	0001101001	0010100000	1011111000	001000
Uca paradussumieri	0101011000	NN10000000	0012110001	001000
Uca perplexa	0101110001	0010000000	1112111110	002000
Uca polita	0011101001	0010000000	00100NNNN0	110000
Uca princeps	0001101000	NN10000000	0011110000	000100
Uca pugilator	1001101001	0110100000	1011111110	012000
Uca pugnax	1001111002	0010000000	1011111110	002000
Uca rapax	1001111002	0010000000	1011111110	001000
Uca rhizophorae	0111101000	NN10000000	0012110000	001000
Uca rosea	02N1111000	NN10000000	0012111000	001000
Uca saltitanta	1011100001	0110000*PPP*	1010111110	112000
Uca seismella	1001001011	0010000000	00100NNNN0	110000
Uca signata	0101101001	0010000000	00100NNNN0	110000
Uca sindensis	0001101000	NN10000000	1011111000	112000
Uca speciosa	0011111001	0111100000	1011111110	112000
Uca spinicarpa	0011111001	0111100000	1011111110	112000
Uca stenodactylus	0111100001	0010000111	10100NNNN0	112000
Uca stylifera	1101100000	NN10000000	010N100000	01N000
Uca subcylindrica	1001100002	0010000000	1010101010	001000
Uca tallanica	1101111001	0110000000	10100NNNN0	112000
Uca tangeri	1001100000	NN11000000	0011111110	001000
Uca tenuipedis	1101111001	0110000000	1010111110	002000
Uca terpsichores	0101101002	0100000111	101111N1N0	102000
Uca tetragonon	0001101000	NN10000000	0011111000	001000
Uca thayeri	1101101002	0110100000	1011111000	012000
Uca tomentosa	1111101001	0110000000	10110NNNN0	112000
Uca triangularis	0101101000	NN10000000	1012100110	112000
Uca typhoni	0101101000	NN10000000	0011110100	001000
Uca umbratila	1101101002	0010100000	1011111000	012000
Uca uruguayensis	1011111001	0010000011	1011111000	002000
Uca urvillei	0101101000	NN10000000	00120NNNN0	110000
Uca virens	1001111002	0010100000	1011111110	002000
Uca vocans	0001010000	NN10000000	0112111000	001000
Uca vocator	1001111001	1010100000	1012111000	001010
Uca vomeris	0001010000	NN10000000	0112111000	001000
Uca zacae	1001111002	0010000000	1011111110	002000