

Fiddler crab claw shape variation: a geometric morphometric analysis across the genus *Uca* (Crustacea: Brachyura: Ocypodidae)

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For decades, the extreme asymmetric chelipeds of male fiddler crabs (genus *Uca*) have been used as 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. In this study, modern methods of describing shape and size, geometric morphometrics, are used to study claw variation across the genus. These analyses are also performed in a phylogenetic context using independent contrasts. Within and among species, major claws show allometric trends in both shape and size. Minor claw growth is isometric within species; across species, these claws are isometric with respect to size, but allometric with respect to 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 length of the pollex relative to the manus and the size of the propodus relative to the carpus. There is some phylogenetic clustering of claw shape and size, but there does not appear to be a significant level of phylogenetic dependence because no conclusions are changed when independent contrasts are used. Regenerated major claws have stronger allometric patterns than unregenerated claws, causing them to have shapes associated with relatively larger claws. Minor claw shape shows a strong correlation with habitat type. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, 75, 147–162.

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INTRODUCTION

Interest in morphological variation has long been a driving force behind many biological studies. Understanding the nature of, and searching for an explanation for, this variety is a major research focus, including fields as diverse as functional morphology, macroevolution, sexual selection, and evolutionary developmental biology. Understanding 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 colours (particularly the colouration of the major claw) easily seen from afar, especially when engaged in 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 (Rosenberg, 2001) which is predominantly right handed (Barnwell, 1982; Jones & 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 direc-

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tion of asymmetry is determined in development (Morgan, 1923, 1924; Vernberg & Costlow, 1966; Yamaguchi, 1973, 1977; Ahmed & Khan, 1978; Ahmed, 1978) to the developmental patterns of asymmetry in the chelipeds (Huxley & Callow, 1933; Miller, 1973) and muscles (Trinka-Randall & Govind, 1985; Rhodes, 1986), as well as description of the asymmetry in walking legs and other appendages (Tazelaar, 1933; Takeda & Murai, 1993). Additional morphological analyses include studies of the feeding morphology (Weissburg, 1991), allometry of the abdomen (Huxley, 1924b; Green & Schochet, 1990) and the claws (Yerkes, 1901; Huxley, 1924a, 1927; 1932; Huxley & Callow, 1933; Gibbs, 1974; Frith & Brunemeister, 1983; Rosenberg, 1997), and the relationship between claw shape and closing force (Brown *et al.*, 1979; Levinton & 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, Veitch & Correll (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; Huxley, 1927) examined the relationship between major claw mass and body mass in *Uca pugnax*. Allometry is the study of shape change 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 discrete molt stages, the size distribution of individuals in a population tends to be continuous (Green & Schochet, 1990).

Despite the large degree of interspecific variation in major claw morphology (Fig. 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 above references), there has been no large-scale interspecific comparative analysis of major claw morphology, especially with respect to behaviour. Furthermore, only Crane (1966, 1967, 1975) has proposed

a functional relationship between discrete major claw characters and behaviour, specifically combat. Crane found that most major claw characters (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 & 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).

MATERIAL AND METHODS

DATA ACQUISITION

Specimens examined were obtained through personal collections by myself and colleagues and from museum collections (Appendix I). Of the 97 recognized fiddler crab species (Rosenberg, 2001), 88 were included in the analysis. The missing species are evenly spread among the subgenera and their exclusion should not change any overall conclusions. Major claw data were available for all 88 species, minor claw data for 86 (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 analysed, 851 major and 801 minor. Although the intraspecific size range could be large, almost all specimens represented adult male crabs.

A full, detailed, mathematical description of geometric morphometrics is beyond the scope of this paper. See Rohlf & Bookstein (1990), Bookstein (1991), Rohlf & Marcus (1993), and Marcus *et al.* (1996) as well as other references in this paper for specific

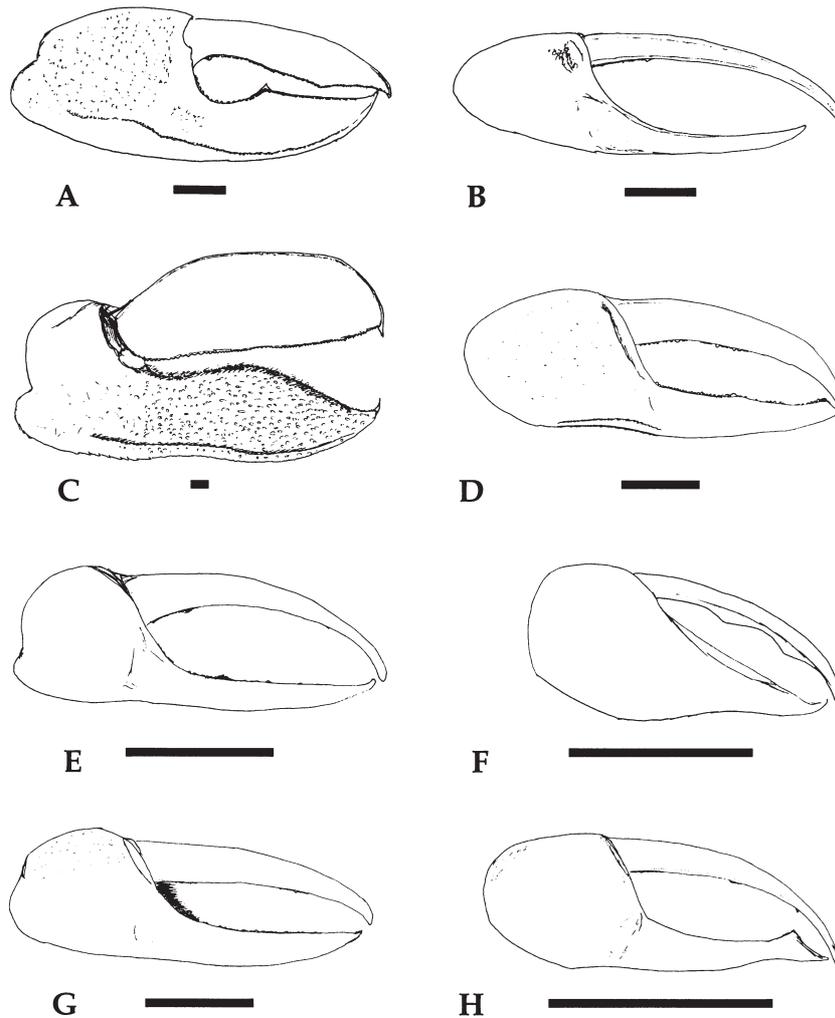


Figure 1. Examples of major claws from different species of *Uca*. Each illustration is of the outer surface of a right major claw; the bar under each claw represents 5 mm. (A) *Uca stylifera*; (B) *Uca festae*; (C) *Uca ornata*; (D) *Uca herradurensis*; (E) *Uca tersichores*; (F) *Uca saltitanta*; (G) *Uca beebei*; (H) *Uca batuenta*.

details. A number of geometric morphometric 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; Fig. 2B) was recorded with calipers to the nearest 1/20th of a millimetre for each individual crab. Previous studies (e.g. Huxley & Callow, 1933; Miller, 1973; Crane, 1975; Frith & 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 is carapace length (Frith & Brunemeister, 1983).

The inner (palmar) surface of each individual claw was photographed with a digital camera. Before we recorded 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 & McIntyre, 1998). Landmark coordinates were digitized from each photograph using tpsDig (Rohlf, 1999b). A pilot study found these shape descriptions to be highly repeatable.

The landmarks (Fig. 2C) used are the same as in Rosenberg (1997). 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

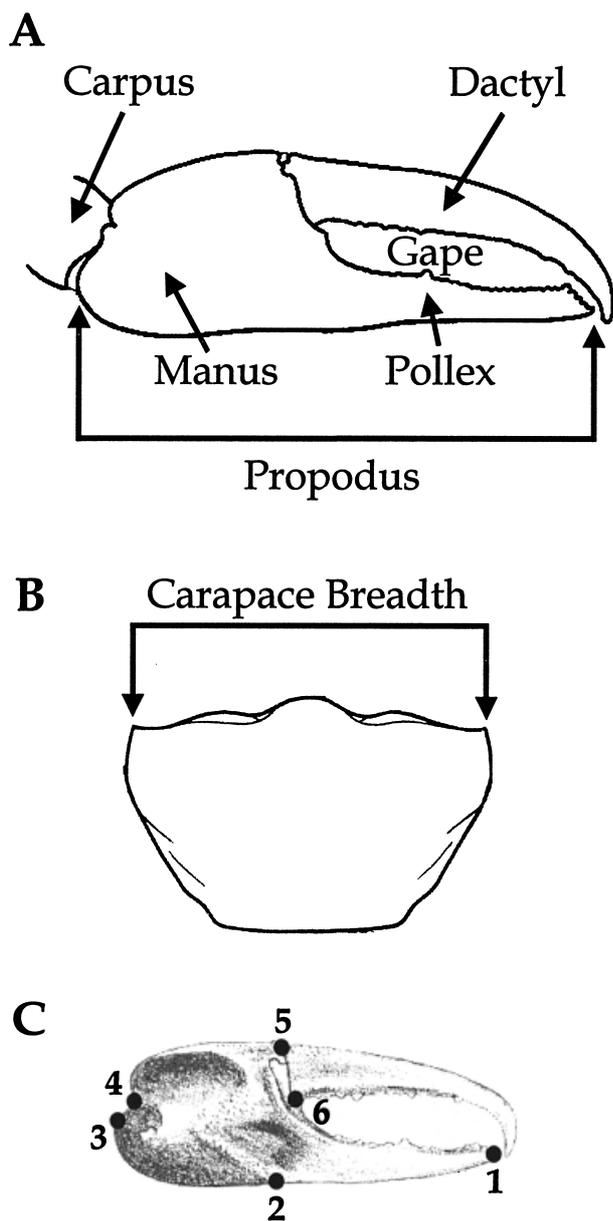


Figure 2. Diagrammatic representation of the morphological features of fiddler crabs described in the text. (A) Outside surface of a right major claw; (B) dorsal view of a carapace; (C) the landmark data collected from each claw. Figure modified from Crane (1975).

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 analyse 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 primarily because only a single landmark could be identified on the dactyl (the tip), and its inclusion would add little to the analyses, given the strong correlation between the length of the dactyl and the length of the pollex. Also, geometric morphometric methods designed to deal with articulated structures are poorly established and still being developed (Adams, 1999a,b).

Centroid size, which is the square-root of 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) to remove the non-shape effects of translation, rotation, and scale (Rohlf & Slice, 1990; Rohlf, 1999a). After superimposition, each landmark configuration corresponds to a single point in a non-Euclidean multidimensional 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 are 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); the present study 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 non-uniform 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 GPA was repeated for each distinct data set depending on the specific analysis (intraspecific, interspecific, major claws, minor claws, etc.; see below) being performed.

ANALYSIS

SIZE ALLOMETRY

The intraspecific relationship of claw size (major and minor separately) to crab size was analysed through linear regression of \ln centroid size onto \ln carapace breadth (\ln , natural logarithm). 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 & Callow,

1933; Miller, 1973; Gibbs, 1974; Frith & Frith, 1977; Frith & Brunemeister, 1983; Levinton *et al.*, 1995). The previous studies used claw length, dactyl length, relative claw proportions, or claw mass.

The regression was also calculated on species means 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 & Pagel, 1991). The interspecific regression was repeated after both carapace and centroid size were standardized using Felsenstein's method of independent contrasts (Felsenstein, 1985). The cladograms from Rosenberg (2001) 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, few characters referred to claw shape; therefore, there should be no concerns about circularity.

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 & Mosimann, 1960; Jolicoeur, 1963); to see whether this holds for these data, the correlation between the scores on the first axis and centroid size was calculated.

SHAPE ALLOMETRY

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 previous 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.

RESULTS

SIZE ALLOMETRY

Every species shows a strong relationship between carapace size and centroid size for both major and minor claws (Table 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 ≈ 1 , while the slopes of the major claw regressions are mostly >1.5 and range to well over 2. In general, within a species, minor claw size grows isometrically, while major claw size grows with positive allometry.

The interspecific regression line for major claws was \ln Centroid Size = $-0.166 + 1.131 \ln$ Carapace Breadth ($r^2 = 0.918$); that for minor claws was \ln Centroid Size = $-1.010 + 0.965 \ln$ Carapace Breadth ($r^2 = 0.960$). The major slope is significantly different from 1; the minor slope is not. Interspecific major claw size shows evolutionary allometry (Klingenberg, 1996); minor claw size is isometric across species.

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 (Rosenberg, 2001) are presented (Fig. 3B). The interspecific regression for major claws (slope, 1.406) is still significantly different from 1, while that of minor claws (slope, 1.005) is not. These are the same as the uncorrected results; the observed interspecific trends in size are not due to shared phylogenetic history.

The within-species allometric slopes differ substantially among species (Table 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 claw 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 (Fig. 4), indicating that the larger species show stronger positive allometry than smaller species. When this analysis is corrected for phylogenetic dependence, however, the relationship becomes non-significant ($F = 1.65$, $P = 0.218$).

SHAPE VARIATION

The first relative warp for the major claws explained 70.09% of the observed variation among species, the second 11.48%, and the third 9.81% (91.38% total) (Figs 5, 6). Visual inspection of the TPS warp grids

Table 1. Results of the linear regression of \ln centroid size onto \ln carapace breadth for individual species (where $n \geq 9$)

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

* $P \leq 0.05$; slope is significantly different from 1 (isometry).

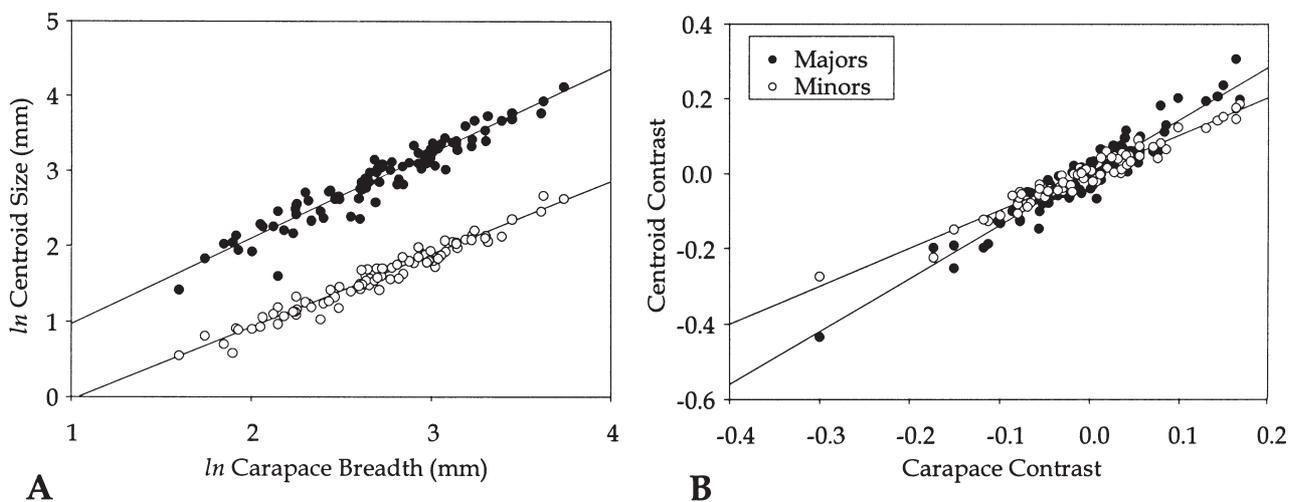


Figure 3. Regression of centroid size on carapace breadth for the species means. (A) Regressions of \ln centroid size on \ln carapace breadth. (B) Regressions of contrast scores of \ln centroid size on \ln carapace breadth.

may lead to generalizations about 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 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 Fig. 5) represents *Uca saltitanta*, a species with an extremely large triangular pollex (Fig. 1F). 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 is due to allometry. Although there are no distinct groupings, there is some separa-

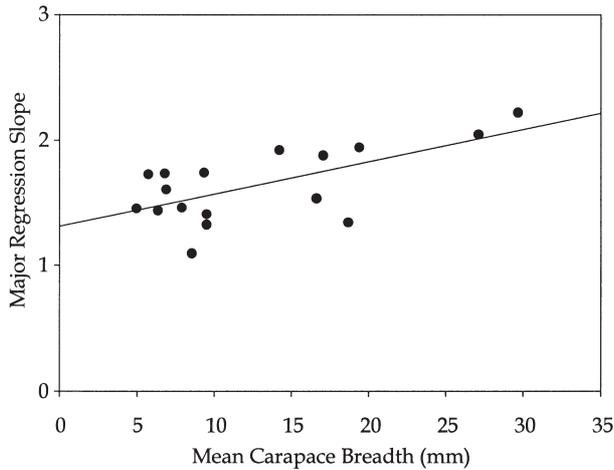


Figure 4. Regression of slope of major claw regression slope on mean carapace size.

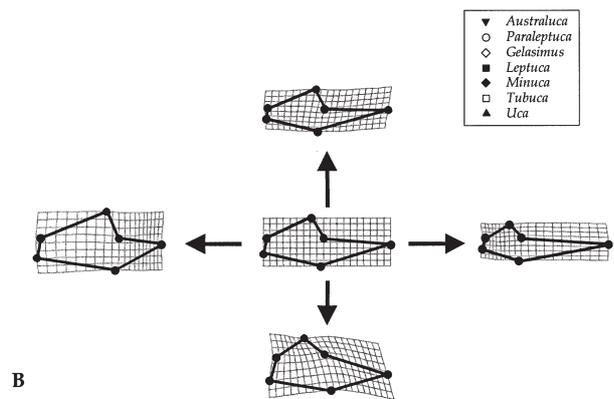
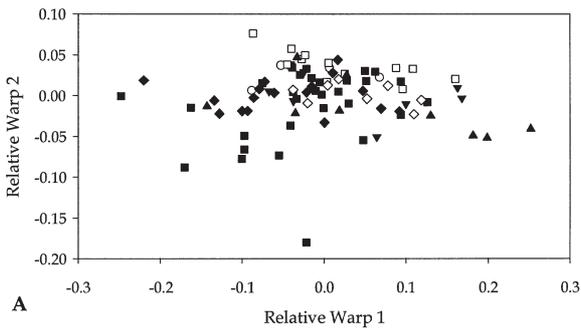


Figure 5. Relative warps 1 and 2 for the species means of the major claws. (A) Plot of relative warp 2 vs. relative warp 1. (B) The centre landmark configuration illustrates the mean major claw shape; the other configurations illustrate the shape change represented by movement along each axis in the direction indicated by the arrows.

tion of the subgenera (*sensu* Rosenberg, 2001) on these plots. In Figure 5, the *Tubuca* make up most of the upper part of the plot. In Figure 6, most of the points in the lower part are the *Leptuca* and *Minuca*.

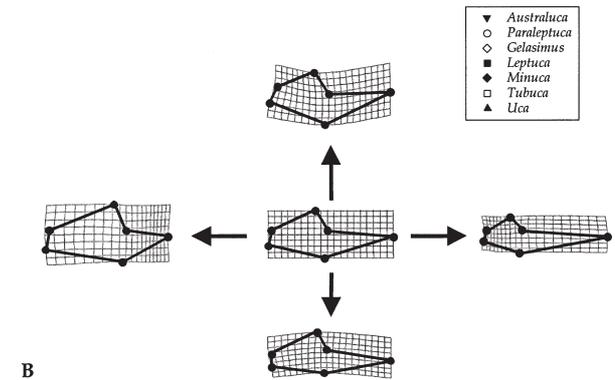
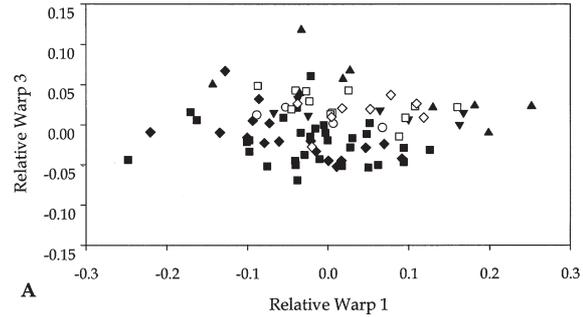


Figure 6. Relative Warps 1 and 3 for the species means of the major claws. (A) Plot of relative warp 3 vs. relative warp 1. (B) The centre landmark configuration illustrates the mean major claw shape; the other configurations illustrate the shape change represented by movement along each axis in the direction indicated by the arrows.

The first relative warp for the minor claws explained 47.50% of the observed variation among species, the second 24.13%, and the third 12.03% (83.66% total) (Figs 7, 8). 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 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 7, the *Minuca* are almost all confined to the far left part of the plot; the *Tubuca* cluster to the right and above them. On the other hand, the *Leptuca* are spread evenly throughout the entire plot.

Figure 9 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

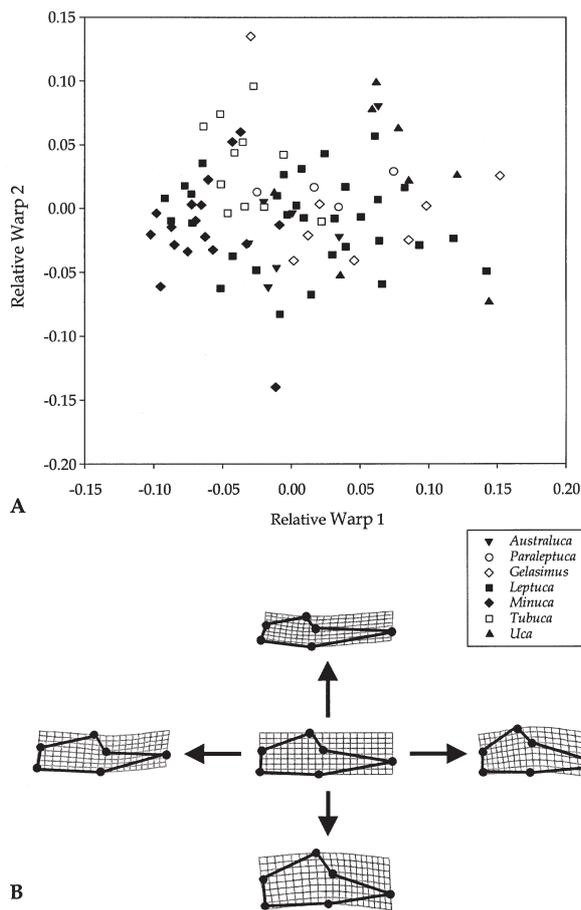


Figure 7. Relative Warps 1 and 2 for the species means of the minor claws. (A) Plot of relative warp 2 vs. relative warp 1. (B) The centre landmark configuration illustrates the mean minor claw shape; the other configurations illustrate the shape change represented by movement along each axis in the direction indicated by the arrows.

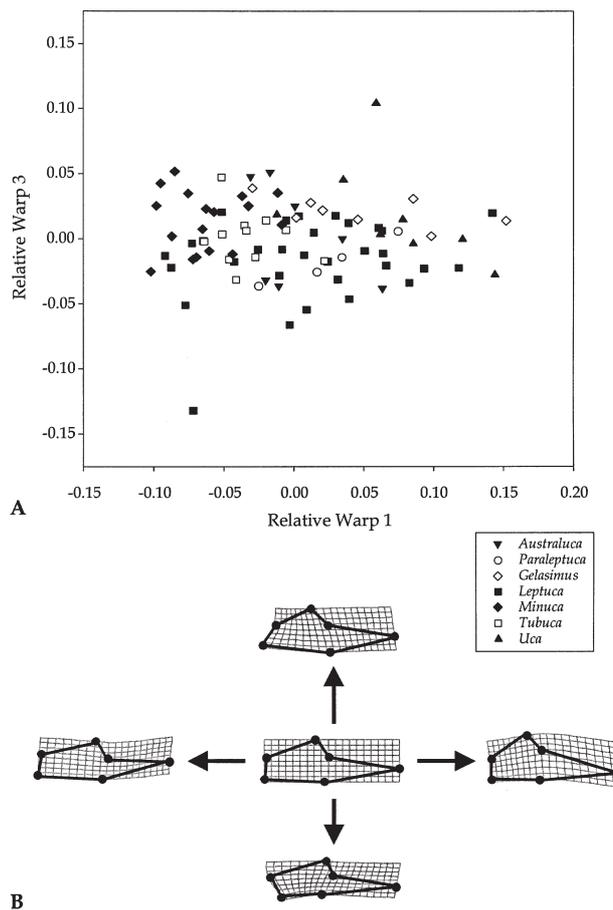


Figure 8. Relative Warps 1 and 3 for the species means of the minor claws. (A) Plot of relative warp 3 vs. relative warp 1. (B) The centre landmark configuration illustrates the mean minor claw shape; the other configurations illustrate the shape change represented by movement along each axis in the direction indicated by the arrows.

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 (Fig. 5). 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.

SHAPE ALLOMETRY

Most species shows strong shape allometry for major claws, but none for minor claws (Table 2). 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 varia-

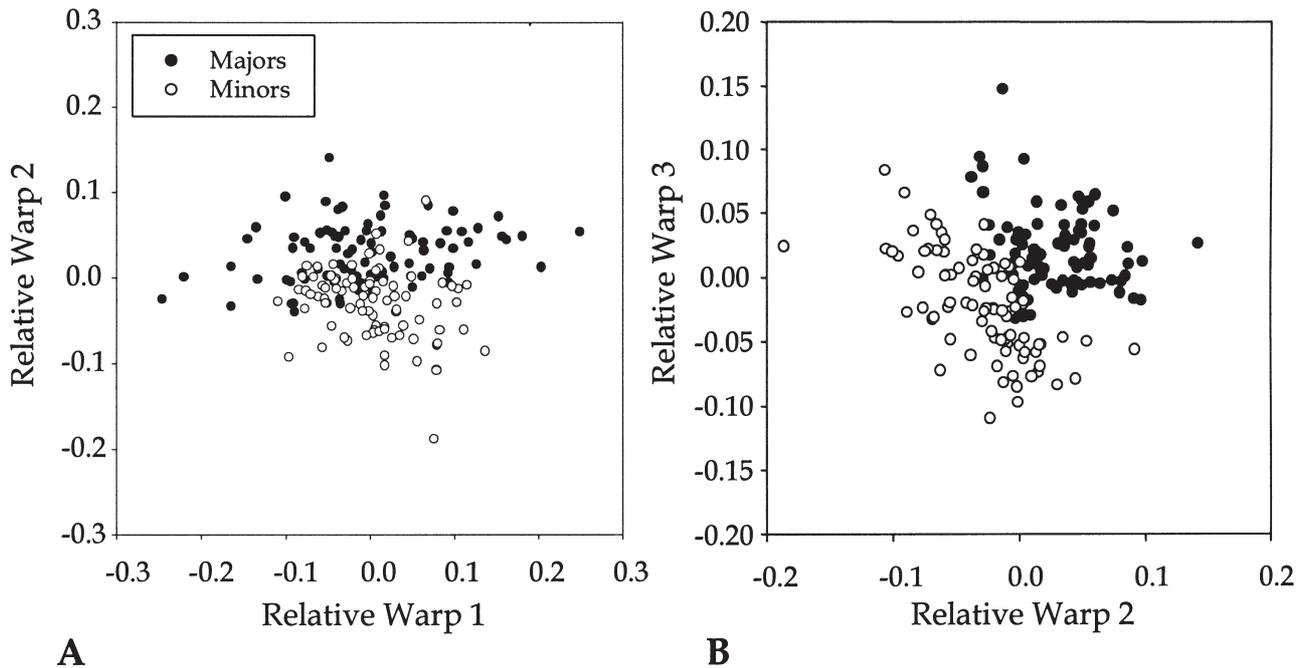


Figure 9. Plot of relative warps of the species means of major and minor claws. (A) Relative warp 2 vs. relative warp 1. (B) Relative warp 3 vs. relative warp 2. Closed circles represent major claws, open circles minor claws.

Table 2. Results of the multiple regression of partial warp scores (including the uniform components) onto carapace breadth for individual species (where $n \geq 15$)

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

tion (about the same as seen within a species), minor claws 6.45%. Figure 10 illustrates the results of the regression. For both major and minor claws, as species get larger, 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

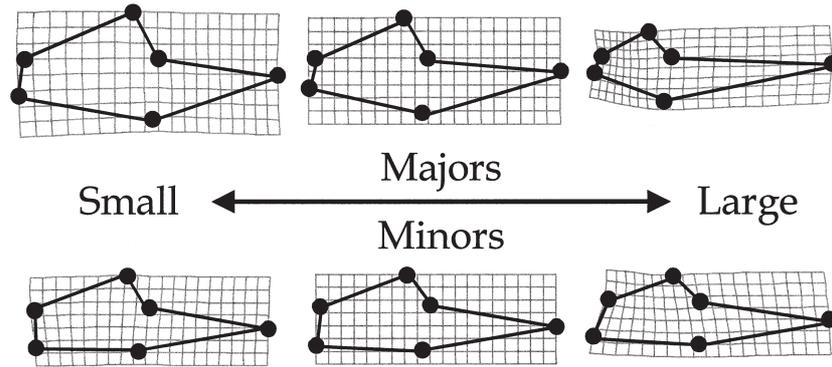


Figure 10. Plot of interspecific multiple regression of partial warp scores on centroid size. The centre configuration illustrates the mean claw shape; the other configurations illustrate the shape change represented by increasing or decreasing centroid size.

species. However, all of the species with particularly short chela (e.g. *U. pygmaea* and *U. latimanus*) are among the smallest in the genus.

DISCUSSION

Although most previous studies of allometry in fiddler crab claws have dealt exclusively with the major claw (Huxley, 1924a, 1927; Miller, 1973; Frith & Frith, 1977; Veitch, 1978; Williams *et al.*, 1980; Frith & Brunemeister, 1983; Green & 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 the first to search for widespread evolutionary allometry in the genus *Uca*. Within species, there is strong allometric growth (of both size and shape) of major claws, while minor claws are isometric for both. Across species, major claws are allometric for both size and shape. Minor claws show isometry for size, but allometry for shape. Evolutionary allometry accounts 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 (Figs 5, 6). This was somewhat unexpected, because, while certain clades appear to have distinctive claw forms, such as the large bladed claws of the American subgenus *Uca* (e.g. *Uca ornata* and *U. stylifera*, Fig. 1A, C) or the heavily toothed claws of the *vocans* species group (Crane, 1975), 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 occurs between the landmarks, especially on the gape face of the pollex (the area between landmarks 1 and 6).

Rather than use landmarks, another approach to the study of shape involves the use of outline data, which might be expected to capture this extra variation. All of the claw outlines were also analysed using elliptical Fourier analysis (Kuhl & Giardina, 1982; Rohlf & Archie, 1984). The results (not shown) were substantially the same as that of the landmark analysis, and there was a very high correlation between the multivariate landmark and outline data sets. See Rosenberg (2000) for more details.

REGENERATION

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; Backwell *et al.*, 2000). Regeneration is likely to have two effects on these results, one on size allometry and one on mean shapes. Regenerating claws are initially smaller than would be expected for a crab of the same size with an unregenerated claw (Hopkins, 1985). In a given population, most of the variance in claw size due to regeneration is likely to be found on the larger crabs for three reasons. First, larger crabs are more likely to be regenerating a claw. Second, it takes longer to regenerate a larger claw than a smaller one. Third, the difference in size between the original and regenerated claw is more extreme when a large claw is regenerating. This will have the effect of lowering the claw size/carapace breadth regression slope. This means that the observed slopes (Table 1) are underestimates of the slope that would be obtained through simple growth without regeneration. For example, there was one clearly regenerate major claw in the

sample of *Uca pugnax*; exclusion of this single individual raised the slope of the size regression (Table 1) and reduced the variance such that the regression became significant.

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) (von Hagen, 1962; Yamaguchi & Takeda, 1973; Yamaguchi, 1973; Crane, 1975; Backwell *et al.*, 2000); other species have claws that look identical. This means that for some species, the average shape 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 two 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 dichotomy. 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 (Wilks' $\Lambda = 0.1049$, $P < 0.001$). The differences are illustrated in Figure 11. 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. Similar results have been reported for *U. annulipes* (Backwell *et al.*, 2000); besides the shape differences, they also found leptochelous claws to be significantly lighter than brachychelous claws.

Furthermore, in *Uca borealis*, 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 (Wilks' $\Lambda = 0.5706$, $P = 0.0035$) significantly differ.

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 chelae. Because regenerated claws are initially 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. If so, this would have important consequences on the relationship of sexual selection and regeneration. Backwell *et al.* (2000) found that in *U. annulipes*,

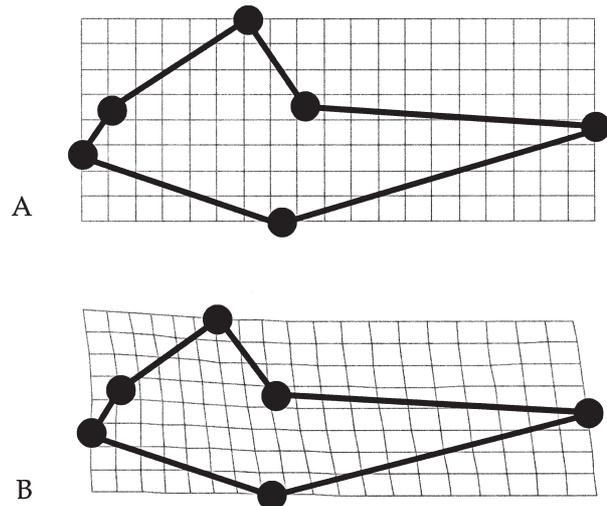


Figure 11. Variant claw forms of *Uca borealis*. (A) Brachychelous claw. (B) Leptochelous claw. The warp grid shows the transformation of the brachychelous form to the leptochelous form.

males with regenerated claws were using dishonest signalling. Although they were likely to lose a fight to a crab with a brachychelous claw, the differential growth pattern of leptochelous claws allowed crabs to bluff their opponents and females into thinking they had stronger, unregenerated claws, thus avoiding fights and gaining mates.

MINOR CLAWS AND PREFERRED SUBSTRATE

The main function of the minor cheliped is to scoop a small amount of material from the substrate and transport it to the mouth for feeding (although it is also used in grooming, reproduction, and, in a few species, waving). 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 (Fig. 12). Both features vary among species. 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, Fig. 2) and the presence of small serrations or teeth may also contribute to the ability of a claw to collect food.

Crane (1975) reported that, in general, 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, Icery & Jones (1978) found that the sand-dwelling species had the longest chela, the widest gape, and the least degree of spoonation at

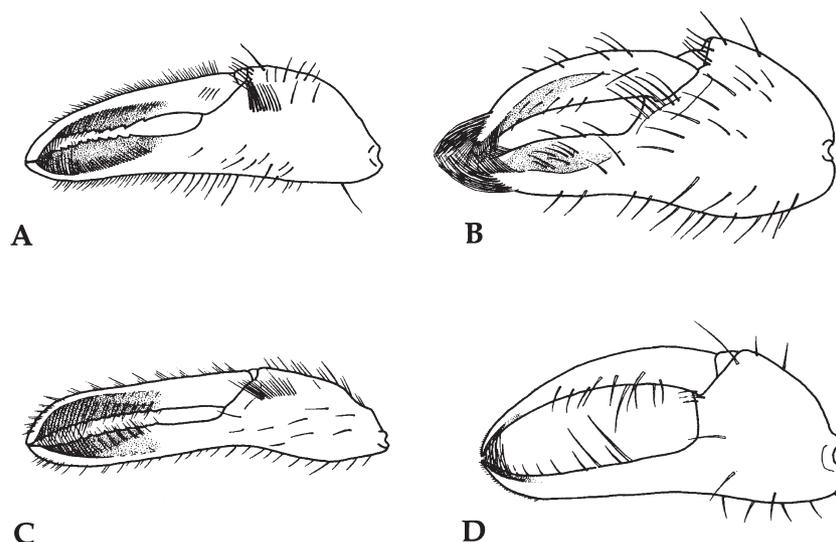


Figure 12. Minor claws of four species, representing some of the variation in specialized feeding structures. (A) *Uca flammua*; (B) *Uca panamensis*; (C) *Uca thayeri*; (D) *Uca terpsichores*. Figure modified from Crane (1975).

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 in the minor chela setae. The general correlation of the mud/sand gradient with gape width was confirmed by Neiman & 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 (Fig. 12b). These setae appear specialized for scraping algae and organic matter off of the rocks upon which they live (Crane, 1975; von Prahl & Guhl, 1981).

The relationship between minor claw shape and habitat type was examined using the geometric morphometric data. 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 the author studied in Panama (Rosenberg, 2000); 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 & Jones, 1978; George & 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 (Bookstein *et al.*, 1996; Rohlf & Corti, 2000). Because one of the data sets (habitat) consisted of a single variable, the analysis simply calculates the covariance between one variable and the others. The analysis was performed with tpsPLS (Rohlf, 1998a); 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 13 illustrates the shape differences at the extreme habitat types. Sand-dwelling species have a relatively shorter manus and a 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), the variation in distance between landmarks 2 and 6 may represent the difference in gape width previously noted by Crane (1975) and Neiman & Barnwell (1997).

Since the habitat designations are fairly coarse and are only approximate, it was necessary to test the

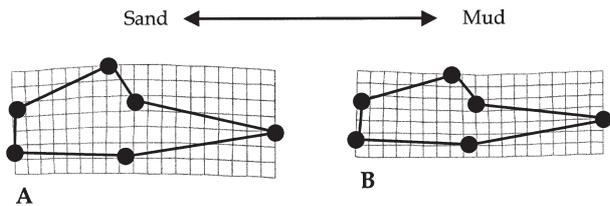


Figure 13. The relationship between minor claw variation and habitat. (A) Shape of minor claw in pure sand habitat (type 1). (B) Shape of minor claw in pure mud habitat (type 5).

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 non-significant ($P > 0.05$).

The description of variation is the 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 behaviour moderated function. Very few structures have been subjected to a rigorous analysis of the interspecific variation as it relates to allometry, function, and behaviour. One set of structures which have been rigorously analysed and which are very similar 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; 1987b; 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 m) 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 vs. intrasexual competition (Packer, 1983). With the greater understanding of the evolutionary patterns of claw shape in fiddler crabs, the study of how these structures are related to their limited functions of display and combat is now possible.

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APPENDIX I. SPECIES EXAMINED

Uca annulipes, *U. arcuata*, *U. argillicola*, *U. batuenta*, *U. beebei*, *U. bellator*, *U. bengali*, *U. borealis*, *U. brevifrons*, *U. burgersi*, *U. capricornis*, *U. chlorophthalmus*, *U. coarctata*, *U. coloradensis*, *U. crassipes*, *U. crenulata*, *U. cumulanta*, *U. dampieri*, *U. deichmanni*, *U. demani*, *U. dorotheae*, *U. dussumieri*, *U. ecuadoriensis*, *U. elegans*, *U. festae*, *U. flammula*, *U. forcipata*, *U. formosensis*, *U. galapagensis*, *U. heradurensis*, *U. hesperiae*, *U. heteropleura*, *U. hirsutimanus*, *U. inaequalis*, *U. insignis*, *U. intermedia*, *U. inversa*, *U. lactea*, *U. latimanus*, *U. leptodactyla*, *U. limicola*, *U. longidigitum*, *U. major*, *U. maracoani*, *U. marguerita*, *U. minax*, *U. mjoebergi*, *U. mordax*, *U. neocultrimana*, *U. oerstedii*, *U. ornata*, *U. panacea*, *U. panamensis*, *U. paradussumieri*, *U. perplexa*, *U. polita*, *U. princeps*, *U. pugilator*, *U. pugnax*, *U. rapax*, *U. rhizophorae*, *U. rosea*, *U. saltitanta*, *U. seismella*, *U. signata*, *U. sindensis*, *U. speciosa*, *U. spinicarpa*, *U. stenodactylus*, *U. stylifera*, *U. subcylindrica*, *U. tallanica*, *U. tangeri*, *U. tenuipedis*, *U. terpsichores*, *U. tetragonon*, *U. thayeri*, *U. tomentosa*, *U. triangularis*, *U. typhoni*, *U. umbratila*, *U. uruguayensis*, *U. urvillei*, *U. virens*, *U. vocans*, *U. vocator*, *U. vomeris*, *U. zacae*

Additional information on the specimens can be found in Rosenberg (2000, 2001).