

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

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A B S T R A C T

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 agonistic 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 an-

alyzing 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 constitutive 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

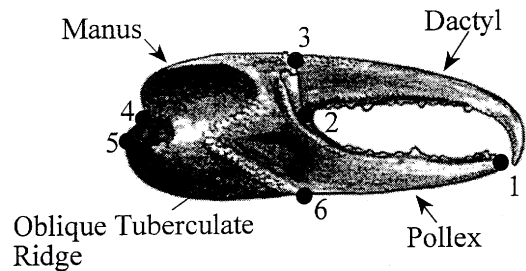


Fig. 1. Diagram of a cheliped with the six morphological landmarks labeled. The landmarks are as follows: 1, tip of the pollex; 2, lower junction between the dactyl and the manus; 3, upper junction between the dactyl and the manus; 4, top of the juncture between the carpus and the manus; 5, base of the 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).

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.

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 $\times$  (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

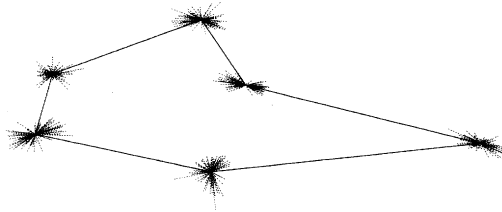


Fig. 2. Generalized Least-Squares superimposition of all 126 chelipeds showing variation at each landmark after the specimens have been scaled, translated, reflected, and rotated. The outline is formed by linking the average of the coordinates of each landmark and represents the consensus configuration.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

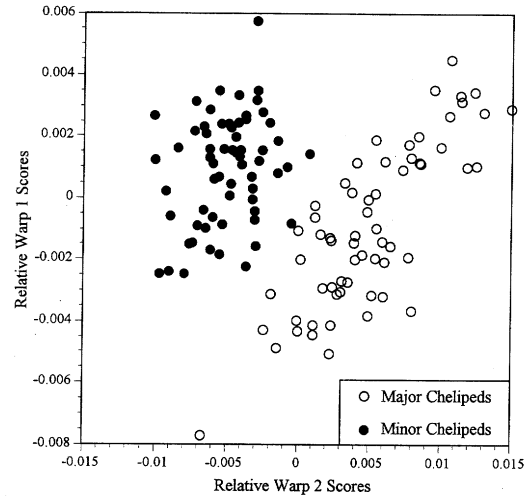


Fig. 3. Bivariate plot of Relative Warp 1 scores versus Relative Warp 2 scores. (Relative Warp scores were calculated by TPSRW, 1992).

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-

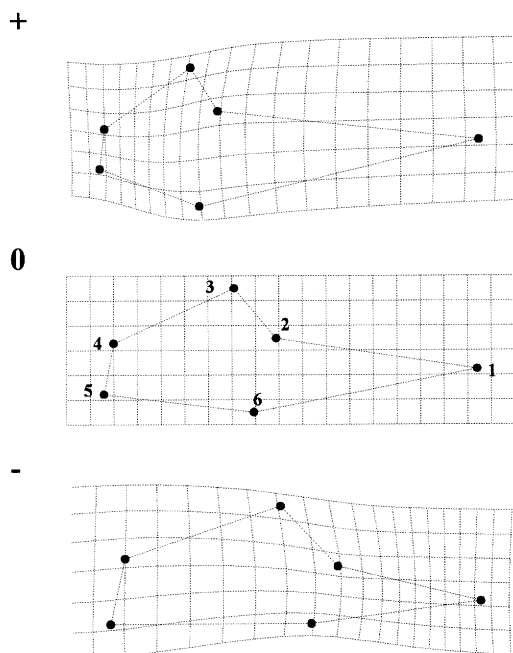


Fig. 4. Overall deformation of shape along the first Relative Warp for all 126 specimens. The first Relative Warp represents the direction of maximal nonuniform shape variation (obtained by a principal components analysis of the **W**-matrix). Positive deformations along this axis represent a short manus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

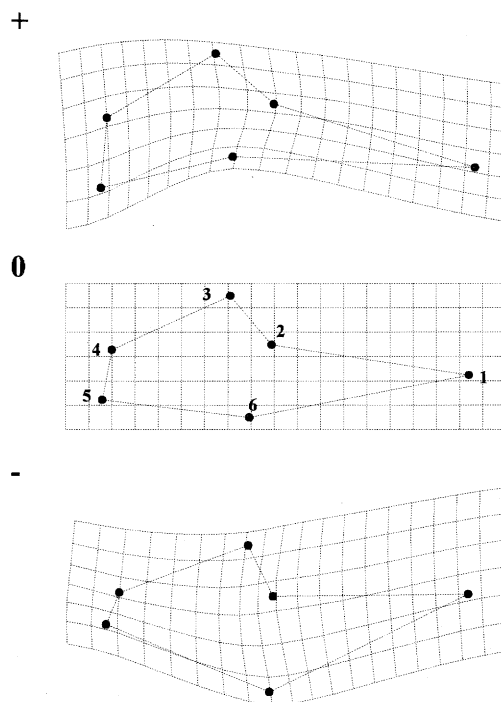


Fig. 5. Overall deformation of shape along the second Relative Warp for all 126 specimens. Positive deformations along this axis represent a narrow cheliped; negative deformations represent a broad cheliped. (Figures produced using TPSRW, 1992).

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 $\Lambda$	$F_s$	$d.f.$	$P$
Nonuniform shape variables ( <b>W</b> -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 $\Lambda$	$F_s$	$d.f.$	$P$
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 uni-

form 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).

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 ( $F_s = 95.6379$ ,  $d.f. = 1, 61$ ,  $P < 0.0001$ ) trend of decreasing mechanical advantage as size increased, while regression for minor chelipeds showed no significant ( $F_s = 0.0048$ ,  $d.f. = 1, 61$ ,  $P = 0.9449$ ) trend. This result is identical to that obtained by Levinton *et al.* (1995).

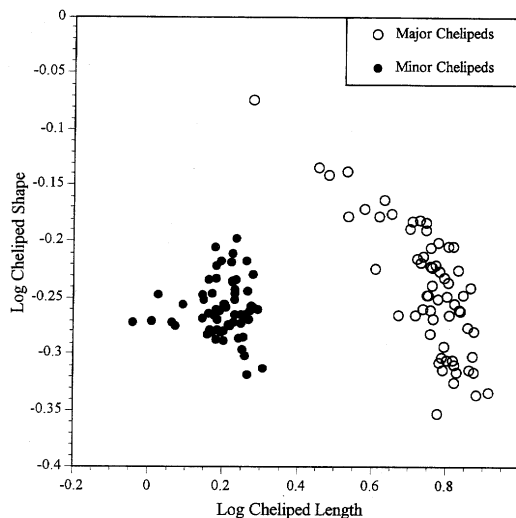


Fig. 6. Relationship between length and shape of chelipeds of *Uca pugnax*. Measurements were extrapolated from landmark data. Shape is the ratio of cheliped height to pollex length. The slope of the least-squares linear regression of shape on length for the major chelipeds is  $-0.396246$  ( $P < 0.0001$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

## DISCUSSION

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

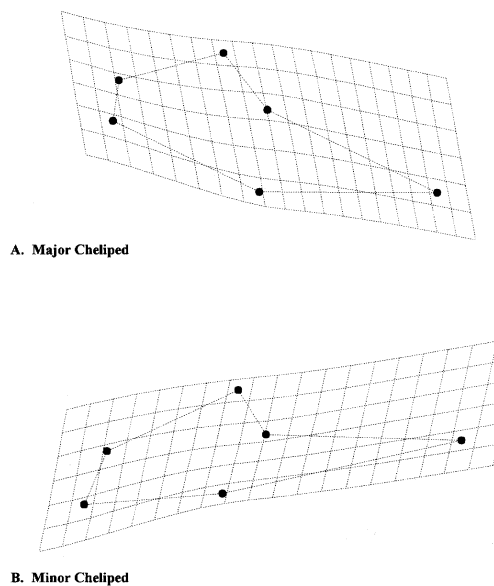


Fig. 7. Predicted cheliped shapes. These figures represent a projection of the exaggerated differences (including both uniform and nonuniform variation) between major (A) and minor (B) chelipeds. The major cheliped has a wider manus and pollex; the minor cheliped is more slender. (Figures produced using 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 (Trinka-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 non-damaging 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 *Megaloceros giganteus* Blumen-

bach. 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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