

# Functional significance of an unusual chela dimorphism in a marine decapod: specialization as a weapon?

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The squat lobster *Munida rugosa* has an unusual chela dimorphism exhibited mainly by large males. Some individuals have 'arched' chelae in which there is a gap between the dactylus and the pollex when closed, and others have a 'straight' morphology in which the dactylus and pollex oppose along most of their length. Geometric morphometric analysis indicated that, compared with males, the arched morphology does not develop fully in females, so further investigation was confined to males. In males, the distal part of the chela was similar in both the forms and seemed to be adapted to hold and shred prey items. Both morphologies had a major cylindrical tooth on the inner proximal part of the dactylus, but the arched morphology had a higher and wider propodus, a greater major tooth-pollex distance and a greater force generation than the straight morphology. The findings suggest that the arched chela morphology in *M. rugosa* is a sexually selected trait adapted to inflict puncture wounds on opponents during agonistic interactions. The arched morphology, therefore, appears to have evolved in males by means of sexual selection because it enhanced the function of the chela as a weapon, while retaining functionality for feeding.

**Keywords:** chela force; *Munida rugosa*; geometric morphometrics; multifunctional structure; puncture wound

## 1. INTRODUCTION

Decapod chelae ('claws') are good models to study evolution of morphology owing to their simple basic structure, their various functions and their well-known mechanics. A chela consists of two main elements: a propodus with a distal extension called the pollex, which opposes the second element, the dactylus, to make the appendage chelate. Although chelae are multifunctional organs (Lee 1995), many species have a particular morphology adapted to a specific use (Brown *et al.* 1979). For example, chelae may be adapted to break the shell of prey in durophagous predators (Yamada & Boulding 1998), shred tissue (Brown *et al.* 1979; Yamada & Boulding 1998), generate snapping sounds or make cavitation bubbles to kill prey (Versluis *et al.* 2000), strike, grab or inflict damage to opponents during agonistic interactions (Crane 1975; Barki *et al.* 1997), collect sediment for feeding (Crane 1975) or even carry sea anemones (Karplus *et al.* 1998).

Small adaptations of the basic structure of decapod chelae allow highly specialized functions (Brown *et al.* 1979). Schenk & Wainwright (2001) considered three distinct aspects of chela mechanics: force generation; force transmission; and force distribution. Force generation depends entirely on the morphological and physiological properties of the chela closer muscle (CCM; Schenk & Wainwright 2001). Force generated by the CCM is transmitted to the dactylus by a lever system, providing a mechanical advantage (MA) that amplifies the force exerted at the point of contact (Warner & Jones 1976). The force distribution on the chela is the result of the

dactylus and pollex morphology, particularly the size, shape and distribution of the denticles (Brown *et al.* 1979). These three aspects of chela mechanics provide a useful basis for analysing the design features of different morphologies in relation to selection pressures that may be suggested by consideration of the species' life history and ecology.

The squat lobster *Munida rugosa* (Fabricius), a galatheid of the northeast Atlantic, has a chela dimorphism unlike any previously analysed. Most individuals have 'straight' chelae (the pollex and dactylus oppose along most of their length), while some large individuals, particularly males, have 'arched' chelae (the proximal sections of the dactylus and pollex are curved, leaving a gap when the chela is closed; Ingrand 1937). The proportion of males with arched chelae increases with size, but even in the largest size classes, a considerable proportion of males have straight chelae (Ingrand 1937). Similar chela morphologies are found in other species of *Munida* (particularly *M. curvimana*; d'Udekem d'Acoz 2003), suggesting that either the straight-arched dimorphism was present in a common ancestor or the extant species had convergent morphological evolution due to similar selection pressures.

Based on the occurrence of puncture wounds, Ingrand (1937) suggested that arched chelae might be better adapted to inflict damage during agonistic interactions between males and to grip females during mating. Berrill (1970) observed an aggressive behaviour in a closely related species (*Munida sarsi*) that also possesses this dimorphism (Hartnoll *et al.* 1992), in which the chelipeds are used for grabbing opponents. However, chelipeds in *Munida* spp. also have functions other than fighting

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Table 1. Results of the multivariate regressions of morphological features and force measurements on chela shape.

dependent variable	Wilks' $\lambda$	$F_{8,31}$	$p$	information explained by the linear model (%)
<i>morphological features</i>				
maximum opening angle	0.63	2.30	0.046	16.7
mechanical advantage	0.30	9.16	<0.001	42.2
propodus height	0.01	306.76	<0.001	69.0
propodus width	0.05	68.73	<0.001	63.6
maximum distance between tips	0.45	4.70	<0.001	34.8
maximum distance between major dactylus tooth and pollex	0.47	4.30	0.001	27.0
width of major dactylus tooth	0.68	1.79	0.117	2.2
length of major dactylus tooth	0.71	1.55	0.182	16.5
distance tooth-fulcrum	0.60	2.54	0.030	17.0
<i>force generation (ln transformed)</i>				
maximal closer muscle contraction force	0.36	6.88	<0.001	43.8
maximal force applied on major tooth	0.24	12.2	<0.001	52.9

(Zainal 1990; Hudson & Wigham 2003), hence the functional significance of the straight-arched dimorphism is unclear.

The aim of the present study was to quantify morphological differences between sexes and investigate whether the arched chelae of males are morphologically better adapted to inflict puncture wounds during agonistic interactions (i.e. to be effective weapons) than straight chelae. Understanding the functional significance of a trait is aided by the knowledge of how its particular features relate to its performance in hypothesized functions compared with other forms (Alcock 1993). Consequently, the study was based on comparing force generation, force transmission and force distribution among morphologies (Schenk & Wainwright 2001).

## 2. MATERIAL AND METHODS

### (a) *Animal collection and maintenance*

A total of 40 male and 35 female *M. rugosa* were collected in the Clyde Sea Area, Scotland (55°45' N, 4°54' W) during the winter 2005–2006, by beam trawling (2 m beam trawl and 50 mm mesh) on a gravely muddy bottom at water depths of 35–40 m. Only large individuals (males greater than 29 mm and females greater than 28 mm carapace length, CL) with both chelipeds intact were sampled (few individuals smaller than this show signs of developing arched chelae). After collection, the animals were maintained in fibreglass tanks supplied with flow-through seawater for at least 24 hours before any measurement and for no more than one week. Animals were fed ad libitum with pieces of frozen fish.

### (b) *Morphological measurements*

Two digital photographs of the lateral surface of each cheliped were taken (chela closed and maximally open) with a digital camera (Fujifilm Finepix F810 in a WP-FX701 waterproof housing) mounted on a custom-made jig holding the cheliped extended. Various dimensions of the chelae (table 1) were measured with vernier callipers (propodus height and width were measured on the distal and the middle parts of the manus, respectively) and from photographs using image analysis software (SIGMA SCAN PRO v. 5.0.0). Squat lobsters were handled carefully during measurements to avoid any damage, particularly to the chelipeds. Geometric morphometric methods were used to analyse variation in shape of the chelae (Marcus *et al.* 1996; Zelditch *et al.* 2004). 'Landmark'

coordinates were recorded from images with the TPSDIG2 program (Rohlf 2005a). The six landmarks used (figure 1a) were homologous to those used by Rosenberg (2002) for fiddler crabs (*Uca* spp.). The generalized least-squares (procruste) method (Rohlf & Slice 1990) was used to superimpose landmark configurations.

Selected cross-sections of the two extreme chela shapes (straight and arched) of males were drawn without setae to highlight morphological differences, observe dentition distribution in the pollex and dactylus and to compare exoskeleton thickness.

### (c) *Measurement of force generated by chelae*

The maximal compressive force of male chelae was measured by the increase in pressure inside a closed, flexible, oil-filled tube pinched by test subjects (Gabbanini *et al.* 1995). Digitized pressure readings were calibrated at the start of each measuring session using a dried chela amputated from a dead animal and glued onto an acrylic support, with weights suspended from the tip of the dactylus.

The maximum force exerted by the CCM ( $F_2$ ) is given by

$$F_2 = \frac{F_1 d_1}{L_2},$$

where  $F_1$  is the maximum force exerted on the tube by the chela;  $d_1$  is the distance from the tube to the fulcrum; and  $L_2$  is the distance from the fulcrum to the insertion of the flexor muscle tendon (figure 1b; Mitchell *et al.* 2003).  $F_2$  is independent of the MA (that is  $L_2/L_1$ ), which varies in relation to chela shape. Force measurements were performed before morphometrics measurement to minimize animal stress.

### (d) *Statistics*

A relative warp analysis (RWA, equivalent to a principal component analysis) was performed on partial warp scores (shape variables) calculated from superimposed landmark coordinates using the TPSRELW program (Rohlf 2005b) to examine major trends of chela shape variation.

The difference in shape (represented by partial warp scores) between sexes was tested with a MANCOVA including the centroid size (the scaling value used during procruste superimposition) of the propodus as covariate using the software MINITAB v. 14.

Relationships between chela shape and other variables were assessed using multivariate regression analysis. Morphological

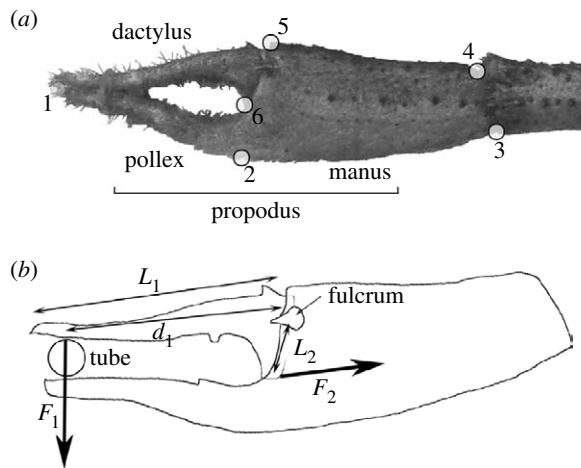


Figure 1. (a) Landmarks whose coordinates were recorded from each chela for analysis of shape. (b) Lever system of *M. rugosa* chela and force measurement (the fulcrum is situated under a large spine).

values and closing force were scaled to the average centroid size of the chela.

For convenient graphical representation of the multivariate results, the first axis of the RWA was used to represent shape variation, because it represented 75% of the variability in shape (§3). If a nonlinear relationship was suspected, an appropriate transformation was applied; otherwise, untransformed values were analysed.

### 3. RESULTS

#### (a) Morphological measurements

Equivalent results were obtained from analysis of left or right chelipeds, hence results only from left chelipeds are presented. The first three axes (or ‘relative warps’) of the RWA together explained 95.7% of the shape variation (75.04% for the first axis, 15.43% for the second and 5.23% for the third). The first axis represented variation in pollex length inversely related to manus length and propodus height. This axis was related to the degree of arching of the chela. The second axis represented the degree of bending of the chela in the vertical plane, with an inflection point at the base of the pollex. The third axis represented the variation in chela height.

The degree of arching was greater in males than in females, in which the arched morphology did not fully develop (MANCOVA, Wilks’  $\lambda=0.41$ ,  $p<0.001$ , figure 2). The degree of arching as represented by RW1 was positively related to propodus centroid size (MANCOVA, Wilks’  $\lambda=0.77$ ,  $p=0.020$ , figure 2) and even the largest females had smaller chelae than males.

In males, compared with straight chelae, arched chelae had a higher and wider propodus (figure 3a), a greater MA (figure 3b) and a smaller distance from the major tooth to the fulcrum (table 1). Arched chelae had a smaller opening angle (table 1), but had a greater pollex–major tooth distance (figure 3c; table 1).

Both arched and straight chelae had a thin dactylus and pollex with a high density of small sharp teeth on the inner surface and terminating with a larger, curved, sharp point (figure 4). In both the morphologies, the dactylus had a major cylindrical tooth with a flat end at a short distance from the fulcrum. However, unlike the straight morphology, arched chelae had a large ovoid gap between

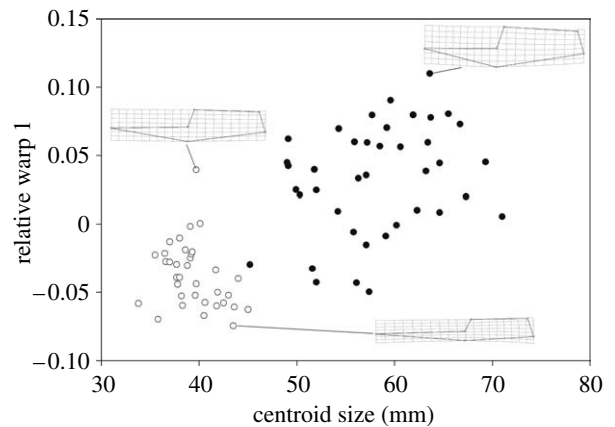


Figure 2. First axis of the RWA as a function of centroid size of the propodus in males (filled symbols) and females (open). Illustrations are the thin-plate spline representations of shape along the first axis representing extreme female and male morphologies.

the dactylus and pollex adjacent to the fulcrum. In the arched morphology, the curvature of the pollex was accentuated by a triangular tooth distal to the dactylus major tooth. Cross-sections showed similar exoskeleton thickness in both the morphologies (but no quantitative assessment was performed). There was thicker calcification in the higher part of the propodus directly opposed to the major tooth, suggesting a greater mechanical resistance to pressure. The cross-section on the tip of the dactylus and pollex showed that there was a close contact between the distal parts of the chela bearing sharp teeth.

#### (b) Force generated by chelae

Force appeared to be exponentially related to chela morphology (figure 3d); consequently, force values were log-transformed. Arched chelae had a stronger CCM than straight chelae (table 1) and as a result of morphology combined with CCM strength, the force applied on the major tooth was 5–10 times greater in arched than in straight chelae (table 1; figure 3d), reaching a maximum recorded value of 52 N. At the tip of the dactylus, this force would correspond to 12 N (for an animal of 35 mm CL and 72 mm propodus length).

### 4. DISCUSSION

The morphological difference between straight and arched chelae in *M. rugosa* is to some extent similar to the difference between the well-known cutter and crusher chela shapes in other decapods (Yamada & Boulding 1998). Arched chelae have a bulkier propodus with a stronger CCM and a greater MA than straight chelae, which results in a greater force production. By contrast, straight chelae have a smaller MA and consequently a higher theoretical closing speed (Levinton & Allen 2005), which could be a better adaptation for catching prey by a snapping motion (as observed in *M. sarsi* by Hudson & Wigham (2003)). Crusher chelae are specialized for breaking open hard-shelled prey and are typically characterized by a  $MA>0.3$  (Yamada & Boulding 1998). *Munida rugosa*, with a maximum MA of 0.16 would be classified as a ‘generalist feeder’ according to Yamada & Boulding’s (1998) criterion. Moreover, *M. rugosa* chelae are not particularly strong, with forces of

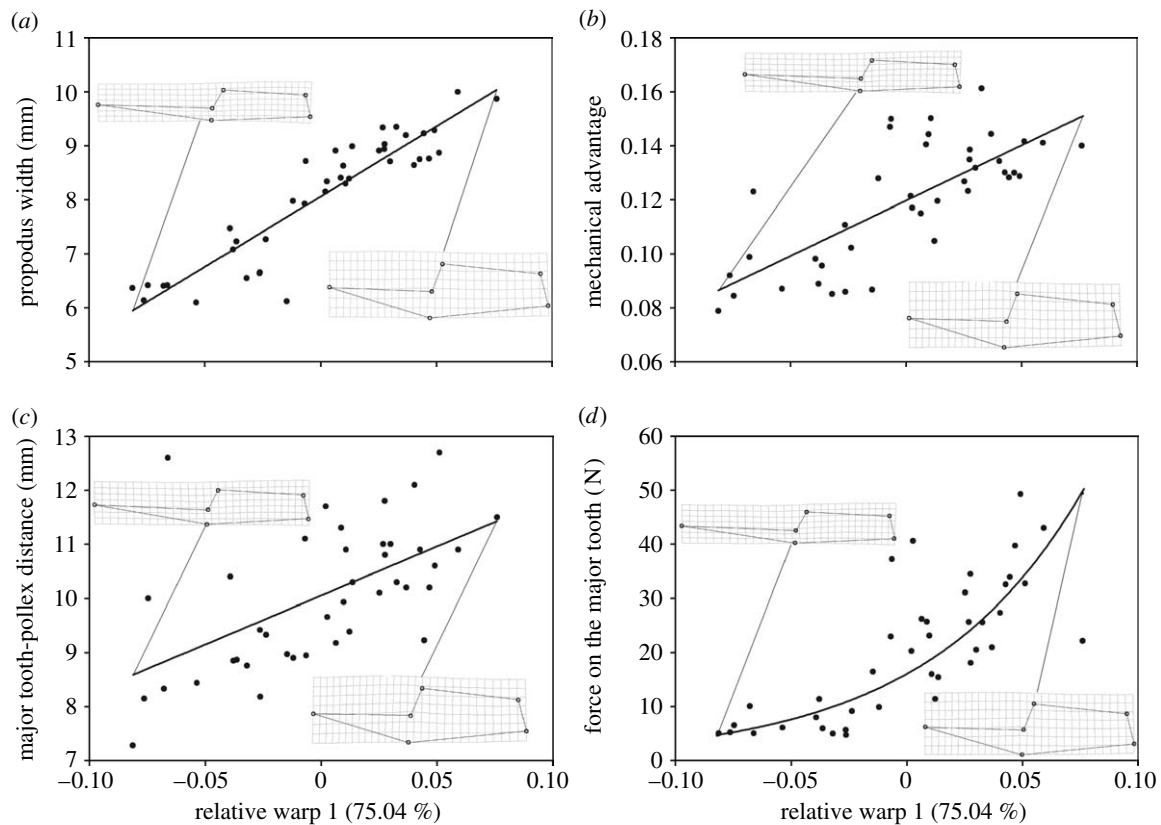


Figure 3. Plots of (a) width of the propodus, (b) MA, (c) major tooth-pollex distance and (d) maximum force generated on the major tooth as a function of the first axis of the RWA. Note that values are scaled to the average centroid size. Shapes represented are thin-plate spline representations of the mean landmark configurations at either extreme of the linear model fitted to the multivariate data.

up to 12 N generated at the tip, compared with equivalent measures for other decapods that can crush mollusc shells, such as *Carcinus maenas* (100 N, Sneddon *et al.* 2000), *Menippe mercenaria*, (380 N, Blundon 1988) and *Homarus americanus* (256 N, Elner & Campbell 1981). The distal part of the chela, which is similar in both the morphologies, has a structure apparently suited to tearing tissue or gripping soft objects (Brown *et al.* 1979), since the opposing surfaces have small sharp spines and teeth. Previous behavioural observations indicated that the distal parts are used to grip food items and pass them to the mouth, but feeding effectiveness did not appear to vary with cheliped morphology (Zainal 1990), although a systematic investigation remains to be made. The proximal part of the chelae appears to be adapted for puncturing hard objects, since there is a large tooth with a small area of contact, increasing the force per unit area (i.e. pressure) that could be applied (Brown *et al.* 1979). In contrast to the straight morphology, arched chelae have an oviform gap that seems better adapted to grip and puncture rounded objects, because the distance from the major tooth of the dactylus to the pollex is greater (owing to the bending of the dactylus and pollex) and there is a smaller distance from the major tooth to the fulcrum, resulting in a greater application of force on the tooth.

Ingrand (1937) noted puncture wounds in male chelipeds and female abdomens in *M. rugosa* and suggested that they could have been caused by the major tooth described previously, but did not draw any further conclusions. A comparison of the major tooth-to-pollex distance with the width of the propodus (merus and carpus are similar in both the morphologies) shows that

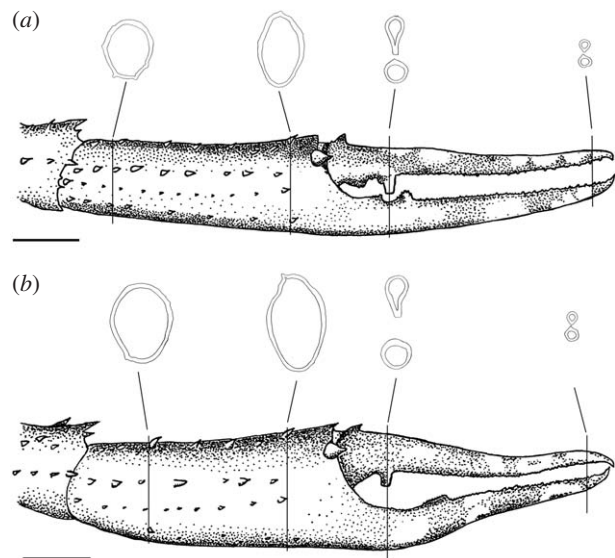


Figure 4. Outer surface of the chelae of male *M. rugosa* shown without setae and slightly open with selected cross-sections (of the same chela closed) for (a) the straight morphology and (b) the arched morphology. Scale bar, 1 cm. Modified drawing from originals by Anna Kerouanton.

arched chelae could fit over the propodus of size-matched animals with any chela morphology, whereas in straight chelae, the major tooth-to-pollex distance would be too small to allow arched chelae to be gripped. Consequently, the present finding suggests that the arched morphology may be better adapted than the straight morphology to inflict damage (puncture wounds) during agonistic

interactions. Moreover, in *M. rugosa*, arched chelae appear to develop fully only in large males, although reduced (intermediate) arching develops in some large females (present study; Ingrand 1937). This suggests a function related to reproduction, such as male competition for access to females. The occurrence of reduced forms of male sexually selected traits in females is common across a range of taxa and was explained by Darwin (1871) as 'transference of characters' between the sexes. These phenomena are attributable to pleiotropy (and linkage) of genes affecting the characters of both the sexes (Lande 1980)

Puncturing of chelae has previously been observed in decapods such as fiddler crabs (Crane 1975) and porcelain crabs (Rypien & Palmer 2007), and has been attributed to a structure with large strength: surface ratio (Crane 1975; Brown *et al.* 1979). Puncturing the exoskeleton can cause haemolymph loss and create an entry for bacterial and ciliate infection (Johnson 1976; Armstrong *et al.* 1981). Infections can affect the general health of the animal, causing a lethargic behaviour and ultimately death (Johnson 1976; Armstrong *et al.* 1981). Moreover, infected or parasitized animals have reduced aggressiveness during interactions (Innocenti *et al.* 2003), leading more often to defeat in encounters with healthy individuals.

In conclusion, the arched chela morphology in *M. rugosa* appears to be a trait that has evolved in males by means of sexual selection owing to its enhanced functionality to inflict injuries to an opponent (i.e. weapon) during agonistic interactions. The distal part of the chela, since it is apparently adapted for feeding, could have remained similar in both chela types due to natural selective pressures. Further work is needed to measure the impact on fitness of puncturing chelae with respect to infection, muscle necrosis, strength, animal health and alteration of behaviour. Behavioural studies to investigate whether arched chelae do, in fact, confer an advantage in agonistic interactions, and whether there are fitness costs of possessing arched chelae in other contexts will be reported elsewhere.

No procedures were used that required licence, and nothing done infringing any ethical guidelines.

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