

# Dimorphism and the functional basis of claw strength in six brachyuran crabs

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## Abstract

By examining the morphological basis of force generation in the chelae (claws) of both molluscivorous and non-molluscivorous crabs, it is possible to understand better the difference between general crab claw design and the morphology associated with durophagy. This comparative study investigates the morphology underlying claw force production and intraspecific claw dimorphism in six brachyuran crabs: *Callinectes sapidus* (Portunidae), *Libinia emarginata* (Majidae), *Ocypode quadrata* (Ocypodidae), *Menippe mercenaria* (Xanthidae), *Panopeus herbstii* (Xanthidae), and *P. obesus* (Xanthidae). The crushers of the three molluscivorous xanthids consistently proved to be morphologically 'strong,' having largest mechanical advantages (MAs), mean angles of pinnation (MAPs), and physiological cross-sectional areas (PCSAs). However, some patterns of variation (e.g. low MA in *C. sapidus*, indistinguishable force generation potential in the xanthids) suggested that a quantitative assessment of occlusion and dentition is needed to understand fully the relationship between force generation and diet. Interspecific differences in force generation potential seemed mainly to be a function of differences in chela closer muscle cross-sectional area, due to a sixfold variation in apodeme area. Intraspecific dimorphism was generally defined by tall crushers with long in-levers, though *O. quadrata* exhibited an extreme dimorphism suggesting that factors unrelated to a speed–strength dichotomy (e.g. sexual selection) have shaped dimorphism of that species. It is concluded here that: (1) the majority of interspecific claw strength variation is a function of closer muscle cross-sectional area; (2) variation in claw morphology related to force production and transmission does have some relation to hardness of diet; (3) claw dimorphism in many species does seem to be related to strength and speed trade-offs; (4) factors besides molluscivory must be considered to understand claw evolution fully; (5) a quantitative assessment of force distribution, lacking in the literature, is essential for a more complete understanding of the relationship between claw design and ecological function.

**Key words:** Brachyura, morphology, dimorphism, force-generation, molluscivory

## INTRODUCTION

Brachyuran crab chelae (claws) function in multiple ecological roles, including prey capture and processing, agonistic interactions, and mate acquisition and handling (see also Hughes, 2000). Besides being multifunctional organs, crab claws are mechanically simple and homogenous, making them an excellent system for studying morphological evolution and the relationship between morphology and ecology. A sizeable body of work has accumulated dealing with crab claw morphology, physiology and associated behaviour,

with the bulk of this work focusing on feeding ecology (Lee & Seed, 1992; Lee, 1995; Seed & Hughes, 1995). Lee and Seed have noted, however, that consideration of organ function in all ecological contexts is necessary for a thorough understanding of evolution in multi-functional structures (Lee & Seed, 1992; Lee, 1995).

Various crab species are known to include hard-shelled prey in their diets, so much of the morphological and physiological work on crab claws has focused on force-generation ability. The primary study organisms have been molluscivorous crabs from three families: Cancridae (e.g. Warner & Jones, 1976; Smith & Palmer, 1994; Rebach & Wowor, 1997; Block & Rebach, 1998), Portunidae (e.g. Warner & Jones, 1976; Elner, 1978; Warner *et al.*, 1982; Blundon, 1989; Kaiser, Hughes &

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Reid, 1990), and Xanthidae (e.g. Cheung, 1976; Blundon, 1988, 1989). While force generation and claw morphology have been studied in non-molluscivorous crab species (e.g. Govind *et al.*, 1992; Levinton & Judge, 1993; Claxton, Govind & Elner, 1994; Levinton, Judge & Kurdziel, 1995), few studies have considered claw design in both molluscivorous and non-molluscivorous crabs (e.g. Brown, Cassuto & Loos, 1979; Skilleter & Anderson, 1986; Yamada & Boulding, 1998), which is necessary to separate elements of claw design related to molluscivory from those elements of claw design common to all crabs, regardless of diet.

It is clear from the current literature that particular elements of claw morphology underlie the ability to crush hard prey, which itself can be divided into three major elements: force generation; force transmission; force distribution. Force generation occurs in the chela closer muscle (CCM) and has both morphological and physiological components. If the physiological component of force generation is known, the maximum force a muscle can generate can be estimated from morphological data (Calow & Alexander, 1973; P. L. Powell *et al.*, 1984). Force transmission is the conference of CCM force to the movable finger (dactyl). This effect can be described exclusively in terms of morphology (i.e. the CCM-dactyl lever system). Force distribution is the focus of stress against an object pinched between the dactyl and pollex (immovable finger), and is determined by their dentition and occlusive geometry. The cumulative result of these elements of claw design includes the crushing or opening of hard prey. The morphology underlying each element sums to determine how much force a claw can generate, which will be referred to here as 'claw strength'.

As first addressed seriously by Vermeij (1977), increased claw strength should generally be associated with increased claw size. However, increased claw size has also been linked to success in sexual and agonistic interactions (e.g. Warner, 1977; Christy & Salmon, 1984; Lee & Seed, 1992). Ultimately, if molluscivory and the need to generate large forces have shaped claw evolution, then 'strong' claws, though large, may also show an overall design cogent to force production (i.e. generate and transmit large forces that are distributed effectively). Crabs not under selection for increased force production may still develop large claws, but may exhibit an overall 'weak' design (i.e. do not transmit or distribute forces effectively). In order to distinguish 'strong' from 'weak' claws and address evolutionary questions (e.g. when does diet-related selection swamp out sexual selection and vice versa?), it is necessary to understand interspecific variation in claw morphology underlying force production. Such variation can be explored through comparative morphological studies that include crabs representing a wide spectrum of claw design.

While much work has gone into general studies of claw design and function, less work has focused on dimorphism in crab claws (e.g. Cheung, 1976; Govind & Blundon, 1985; Abby-Kalio & Warner, 1989). In many

crab species, both male and female crabs exhibit dimorphic claws that are generally identified as the 'crusher' (larger claw) and 'cutter' (smaller claw) in accordance with presumed functional differences. It is assumed that the dimorphism compensates for a trade-off between strength and speed, allowing the crab one 'strong' and one 'fast' claw. The most extreme case of dimorphism known in crabs occurs in the genus *Uca*, where claw dimorphism is seen only in males, suggesting that the difference in claw shape is, at least in part, related to sexual selection. Given the link between claw size and agonistic and sexual interactions, it is apparent that intraspecific claw dimorphism may not be directly related to feeding ecology in general, and force generation in particular. While several studies have considered claw dimorphism in crab genera other than *Uca*, there has been little effort to describe dimorphism in multiple crab species and identify relationships between claw design and potential function.

This study considers the morphological variation underlying force production in six brachyuran crab species representing four families (Majidae, Ocypodidae, Portunidae, and Xanthidae). The crabs selected for this study exhibit a range in diet (from algae grazing to molluscivory) and in force generating ability (from relatively 'weak' to very 'strong' claws). Additionally, five of the six species exhibit varying degrees of claw dimorphism. We have three primary goals: (1) to determine whether interspecific variation in claw morphology is suggestive of a possible relationship between claw function and diet; (2) to determine how claws have been modified during evolution to produce diversity in force production potential; (3) to determine whether the nature of intraspecific dimorphism is consistent for all species and whether the dimorphism seems to be related to claw function.

## MATERIALS AND METHODS

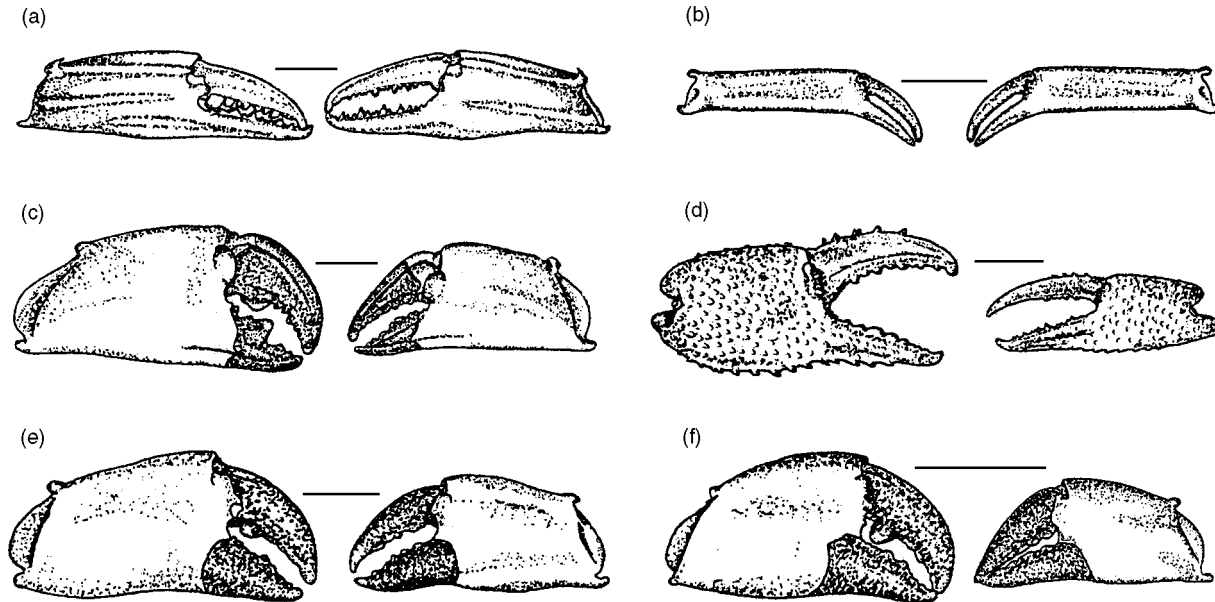
### Study organisms

Six brachyuran crab species (Table 1) representing 4 families were selected for this study based on their variation in claw morphology (Fig. 1) and diet, and their relative abundance along the Gulf Coast of northern Florida (U.S.A.). Two species included here have been subjects of previous morphometric studies: the blue crab *Callinectes sapidus* (e.g. Brown *et al.*, 1979; Blundon & Kennedy, 1982; Govind & Blundon, 1985; Seed & Hughes, 1997) and the Florida stone crab *Menippe mercenaria* (e.g. Cheung, 1976; Brown *et al.*, 1979; Blundon, 1988). Five of the 6 species exhibit a claw dimorphism in size. The larger claw of dimorphic crabs was designated the 'crusher,' and the smaller claw the 'cutter'. All crabs used in this study were collected from the northern Gulf of Mexico between 1 December 1998 and 1 August 1999.

The crusher of *C. sapidus* is slightly larger than the cutter, and possesses a molariform-crushing surface

**Table 1.** Crab species examined, sample size, and crab size range

Crab species	Family	<i>n</i>	Carapace width range (mm)
<i>Callinectes sapidus</i>	Portunidae	30 (19 male, 11 female)	50.8–159.9
<i>Libinia emarginata</i>	Majidae	7 (4 male, 3 female)	43.6–61.0
<i>Ocypode quadrata</i>	Ocypodidae	17 (12 male, 5 female)	30.8–41.3
<i>Menippe mercenaria</i>	Xanthidae	30 (18 male, 12 female)	33.7–90.2
<i>Panopeus herbstii</i>	Xanthidae	12 (8 male, 4 female)	26.3–38.7
<i>Panopeus obesus</i>	Xanthidae	20 (15 male, 5 female)	31.3–55.8



**Fig. 1.** Claws of the six species examined: (a) *Callinectes sapidus* (Portunidae); (b) *Libinia emarginata* (Majidae); (c) *Menippe mercenaria* (Xanthidae); (d) *Ocypode quadrata* (Ocypodidae); (e) *Panopeus obesus* (Xanthidae); (f) *Panopeus herbstii* (Xanthidae). Scale bar = 10 mm for each pair of claws.

near the base of the dactyl (Fig. 1a). Blue crabs have a very catholic diet that includes a variety of gastropods and bivalves, as well as other decapod crustaceans, fish, and algae (S. K. Alexander, 1986; Ropes, 1989; Hsueh, McLintock & Hopkins, 1992). Of the crabs in this study, *C. sapidus* includes the highest percentage of elusive prey in its diet (Fitz & Wiegert, 1991). *Callinectes sapidus* was taken from a sandy bottom habitat near Turkey Point (Franklin County, Florida, U.S.A.) by either dip-net or seine.

The spider crab *Libinia emarginata* is the only species that does not exhibit claw dimorphism, possessing long claws with minimal dentition (Fig. 1b). All interspecific claw comparisons involving crushers of dimorphic crabs are made to the left claws of *L. emarginata*. The bulk (up to 75%) of this species' diet is plant matter, though it is known to consume some animal matter, including molluscs (Ropes, 1989). *Libinia emarginata* was taken by hand from turtle grass beds in St Joseph's Bay (Gulf County, Florida, U.S.A.).

The claws of *M. mercenaria* are highly dimorphic, the

larger crusher having a broad molariform surface at the dactyl base (Fig. 1c). It feeds almost exclusively on a wide range of hard prey, including bivalves, gastropods, and hermit crabs (Powell & Gunter, 1968; Kent, 1983; pers. obs.). Stone crabs were taken by hand from oyster beds at Turkey Point (Franklin County, Florida, U.S.A.). This stone crab collection site falls within a zone of hybridization for *M. mercenaria* and the western-Gulf stone crab *M. adina* (Williams & Felder, 1986; Bert & Harrison, 1988). All specimens collected from Turkey Point more closely resembled *M. mercenaria* and are identified as such in this study.

The claws of the ghost crab *Ocypode quadrata* exhibit a clear dimorphism, though molariform dentition is not evident on the crushers (Fig. 1d). This semi-terrestrial crab takes a variety of prey including carrion, coquina clams, mole crabs and other arthropods, and juvenile birds and terrapins (Sprunt, 1948; Fales, 1976; Wolcott, 1978; Arndt, 1991), with coquinas being the only hard-shelled prey making up a substantial proportion of the diet. Ghost crabs were taken at night by dip-net on the

sandy beaches of St George Island (Franklin County, Florida, U.S.A.).

Both species of mud crabs examined, *Panopeus obesus* and *P. herbstii*, have dimorphic claws with a prominent basal tooth on the dactyl of the crusher (Fig. 1e,f). Both species are known to be aggressive predators of oysters and other bivalves (Bisker & Castagna, 1987; Bisker, Gibbons & Castagna, 1988; Abbe & Breitburg, 1992; Turner, Tammi & Starr, 1996). All mud crabs used in this study were collected by hand from oyster reefs at Wakulla Beach (Wakulla County, Florida, U.S.A.).

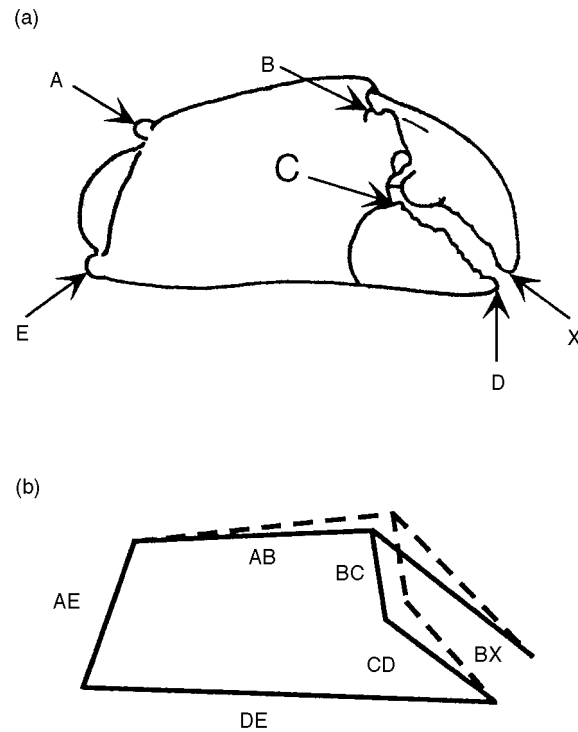
Crabs collected from each location were returned to Florida State University (Tallahassee, Florida, U.S.A.) and maintained in salt water aquaria (33–35‰, ~21 °C) for no more than 1 week before claw dissection. *Ocypode quadrata* was maintained in aquaria with *c.* 2.5 cm of sand on the bottom, which was moistened daily with seawater.

Previous data indicated that crushers and cutters in male and female *C. sapidus*, *M. mercenaria*, and *P. obesus* had indistinguishable shapes in spite of sexual size dimorphism (S. C. Schenk, pers. obs.). That is, if a male and female of similar size were compared, the male would have bigger claws, but the female's crusher would be more similar in size and shape to the male's crusher than his cutter. As our focus in this study was primarily on claw shape, both male and female crabs were collected.

Current systematic work on crabs has focused on resolving relationships among the 'higher' and 'lower' Brachyura (Spears, Abele & Kim, 1992; Guinot, Jamieson & Richer de Forges, 1994; Jamieson, 1994), relationships among freshwater and marine crabs (von Sternberg, Cumberlidge & Rodriguez, 1999), or relationships within families (e.g. Bellwood, 1998; Pohle & Marques, 1998; Tucker, 1998; Harrison & Crespi, 1999). As such, there is no robust phylogenetic hypothesis for infraorder Brachyura, which limits our ability to make evolutionary inferences. For example, the 3 most aggressive molluscivores included in this study are in the same family (Xanthidae) and probably do not represent independently derived molluscivory. The 6 study species represent 4 diverse crab clades and might be expected to show some group-specific design features. Even so, we can still gain insight into potential patterns of claw evolution by comparing aspects of claw design among the 6 species above and describing the intraspecific variation.

#### External morphological measurements: claw shape and force transmission

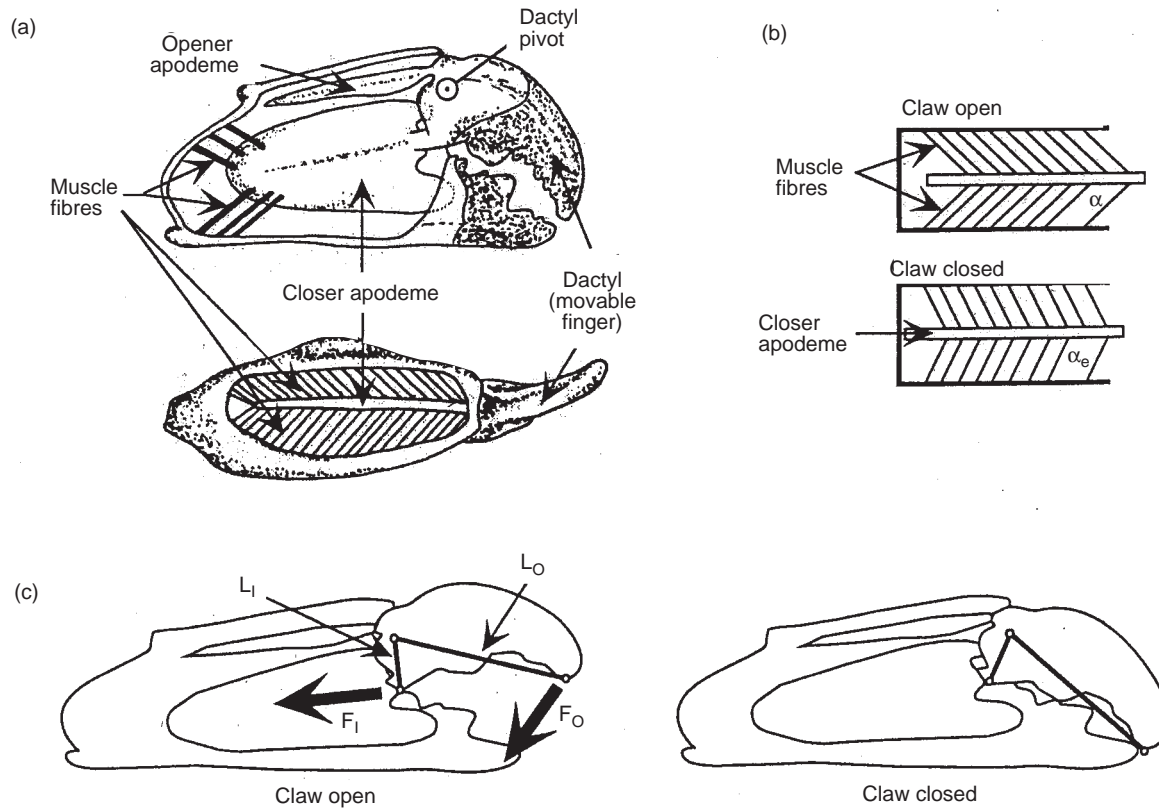
Specific aspects of claw muscle anatomy are expected to be most closely related to claw strength, but one aim of this study was to evaluate the accuracy of external shape measures for predicting claw strength. In particular, certain external claw dimensions may relate directly to components of claw force generation such as physiological cross-sectional area and mechanical advantage.



**Fig. 2.** Claw landmarks and external dimensions measured. (a) Landmarks are morphologically homologous points found on all crab claws: A, dorsal and E, ventral prodopus–carpus articulation points; B, the dactyl pivot point; C, the dorsal base of the pollex; D, tip of the pollex; X, tip of the dactyl. (b) Measurements of external dimensions were taken with dial callipers on the exterior lateral face of the claw: AB, dorsal prodopus–carpus articulation to pivot point; BC, the in-lever proxy; CD, the pollex descent; DE, the ventral prodopus–carpus articulation to pollex tip; AE, the prodopus–carpus gap; BX, the dactyl length/out-lever proxy. Where possible, measurements were also taken on the interior lateral face, and are indicated by dotted lines in the figure (AB', B'C', C'D, and B'X). Additionally, PH, maximum prodopus height and PW, maximum prodopus width, were measured for each cheliped.

For this reason, a series of external linear measurements were made for each claw so that interspecific variation in claw shape could be considered.

Immediately before claw dissection, crabs were placed on ice for 20–30 min, depending on body size. Once inactive, the crab's carapace width and external claw dimensions were measured using dial callipers. Claw dimensions were defined in terms of 6 homologous landmarks found on all crab claws (Fig. 2a). Measurements between points were taken from external (lateral) and internal (medial) claw faces where possible (Fig. 2b), and all linear measurements were  $\log_{10}$ -transformed. CCM lever arms (Figs 2 & 3) were identified as lines BC (in-lever) and BX (out-lever). These lines lie at right angles to the force vectors, and were used to calculate the mechanical advantage (MA) for force generation (BC:BX). Although force can be applied at any point along the dactyl, the distance BX



**Fig. 3.** Schematic diagrams of claw internal anatomy and mechanical function. (a) Dorsal and lateral cutaway showing structures involved in claw mechanical function and force generation. Note that in the dorsal cutaway, the claw opener muscle and apodeme have been removed. (b) Dorsal view of apodeme movement, indicating stretched (open) angle of pinnation ( $\alpha$ ) and relaxed (closed) angle of pinnation ( $\alpha_e$ ). As muscle fibres shorten and the angle of pinnation increases, the apodeme is drawn back into the prodopus, rotating the dactyl around its pivot point. (c) Lateral view of apodeme movement showing relative change in position of dactyl, opener apodeme, and closer apodeme during claw function. The closer muscle induces a force on the closer apodeme ( $F_1$ ) that is transmitted through the in-lever ( $L_1$ ) to the out-lever ( $L_0$ ), producing a force at the claw tip ( $F_0$ ) or anywhere along the dactyl.

was used to determine out-lever length as it is the only easily identified homologous distance on all claws. Once external measurements were taken for both claws, 1 was detached at its breakage plane with wire cutters, and the crab was returned to ice. The second claw would be removed by the same means following dissection of the first claw.

Variation in external claw shape was examined using a principal components analysis (PCA) of the covariance matrix of all distance measurements. The principal components (PCs) that provided the best resolution of claw groupings were used to summarize interspecific differences in claw shape. External claw asymmetry was examined in each species using multivariate analysis of variance (MANOVA) of the distance measurements. Additionally, distance measurements for both claw types were analysed with separate PCAs for each species. Plots of the PCs providing the best separation of crushers and cutters allowed for the identification of external dimensions that most contributed to intraspecific asymmetry.

#### Internal morphological measurements: claw force generation

As shown by Calow & Alexander (1973), maximum force generation for a pinnate muscle can be calculated from the equation:

$$P' = 2 (V/w) \sigma \sin \alpha \cos \alpha_e \quad (1)$$

where  $P'$  is the force exerted by the muscle,  $V$  is the muscle volume,  $w$  is muscle width,  $\sigma$  is the stress generated per unit of muscle cross-sectional area,  $\alpha$  is the angle of pinnation when the muscle is stretched, and  $\alpha_e$  is the angle of pinnation when the muscle is relaxed. If  $\alpha$  and  $\alpha_e$  are similar, the equation can be reduced to:

$$P' = (V/w) \sigma \sin 2\alpha \quad (2)$$

(Alexander, 1969). As  $V/w$  is muscle cross-sectional area ( $A$ ), the equation becomes:

$$P' = A \sigma \sin 2\alpha \quad (3)$$

where  $A$  in crab claws is apodeme area. The morpholo-

gical contributions to crab claw force generation are thus CCM  $A$  and  $\alpha$  (it can be shown using equation 3 that a pinnate muscle generates the greatest force when  $\alpha$  approaches  $45^\circ$ ; see Paul & Gronenberg, 1999). For comparative purposes we assumed that  $\sigma$  was constant across species. This is a conservative step that probably underestimates rather than overestimates real differences among species in claw strength.

CCM morphology was observed through dissection of freshly detached crab claws. Muscle fibres in the dorsal portion of the prodopus are associated with the chela opener muscle (COM) (Fig. 3a, lateral view) and are not involved in claw force production (Fig. 3c). A portion of the dorsal exoskeleton was removed, and the COM and its apodeme were removed from the prodopus, exposing the dorsal surface of the CCM (Fig. 3a, dorsal view).

A Cohu solid state video camera and SigmaScan Pro software (version 4.0, Jandell Scientific) were used to acquire a digital image of the CCM's dorsal surface. Muscle fibres were photographed in the fully stretched position by manually opening the claw to maximum gape. Relaxed fibres were then photographed by holding the claw completely closed. Although the best estimate of  $\alpha$  in equation 3 is stretched angle of pinnation, the relaxed angle of pinnation (when combined with the stretched angle of pinnation) establishes the range of angles a given CCM can assume.

Once the CCM was photographed, the claw was dismantled and the CCM apodeme removed. All muscle fibres were scraped from the apodeme and an image taken of its lateral surface. Apodeme surface area and angle of pinnation were measured on digital images using the software package MeasurementTV (version 1.90, Garr Updegraff/DataCrunch). Angle of fibre pinnation was measured for between 1 and 5 fibres, depending on how many could be reliably discriminated, and a mean angle of pinnation (MAP) was calculated for each claw. Stretched fibre angle was measured directly from the given fibre. As the claws were detached, the muscles did not shorten when the claw was held closed manually. Closed claw fibre angles were measured as the angle between the points of fibre insertion and origin.

Apodeme area, which was expected to scale with body size in all crabs, was compared between claw type and species using least squares linear regression of  $\log_{10}$ -transformed data and analysis of covariance (ANCOVA) to identify interspecific differences in size and intraspecific size dimorphism. If slopes were not homogeneous for intraspecific comparisons, apodeme areas were compared using Wilcoxon-Kruskal-Wallis rank sums non-parametric tests. MAPs and MAs (see above) were not expected *a priori* to scale with body size, were compared using analysis of variance (ANOVA) and *post-hoc* pairwise comparisons.

The functional consequences of claw apodeme size, MAP and MA were assessed by examining the difference between the potential force produced by the CCM and the potential force transmitted to the dactyl tip.

This was done by making interspecific comparisons of the ability of a claw to generate (physiological cross-sectional area, PCSA) and transmit (force potential estimate) force. PCSA was calculated from equation 3 as  $A \sin 2\alpha$ . Force potential estimate (FPE) was calculated assuming no friction as equation 3 times MA, or:

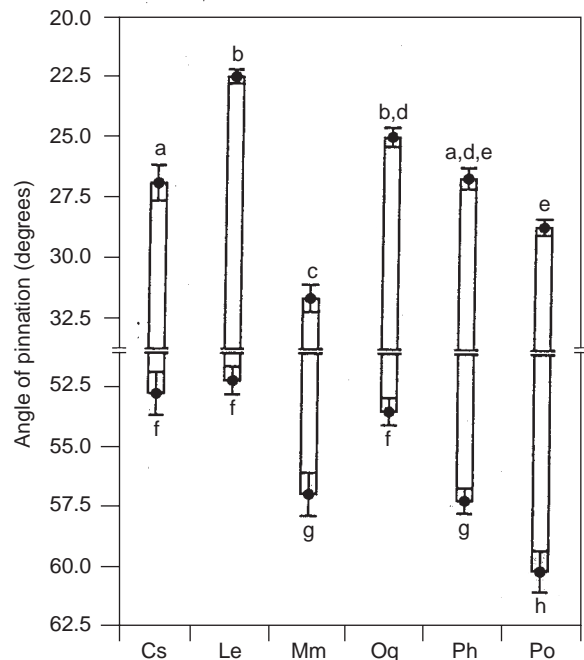
$$(A \sigma \sin 2\alpha) \text{ MA.} \quad (4)$$

All statistical analyses were performed with JMP version 3.1.5 software.

## RESULTS

### Morphology underlying force production

Crusher mean angle of pinnation (MAP) did not vary with body size ( $r^2 < 0.25$  and  $P > 0.05$  for all species), and one way ANOVA indicated a significant difference among species for open claws ( $F = 17.37$ ,  $P < 0.0001$ ; Fig. 4). *Post-hoc* comparisons for open crusher MAP ( $P = 0.05$ ) indicated that *M. mercenaria* had the largest MAP. *Panopeus obesus*, *P. herbstii*, and *C. sapidus* had the next largest MAPs, though *C. sapidus* did not differ



**Fig. 4.** Mean angle of pinnation (MAP) for chela closer muscles (CCMs) in opened and closed crusher claws. The smaller angles indicate mean angles for open claws, and the larger angles indicate mean angles for closed claws. Boxes connecting opened and closed means indicate that species range in CCM pinnation angle. Data points sharing a letter are not significantly different from one another. Cs, *Callinectes sapidus*; Le, *Libinia emarginata*; Mm, *Menippe mercenaria*; Oq, *Ocypode quadrata*; Ph, *Panopeus herbstii*; Po, *Panopeus obesus*. Data shown for *L. emarginata* are for left-hand claws.

**Table 2.** Closer apodeme allometry for crushers and cutters in all species. Results for a regression of  $\log_{10}$  apodeme area ( $\text{mm}^2$ ) regressed against  $\log_{10}$  carapace width (mm). Slope and intercept values given  $\pm$  standard error (SE)

Crab Species	Claw	Slope	Intercept	$r^2$	$n$
<i>Callinectes sapidus</i>	Crusher	$2.92 \pm 0.11$	$-3.68 \pm 0.22$	0.96	30
	Cutter	$2.61 \pm 0.15$	$-3.23 \pm 0.29$	0.92	30
<i>Libinia emarginata</i> <sup>a</sup>	Crusher	$4.68 \pm 1.44$	$-6.24 \pm 2.50$	0.68	7
	Cutter	$4.70 \pm 1.45$	$-6.27 \pm 2.52$	0.68	7
<i>Ocypode quadrata</i>	Crusher	$2.18 \pm 0.26$	$-1.46 \pm 0.41$	0.82	17
	Cutter	$3.21 \pm 0.26$	$-3.44 \pm 0.40$	0.92	16
<i>Menippe mercenaria</i>	Crusher	$2.30 \pm 0.09$	$-1.60 \pm 0.16$	0.96	29
	Cutter	$2.48 \pm 0.08$	$-2.31 \pm 0.14$	0.98	29
<i>Panopeus herbstii</i>	Crusher	$1.73 \pm 0.16$	$-0.56 \pm 0.25$	0.92	12
	Cutter	$3.00 \pm 0.30$	$-3.00 \pm 0.44$	0.91	12
<i>Panopeus obesus</i>	Crusher	$2.02 \pm 0.08$	$-1.08 \pm 0.12$	0.97	20
	Cutter	$2.82 \pm 0.15$	$-2.73 \pm 0.24$	0.95	20

<sup>a</sup> For *L. emarginata*, data shown are for left chela = crusher and right chela = cutter.

**Table 3.** Closer force generation potential for crushers. Results for a regression of  $\log_{10}$  physiological cross-sectional area ( $\text{mm}^2$ ) against  $\log_{10}$  carapace width (mm). Physiological cross-sectional area is defined as  $A \sin 2\alpha$ , where  $A$  is the apodeme area and  $\alpha$  is angle of pinnation. Slope and intercept values given  $\pm$  standard error (SE)

Crab species	Slope	Intercept	$r^2$	$n$
<i>Callinectes sapidus</i>	$3.03 \pm 0.12$	$-4.00 \pm 0.23$	0.96	28
<i>Libinia emarginata</i> <sup>a</sup>	$4.57 \pm 1.40$	$-6.18 \pm 2.44$	0.68	7
<i>Ocypode quadrata</i>	$3.34 \pm 0.41$	$-3.33 \pm 0.64$	0.82	17
<i>Menippe mercenaria</i>	$2.27 \pm 0.11$	$-1.61 \pm 0.19$	0.94	29
<i>Panopeus herbstii</i>	$1.68 \pm 0.18$	$-0.54 \pm 0.28$	0.89	12
<i>Panopeus obesus</i>	$1.93 \pm 0.10$	$-1.02 \pm 0.17$	0.93	20

<sup>a</sup> For *L. emarginata*, data shown are for 'left' chelae.

significantly from *O. quadrata* and *P. herbstii* did not differ significantly from *O. quadrata* and *L. emarginata*. *Post-hoc* comparisons for closed crusher MAP ( $P=0.05$ ) indicated that the three xanthids had the largest MAPs, followed by the three non-xanthids (Fig. 4). Opened to closed angle of pinnation varied significantly among species ( $F=10.33$ ,  $P<0.0001$ ). *Post-hoc* tests of angle range ( $P=0.05$ ) indicated that largest angle ranges occurred in the two *Panopeus* species and *L. emarginata*, and the smallest ranges occurred in *C. sapidus* and *M. mercenaria*. It should be noted that although magnitude of angle range was similar in some species, actual angle ranges did not necessarily overlap. For example, both *M. mercenaria* and *C. sapidus* had total angle ranges of  $c. 25^\circ$ , but *M. mercenaria* ranged from  $c. 32^\circ$  to  $57^\circ$ , while *C. sapidus* ranged from  $c. 27^\circ$  to  $52^\circ$ . The mean range of all species included a  $45^\circ$  angle of pinnation (Fig. 4).

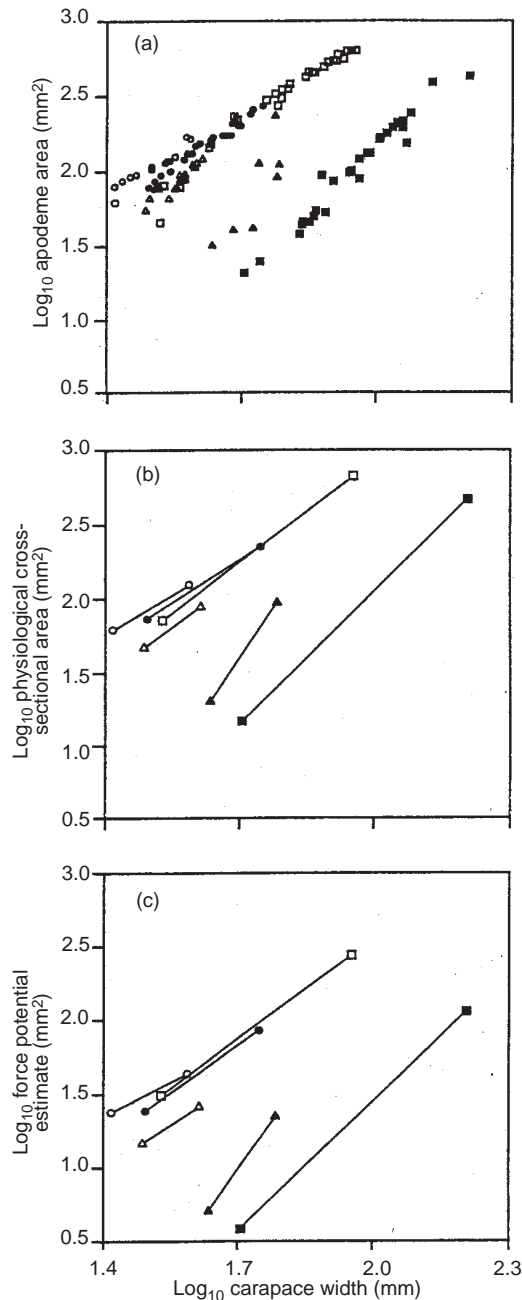
$\log_{10}$ -transformed crusher apodeme area was regressed against  $\log_{10}$ -transformed body size (carapace width) for all species (Fig. 5a, Table 2), and these regressions were compared by ANCOVA. Interspecific

crusher comparisons could not be made, as slopes were not homogeneous and no combination of species produced homogeneous slopes ( $P<0.05$  for ANCOVA interaction in all). However, PCSA was calculated ( $A \sin 2\alpha$  from equation 3),  $\log_{10}$ -transformed, and regressed against  $\log_{10}$ -transformed carapace width (Fig. 5b), as plots of PCSA against body size were similar to plots of apodeme area against body size (Fig. 5a,b), and produced homogeneous slopes for the three xanthids and the three non-xanthids, respectively ( $P=0.21$  and  $P=0.08$ , respectively; Fig. 5b). While members of these two groups could not be compared directly, the xanthid group does appear to have larger PCSAs than the non-xanthid group (Fig. 5a). Differences did not exist among the xanthid crab PCSAs ( $P=0.08$ ), but did among the non-xanthids ( $P<0.0001$ ). *Post-hoc* multiple comparisons for non-xanthids indicated that *O. quadrata* had the largest PCSAs, followed by *L. emarginata* and *C. sapidus* in order ( $P<0.0001$  for all three comparisons) (Table 3).

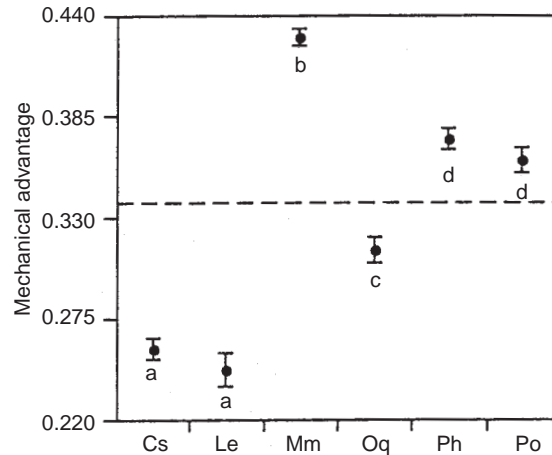
### Morphology underlying force transmission

Crusher mean MA did not vary with body size ( $r^2<0.25$  and  $P>0.05$  for all species), and one way ANOVA indicated a significant difference among species ( $F=106.56$ ,  $P<0.0001$ ; Fig. 6). *Post-hoc* pairwise comparisons for crusher MA ( $P=0.05$ ) indicated that *M. mercenaria* had a significantly higher mean MA than any other species. The two *Panopeus* species were next highest, followed by *O. quadrata*, and then by *C. sapidus* and *L. emarginata*.

The potential maximum forces generated (FPE) at the crusher tip were calculated ( $\text{PCSA} \times \text{MA}$ ),  $\log_{10}$ -transformed, and plotted against body size (Fig. 5c). Forces generated at dactyl tips were lower than forces generated by CCMs (Fig. 5b,c). As the three xanthid crabs had significantly higher MAs than the three non-xanthid crabs, they seem to experience a smaller



**Fig. 5.** Least squares linear regression of: (a)  $\log_{10}$ -transformed apodeme area ( $\text{mm}^2$ ); (b)  $\log_{10}$ -transformed crusher claw closer muscle physiological cross-sectional area (PCSA)( $\text{mm}^2$ ); (c)  $\log_{10}$ -transformed crusher claw force potential estimate (FPE) ( $\text{mm}^2$ ) against  $\log_{10}$ -transformed carapace width (mm) for crushers in all six species examined. PCSA was calculated from  $\text{PCSA} = A \sin 2\alpha$ , where  $A$  is apodeme surface area and  $\alpha$  is closer muscle mean angle of pinnation stretched for each crusher claw. FPE was calculated by multiplying PCSA and mechanical advantage (MA). Regression lines in (b) and (c) span only the actual size range examined for each species. Filled squares, *Callinectes sapidus*; open squares, *Menippe mercenaria*; filled circles, *Panopeus obesus*; open circles, *Panopeus herbstii*; filled triangles, *Libinia emarginata*; open triangles, *Ocypode quadrata*. Data for *L. emarginata* are from left-hand claws.



**Fig. 6.** Mean mechanical advantage (MA) for crusher claws. Means sharing a letter in common are not significantly different from one another. Cs, *Callinectes sapidus*; Le, *Libinia emarginata*; Mm, *Menippe mercenaria*; Oq, *Ocypode quadrata*; Ph, *Panopeus herbstii*; Po, *Panopeus obesus*. Data shown for *L. emarginata* are for left-hand claws.

difference between force generated (Fig. 5b) and force transmitted (Fig. 5c) than the three non-xanthids.

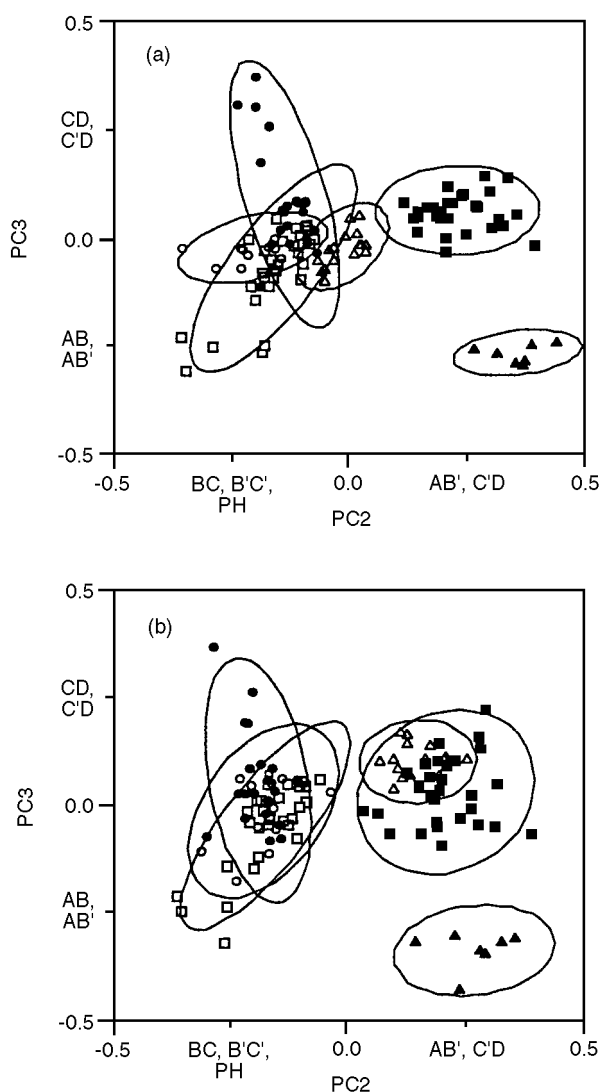
#### Claw shape and asymmetry

Following a PCA of external crusher morphology, PC2 and PC3 were plotted against one another (Fig. 7a) to determine how the six species differed in claw shape. The three xanthid species grouped together, having relatively larger prodopus heights (PH) and in-lever (BC) lengths than the three non-xanthids. *Ocypode quadrata* crushers seem to group with the three xanthids, but the 95% density ellipse is located near the centre of both PC axes. The left claws of *L. emarginata* and the crushers of *C. sapidus* formed separate groups, both having longer claws (AB, AB') than the other four species, but with *C. sapidus* having a longer pollex (CD, C'D) and relatively shorter claws (AB, AB') than *L. emarginata*.

PCA results for cutters produced a PC plot similar to the crusher PC plot (Fig. 7). PC axes 2 and 3 were defined by the same variables as in the crusher PCA, and five of the six species were distributed in PC space in the same manner as in the crusher PC plot. Only *O. quadrata* grouped differently, exhibiting relatively long prodopus (AB') and pollex (CD, C'D) measurements like *C. sapidus* (Fig. 7b).

Intraspecific comparisons of apodeme area indicated that crushers and cutters had homogenous slopes for all species except *P. herbstii* and *P. obesus* ( $P > 0.05$  in all crabs except *Panopeus* species where  $P < 0.05$ ). In *M. mercenaria*, *C. sapidus*, and *O. quadrata* crushers had significantly larger apodemes than did cutters ( $P < 0.0001$  for all), while left and right claws of *L. emarginata* exhibited no difference in CCM apodeme





**Fig. 7.** Principal component (PC) plots from PC analysis on  $\log_{10}$ -transformed external morphological data for: (a) crusher claws; (b) cutter claws. Axes are PC 2 and PC 3, and letters along the ends of each axis indicate which linear variable(s) contribute(s) most strongly to defining the particular end of that PC axis. All variables had correlation values  $\geq 0.30$ . Lines indicate 95% density ellipses. Filled squares, *Callinectes sapidus*; open squares, *Menippe mercenaria*; filled circles, *Panopeus obesus*; open circles, *Panopeus herbstii*; filled triangles, *Libinia emarginata*; open triangles, *Ocypode quadrata*. Data for *L. emarginata* are from left-hand claws in (a) and from right-hand claws in (b).

size ( $P=0.96$ ). Claws of *P. herbstii* and *P. obesus* were compared using a Wilcoxon–Kruskal–Wallis rank sums test, and both species exhibited significantly larger CCM apodeme areas in crushers (*P. herbstii*,  $\chi^2 = 10.7$ , d.f. = 1,  $P=0.0011$ ; *P. obesus*,  $\chi^2 = 17.3$ , d.f. = 1,  $P < 0.0001$ ).

The three xanthids exhibited highly significant differences between crusher and cutter MAP ( $P < 0.0001$ ), while *C. sapidus* exhibited a significant difference ( $P=0.01$ ) and *O. quadrata* and *L. emarginata* showed

no dimorphism in MAP (Table 4). In all crabs, MA and MAP were larger in crushers than in cutters. All species examined exhibited highly significant differences ( $P < 0.0001$ ) between the crusher and cutter in MA except *L. emarginata* (Table 5).

MANOVAs performed on external morphological data for each species indicated shape dimorphism in five of the six species, with only *L. emarginata* ( $P=0.6$ ) possessing monomorphic claws (Fig. 8b, Table 6). Relatively long in-levers (BC, B'C') and tall claws (PH) generally defined crushers, while cutters frequently had a long pollex (CD, C'D) and long dactyl (BX, B'X) (Fig. 8), though PC plots indicated some variation in which variables defined the various dimorphisms. *Callinectes sapidus* crushers were defined primarily by long in-levers (BC, B'C'), while cutter claws were defined primarily by a wide prodopos–carpus articulation gap (AE) and shorter in-levers (BC, B'C') (Fig. 8a). *Menippe mercenaria* crushers were defined primarily by large in-levers (BC, B'C') and tall claws (PH), while cutters had a long pollex (CD, C'D) and dactyl (B'X) (Fig. 8c). *Ocypode quadrata* crushers were long, tall, relatively wide claws (AB, AB', PH, PW) with long in-levers (BC, B'C'), while cutters were typically shorter in height, length, and width, with a longer pollex (CD, C'D) and dactyl (BX, B'X) (Fig. 8d). *Panopeus obesus* crushers generally were tall claws (PH) with long in-levers (BC, B'C'), while cutters were longer (AB, AB') with a long dactyl (BX, B'X) and a wide prodopos–carpus articulation gap (AE) (Fig. 8e). *Panopeus herbstii* crushers were generally long from dorsal articulation to pivot point (AB, AB') and tall (PH) with large in-levers (BC, B'C'), while cutters had a long pollex (CD, C'D) and were longer from ventral articulation to pollex tip (DE) (Fig. 8f).

## DISCUSSION

Examination of CCM morphology in six crab species revealed that the three xanthid crabs had significantly larger open claw MAPs and larger CCM cross-sectional areas than the other crabs examined (Figs 4 & 5), and all six crab species have angle of pinnation ranges that include  $45^\circ$  (Fig. 4). External claw measurements indicated that, as with MAP, the three xanthid crabs exhibited the largest mean MAs at the dactyl tip (BC, Fig. 2). Crusher and cutter claws segregated in PC space according to species, and crushers of a given species were generally similar in shape to their respective cutters, except for *O. quadrata* (Fig. 7). In addition, the five dimorphic species exhibited a crusher–cutter asymmetry that was defined largely by tall crushers with long in-levers, and cutters with long out-levers (Fig. 8).

### Interspecific variation in claw strength

Several aspects of claw morphology could potentially be modified during evolution to produce stronger claws. A

**Table 4.** Results for *t*-tests on asymmetry of mean angle of pinnation (MAP). All *t*-tests were performed against claw type<sup>a</sup> (crusher or cutter) for each species. Significant *P*-values ( $P < 0.05$ ) indicate a significant difference between crushers and cutters. Values for crusher and cutter MAP are given as means  $\pm$  standard error (SE)

Crab species	Open crusher MAP	Open cutter MAP	MAP <i>t</i> -value	d.f.	MAP <i>P</i> -value
<i>Callinectes sapidus</i>	27.0 $\pm$ 0.8	24.3 $\pm$ 0.6	2.66	55	0.01
<i>Libinia emarginata</i> <sup>a</sup>	22.6 $\pm$ 0.4	22.6 $\pm$ 0.5	0.08	12	0.94
<i>Ocypode quadrata</i>	25.1 $\pm$ 0.5	24.3 $\pm$ 0.6	1.10	31	0.28
<i>Menippe mercenaria</i>	31.8 $\pm$ 0.6	25.6 $\pm$ 0.5	7.88	55	< 0.0001
<i>Panopeus herbstii</i>	26.8 $\pm$ 0.5	21.2 $\pm$ 0.4	9.08	22	< 0.0001
<i>Panopeus obesus</i>	28.8 $\pm$ 0.4	21.3 $\pm$ 0.3	13.82	38	< 0.0001

<sup>a</sup>For *L. emarginata* claw type is defined as 'left' and 'right'.

**Table 5.** Results for *t*-tests on asymmetry of mean mechanical advantage (MA). All *t*-tests were performed against claw type<sup>a</sup> (crusher or cutter) for each species. Significant *P*-values ( $P < 0.05$ ) indicate a significant difference between crushers and cutters. Values for crusher and cutter MA are given as means  $\pm$  standard error (SE)

Crab species	Crusher MA	Cutter MA	MA <i>t</i> -value	d.f.	MA <i>P</i> -value
<i>Callinectes sapidus</i>	0.259 $\pm$ 0.006	0.192 $\pm$ 0.005	8.32	58	< 0.0001
<i>Libinia emarginata</i> <sup>a</sup>	0.248 $\pm$ 0.010	0.231 $\pm$ 0.013	1.02	12	0.33
<i>Ocypode quadrata</i>	0.312 $\pm$ 0.008	0.166 $\pm$ 0.003	17.08	31	< 0.0001
<i>Menippe mercenaria</i>	0.428 $\pm$ 0.005	0.329 $\pm$ 0.003	15.56	57	< 0.0001
<i>Panopeus herbstii</i>	0.372 $\pm$ 0.006	0.260 $\pm$ 0.007	12.53	22	< 0.0001
<i>Panopeus obesus</i>	0.361 $\pm$ 0.008	0.303 $\pm$ 0.006	6.02	38	< 0.0001

<sup>a</sup> For *L. emarginata* claw type is defined as 'left' and 'right'.

**Table 6.** Results for external asymmetry multivariate analyses of variance (MANOVA). All external measurements were examined by MANOVA against claw type<sup>a</sup> (crusher or cutter) for each species. Significant *P*-values ( $P < 0.05$ ) indicate a difference between crushers and cutters in at least one external dimension.

Crab species	Wilks'			
	lambda	<i>F</i> -value	d.f.	<i>P</i> -value
<i>Callinectes sapidus</i>	0.091	9.9	22, 94	< 0.0001
<i>Libinia emarginata</i> <sup>a</sup>	0.007	1.0	22, 2	0.61
<i>Ocypode quadrata</i>	0.016	12.7	22, 40	< 0.0001
<i>Menippe mercenaria</i>	0.026	21.7	22, 92	< 0.0001
<i>Panopeus herbstii</i>	0.010	9.2	22, 22	< 0.0001
<i>Panopeus obesus</i>	0.007	26.4	22, 54	< 0.0001

<sup>a</sup> For *L. emarginata* claw type is defined as 'left' and 'right'.

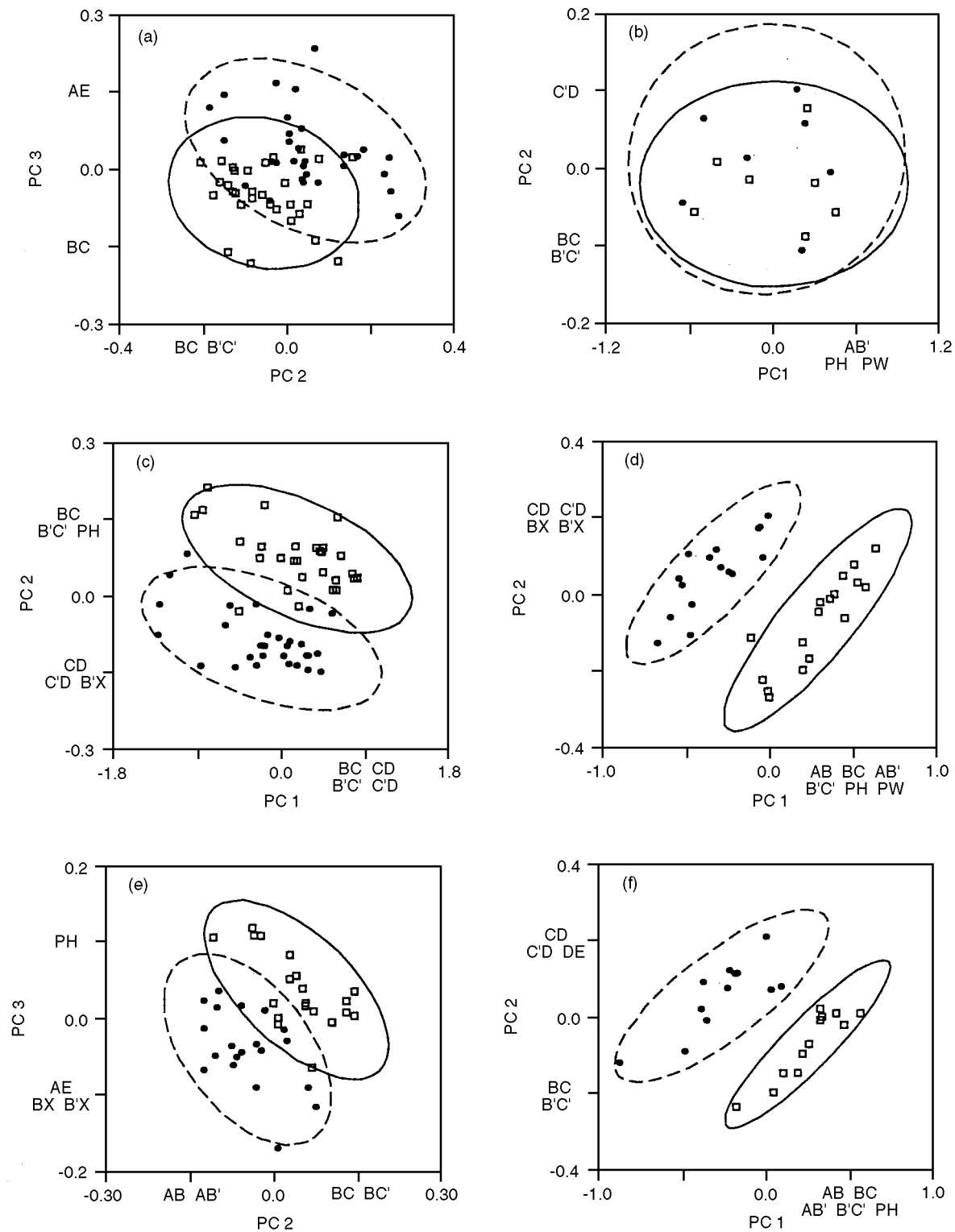
main goal of this study was to determine to what degree these variables (muscle cross-sectional area (apodeme area), MAP, and MA) have been modified. The effect of each variable on claw force generation can be estimated by considering the interspecific range of its effect on equation 4 (i.e.  $MA \times \text{apodeme area} \times \sin 2\alpha$ ).

In crushers, the largest apodemes (*M. mercenaria*) were 6.3-fold larger than the smallest apodemes (*C. sapidus*). The apodeme area range was considerably greater than the differential effects on claw force generation of the largest and smallest MAs (a 2.2-fold range) and the largest and smallest MAPs (1.4-fold range in values of  $\sin 2\alpha$ ). This suggests that most of the interspecific variation seen in claw strength is a function of

CCM cross-sectional area. Besides having a small interspecific range for open claw MAP, the crushers of all crabs examined include 41–45° in their CCM range of fibre angles (Fig. 4). This means that, in theory, all six species can modulate their angle of pinnation to gain the maximum effect on force production, further reducing the overall contribution of MAP to interspecific variation in force generation.

### Morphology underlying force production

The largest open crusher MAPs were observed in the xanthid crabs (Fig. 4), which consume the largest variety and amount of molluscan prey. This suggests a potential relationship between diet and claw morphology, and observed claw morphology could be a product of selection for molluscivory (i.e. for 'stronger' claws). All crabs do not exhibit the same ranges in pinnation angle, though, and it is worth noting that while *M. mercenaria* and *C. sapidus* exhibit a smaller absolute angle range than the other species, their range spans are not identical (Fig. 4). The *M. mercenaria* open CCM begins closer to 45° than does that of *C. sapidus*, suggesting that *M. mercenaria* is stronger than *C. sapidus* through a wider range of claw gapes and at larger percentages of maximum gape. A similar pattern can be seen in the angle ranges of the other crabs (Fig. 4). This suggests that while open claw MAP may not contribute greatly to interspecific differences in claw strength, range of pinnation angle may be important in the execution of molluscivorous behaviour.



**Fig. 8.** Principal component (PC) plots for PC analysis on  $\log_{10}$ -transformed external morphological data for each species examined, indicating claw dimorphisms. PC axes were selected based on which axes provided the best visual separation of crusher (open square) and cutter (filled circle) claws. The letters along the ends of each axis indicate which linear variable(s) contribute(s) most strongly to defining the particular end of that PC axis. All variables had correlation values  $\geq 0.30$ . Lines indicate 95% density ellipses. (a) *Callinectes sapidus*; (b) *Libinia emarginata*; (c) *Menippe mercenaria*; (d) *Ocypode quadrata*; (e) *Panopeus obesus*; (f) *Panopeus herbstii*. Data for *L. emarginata* are from left-hand (open square) and right-hand (closed circle) claws.

Blundon (1988) previously reported that MAP for *M. mercenaria* cutters is *c.* 24° in all claws, while crusher MAP increases from *c.* 25° in small claws to *c.* 35° in larger claws (Blundon, 1988). While both we and Blundon found high MAP for *M. mercenaria* crushers, our results showed no discernible relationship between crusher MAP and body size. Blundon's measurements of MAP were taken from claws fixed with a constant dactyl–pollex gape. Because gape distance was constant, smaller claws were probably fixed with the dactyl at a larger angle. A larger open angle would lead to greater stretching of the muscle fibres, which would lead to smaller MAP measurements in smaller crabs.

Comparisons of crusher apodeme area suggest that the three xanthid crabs have similar-sized apodemes and the largest apodemes overall (Fig. 5a). However, all six species vary greatly in body size (Table 1). Although *C. sapidus* seems to have the smallest apodeme area and PCSA, it attains a larger size than any crab here except *M. mercenaria*. *Callinectes sapidus* has absolute apodeme areas larger than most of the crabs examined (Fig. 5a) and hence the potential to produce larger absolute crushing forces than most of the other crabs (Fig. 5b, c), as does *M. mercenaria*.

### Morphology underlying force transmission

Only two crab species examined here have been subjects of previous work dealing explicitly with MA: *M. mercenaria* (Brown *et al.*, 1979; Blundon, 1988) and *C. sapidus* (Brown *et al.*, 1979; Blundon & Kennedy, 1982; Govind & Blundon, 1985; Seed & Hughes, 1997). Our values for MA (Table 5) fall within the range of those previously reported for both *M. mercenaria* crushers (0.384–0.503) and cutters (0.298–0.364), as well as for *C. sapidus* crushers (0.230–0.293) and cutters (0.171–0.232).

The out-lever measurement used in calculating MA is the distance from pivot-to-tip on the dactyl (BX, Fig. 2) because this is the only morphologically homologous measurement across species. Crushing forces are generally applied at the base of the dactyl, and it has been shown that MAs near the dactyl base approach one, even if MA at the dactyl tip is small (e.g. Vermeij, 1977). The largest dactyl-tip MAs we observed were in the three xanthid species (Fig. 6). Although MA at the dactyl base is probably similar for all species, and although interspecific variation in dactyl-tip MA is small compared to CCM cross-sectional area (see above), the significant differences observed in dactyl-tip MA are suggestive of a relationship between diet and claw design.

Consider the fact that *O. quadrata* has a larger MA than *C. sapidus* at the claw tip. *Callinectes sapidus* is known to take more elusive prey than the other crabs examined, so its long BX measurements and lower overall MA may be the product of selection for faster claws. It is probable, however, that *C. sapidus* and *O. quadrata* have similar MAs at their respective

crushing surfaces, which are molariform in *C. sapidus* (Fig. 1a,d). Basal molariform dentition, then, might allow *C. sapidus* to retain efficient force transmission at the crushing surface in an otherwise fast claw. On the other hand, the three xanthids may transmit crushing forces with the same efficiency as *C. sapidus* at the primary crushing surfaces, but have overall larger MAs. Hence, the xanthids transmit forces more efficiently throughout the full dactyl length, potentially allowing them to attack larger molluscs more efficiently. The fact that *P. herbstii* is known to handle oyster prey more efficiently than similar-sized *C. sapidus* (Bisker & Castagna, 1987) supports this idea.

### Intraspecific claw dimorphism

The basic elements of claw dimorphism are consistent with an asymmetry based on a force–speed trade-off. Tall crushers (PH) with long in-levers (BC, B'C') have larger apodeme areas and MAs. Shorter cutters with long dactyls and polices (CD, C'D) have smaller apodeme areas and MAs. In general, intraspecific differences in the elements of dimorphism were consistent for all five dimorphic species (Fig. 8, Tables 4 & 5), though other interesting patterns do emerge.

The dimorphism in *C. sapidus* claw shape is defined primarily by crushers with larger in-levers and cutters with larger carpus–prodopus gaps (AE) (Fig. 8a). Prodopus height (PH) can be related to apodeme size and has been used as a proxy for claw strength (Lee, 1993). As the carpus–prodopus gap is not always in the same plane as prodopus height, it is not intuitively related to apodeme size. We see no *a priori* reason to expect weak or fast claws to have a large AE measurement. As this dimension defines the carpus–prodopus joint, it could be related to whole cheliped force–speed dimorphism, or may be a non-functional difference in crushers and cutters.

*Ocypode quadrata* is the only dimorphic species examined with crushers and cutters occupying different areas of interspecific PC space (Fig. 7). It is also the only species to exhibit no MAP dimorphism (Table 4). That the cutters of *O. quadrata* are similar to those of *C. sapidus* and its crushers similar to those of the xanthids certainly suggests a dimorphism related to strength and speed. However, every other dimorphic species examined possesses cutters and crushers of relatively similar shape (Fig. 7). This stark difference suggests that although the dimorphism may be related to force generation, other factors have probably shaped the dimorphism of this crab. The most striking claw dimorphism seen in any crab occurs in males of the genus *Uca* (see Weissburg, 1991; Levinton *et al.*, 1995; Rosenberg, 1997) which, like *O. quadrata*, is a member of family Ocypodidae. As the *Uca* dimorphism has been attributed to sexual selection, the stark dimorphism in *O. quadrata* may not be merely the product of a strength–speed trade-off, but a product of other evolutionary factors, including sexual selection.

### Consequences of morphology

In showing a relationship between large claws and success in mating and agonistic interactions, Lee & Seed (1992) identified claw height (PH here) as one important size variable. Tall claws are likely to have tall CCM apodemes with large apodeme surface areas, and as pointed out above, large apodeme area translates into large PCSA, regardless of MAP, and thus large force-generating ability. Data such as those of Lee and Seed suggest that claws could increase in size independently of selection for increased force generation, so large claw size alone does not indicate a linkage between claw design and selection for increased force generation. Other elements of claw design need to be examined to determine whether or not their patterns of variation are consistent with increased force production. As claw strength increases with increasing MAP, it is one such element. The physiological component ( $\sigma$ ), though not examined here, is another.

Most crushing of hard prey occurs at the dactyl base where MA approaches one. In describing patterns of claw dentition and occlusive geometry in five decapod crustacean species, Brown *et al.* (1979) identified 'specialized occlusive regions' in all claws examined. It is known that many crabs use tactics other than crushing (e.g. chipping and peeling) when attacking shelled prey. If regional occlusive differences translate into functional differences related to non-crushing feeding behaviours, large MA might be ecologically important throughout the length of the dactyl.

### Morphological evolution

The crabs in this study consuming the largest percentage and varieties of hard prey also exhibit the strongest claw morphologies, indicating possible selection for strong claws in these crabs. The idea that an animal's ability to produce force predicts its ability to consume hard prey is not a novel one, and has been applied to other durophagous animals, such as labrid fishes (Wainwright, 1988). It should be noted that the three xanthid crabs (i.e. the 'strongest' crabs) are almost certainly the most closely related of the species examined, and their similar design can be seen as a phylogenetic constraint, not independent examples of specialization for force generation. However, these xanthids illustrate how selection for increased force generation related to molluscivory may have played an important role in shaping the claws of a particular family. Further, comparisons of xanthid morphology to that of other potentially molluscivorous crab species with robust claws (e.g. the portunid *Scylla serrata* and the parthenopid *Daldorfia horrida*) could make a stronger case for the importance of diet (especially molluscivory) in shaping the claw design of individual species.

Morphological differences in the claws of dimorphic crabs suggest that the dimorphism may be related to a functional trade-off between force generation and

speed, and selection to compensate for this trade-off. In all five dimorphic crabs, crushers were generally taller than cutters and possessed higher MAs.

*Callinectes sapidus* and *O. quadrata* clearly possess morphological designs suggestive of functions other than force production. Long dactyls and low MAs in *C. sapidus* are suggestive of selection for fast claws. *Ocypode quadrata* exhibits a very strong claw dimorphism that may represent extreme strength-speed differentiation, but could also be a product of selection related to sexual and agonistic display. This latter notion is reinforced by the absence of dimorphic dentition observed in the other dimorphic crabs.

Force distribution (as indicated by dentition and occlusive geometry) was not considered in this study. It has been shown that patterns of dentition and occlusion determine the stress that a given claw can exert (Brown *et al.*, 1979). While dentition and occlusion have been considered in the literature (e.g. M. J. Williams, 1978; Juanes & Hartwick, 1990; Yamada & Boulding, 1998), they have generally not received a quantitative treatment. Yet shell failure should ultimately be determined by the stress produced, not simply the force. Interspecific variation in force production morphology seems to suggest that *M. mercenaria* is proportionally no stronger than the other two xanthids, and that *O. quadrata* and *L. emarginata* are both proportionally stronger than *C. sapidus*. Dietary evidence, however, indicates that *M. mercenaria* takes a much wider range of hard prey than any of the other crabs considered here, and *C. sapidus* takes more and harder molluscan prey than either *L. emarginata* or *O. quadrata*. Besides differing from the other crabs in body size, *M. mercenaria* and *C. sapidus* seem to differ from the other crabs in dentition, which could modify the effectiveness of their crushing attacks. In this way, our study suggests that the relationship between diet, force generation ability, and claw evolution cannot be fully understood without considering force distribution quantitatively as well as qualitatively (Hughes, 1989; Hughes & Elner, 1989).

Of the three factors examined here that determine claw strength (apodeme area, MAP, and MA), apodeme area is primarily responsible for producing the interspecific variation in claw strength, and though significant variation exists in both MA and MAP, the overall strength variation explained by these variables is small in comparison to that explained by CCM cross-sectional area. This is especially clear in light of the fact that the MA of all species examined should approach one near the dactyl base, and the pinnation angle range for all species includes 45°.

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