Pronounced heterochely in the ghost shrimp, *Neotrypaea californiensis* (Decapoda: Thalassinidea: Callianassidae): allometry, inferred function and development

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(With 1 plate and 6 figures in the text)

To understand their function and ontogeny better, we conducted a morphometric analysis of claw size and shape variation in the strikingly heterochelous, north-eastern Pacific ghost shrimp, *Neotrypaea* (formerly *Callianassa*) *californiensis*. Master claws approached 25% of total body weight in mature males, but rarely exceeded 10% in females. Minor claws were less than 3% of body weight in both sexes. The proportions of right and left master claws did not differ significantly from 50:50. Males exhibited a greater positive allometry than females in both master and minor claw size, though master claws differed more than minor claws. Sexual dimorphism was also observed in master but not minor claw shape: compared to females, mature male master claws: a) were proportionally higher relative to their length; b) exhibited a deeper propodal notch and consequently a larger gape; c) developed a more slender and more distally hooked dactyl; and d) exhibited more well-developed teeth about the periphery of the claw gape.

The shape of the conspicuous gape in mature male master claws bore a close resemblance to the cross-section of similar-sized master claws. The shape of this gape, and the presence of fine teeth about its periphery, strongly suggests that master claws function in a highly stereotyped form of grappling during agonistic encounters or perhaps during mating between similar-sized conspecifics. In addition, a landmark morphometric analysis of relative growth suggested that the pronounced propodal notch develops via localized deformations near the base of the fixed finger rather than via a more generalized contraction of the ventral manus region. Finally, a preliminary survey suggests that the distinctive propodal notch, which may be diagnostic of the hypothesized grappling function, has evolved at least twice in the Callianassidae, once in the Callianassinae and once in the Callichirinae. Sexual selection may have significantly influenced the evolution of these unusual master claws.

Introduction

Incidence and adaptive significance of prominent heterochely

Hypertrophied claws in crustaceans are used primarily for feeding and defence, and simple mechanical principles tell us the form they should take to maximize speed or strength (Warner, 1977). Yet some claws are sufficiently unusual in form or magnitude of asymmetry that they must have evolved for some other primary function, such as mating, sexual signalling, or intra-sexual

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combat. Hence, prominent claw asymmetries may reveal a great deal about the interplay between sexual and natural selection. Furthermore, the sometimes peculiar shapes of these hypertrophied claws raise questions about how they arise developmentally.

Pronounced heterochely appears to have evolved several times in clades of otherwise bilaterally symmetrical decapod crustaceans. It can reach rather surprising proportions in brachyuran crabs (e.g. fiddler crabs, Ocypodidae) (Crane, 1975), lobsters (Astacidea) (Herrick, 1895), and various shrimp, including snapping and river shrimp (Caridea: Alpheidae, Paleomonidae) (Williams, 1965), and mud or ghost shrimp (Thalassinidea: Callianassidae, Ctenochelidae) (Biffar, 1971; Manning & Felder, 1991). For most of these groups, the function of the hypertrophied master claw is reasonably well understood. Male fiddler crabs use their claws to attract females or to combat other males for territory or mates (Crane, 1975; Hyatt & Salmon, 1978). Lobsters use them for crushing hard-shelled invertebrates (Elner & Campbell, 1981), or in intraspecific agonistic encounters (Douglis, 1946), while those in snapping shrimp may aid in territorial interactions (Nolan & Salmon, 1970). Curiously, even though the magnitude of claw asymmetry in many callianassid shrimp approaches that of the more widely studied fiddler crabs, snapping shrimp and lobsters, virtually nothing is known about how their hypertrophied and seemingly specialized master claws actually function. This lack of information is especially puzzling given the impressive variety of master-claw form within the family (Edmondson, 1944; Biffar, 1971; Manning & Felder, 1991).

Inferring function from form

Claw function is most easily determined by direct field or laboratory observations. The paucity of such information for callianassid shrimp no doubt results from their retiring, almost exclusively subterranean habit (Pohl, 1946). Even though they will construct artificial burrows in laboratory fossaria, observations in such a setting have yielded information mainly about feeding (MacGinitie, 1934; Devine, 1966; Dworschak, 1987a), respiratory (Torres, Gluch & Childress, 1977), or burrowing behaviour (Dworschak, 1983; Griffis & Chavez, 1988). The impressive master claws are thought to be used in aggressive interactions or mating (MacGinitie, 1934; Felder & Lovett, 1989), but direct observations of such behaviours are either lacking (Devine, 1966) or a potential artefact of unnatural forced encounters outside of burrows (Rowden & Jones, 1994). Although relative growth has been examined in other species [*Callianassa kraussi* (Forbes, 1977), *Callichirus major* (Rodrigues, 1985), *Lepidophthalmus louisianensis* (Felder & Lovett, 1989), *Callianassa subterranea* (Rowden & Jones, 1994)], these studies used relatively crude measures of claw size and shape, and hence shed little light on the details of master claw growth and use.

Detailed morphometric analyses can yield strong inferences about the function of particular structures, even where behavioural observations are impossible, as in extinct but well fossilized organisms (e.g. the toes and feathers in *Archaeopteryx* (Feduccia, 1993; Speakman & Thomson, 1994). We report the results of a morphometric study of relative claw growth in *Neotrypaea* (previously *Callianassa*) *californiensis* Dana (1854), whose master claws are unusual even by callianassid standards [relations within the Callianassidae have recently been revised, and we follow Manning & Felder's (1991) classification throughout]. These analyses lead to specific predictions about how their master claws may function and about the developmental processes that give rise to such a peculiar shape. They also set the stage for a more thorough understanding of the evolution of heterochely within the Thalassinidea.

Materials and methods

Thalassinidean biology and collection

Mud or ghost shrimp (Thalassinidea) are a distinctive, geographically widespread group that is heterogeneous both ecologically and morphologically. Fossils attributed to *Callianassa* (*sensu latu*) are known from the Mesozoic (Rathbun, 1926). Living species range in size from *Biffarius biformis*, which mature at 20 mm (Manning & Felder, 1991), to *Callichirus major* and *Neotrypaea gigas*, which can reach or exceed 150 mm body length (Pohl, 1946; Haig & Abbott, 1980). Some feed on decaying plant material, while others are deposit- or suspension-feeders (Griffis & Suchanek, 1991), but their conspicuous master claws appear to play only a minor role in feeding (Dworschak, 1987a).

Thalassinidean shrimp are almost exclusively fossorial. They can reach high densities in habitats that range from high intertidal mud flats to the margins of the continental shelf (Dworschak, 1987b), and their burrowing activities can have a major impact on sediment dynamics (Rowden, Jones & Morris, 1996). Burrow form appears to be related to mode of feeding (Suchanek, 1985; Griffis & Chavez, 1988), and ranges from simple U- or Y-shaped tubes to networks of tunnels with multiple branches or chambers that can exceed depths of 100 cm (Dworschak, 1983). Most burrows appear to be inhabited by only 1 or sometimes 2 shrimp at a time. Among callianassid species, only one (*Neotrypaea affinis*) has been confirmed to live in pairs (Dworschak, 1983), although MacGinitie (1934) has suggested that the burrows of *N. californiensis* interconnect.

Neotrypaea californiensis occurs along the west coast of North America from Alaska to lower California, and can reach great numbers on intertidal bottoms of mixed sand and mud in bays and estuaries (Haig & Abbott, 1980). Individuals of both sexes, ranging from 18 to 90 mm total length, were collected from a single intertidal population in a sandy beach on Fleming Island (48° 53′ N, 125° 08′ W), in Barkley Sound on the west coast of Vancouver Island, Canada. They were distinguished from a potential congener, *N. gigas*, based on diagnostic characteristics of the master claw (Kozloff, 1987). Samples were collected in August, 1994 by shovelling trenches in the substratum and capturing shrimp as they struggled to the surface of the collapsing sediment. Shrimp were transported to the laboratory alive and subsequently frozen. Sex was determined by examining the pleopods, 2 pairs of which occur on the anterior abdominal segments of females but not males. Wet-weights of intact individuals, as well as cephalothorax weight, abdomen weight, and weights of the master and minor chelipeds (all limb segments were included in cheliped weight) of disarticulated shrimp, were determined using a Mettler balance (BB240) accurate to 0.1 mg. To ensure a standard measure of live weight, shrimp frozen prior to weighing were corrected for small weight losses due to freezing (approx. 10%) by least-squares linear regression techniques.

Measurements

All body dimensions were measured along the dorsal midline of intact, straightened specimens whose pre-abdominal membranes had been folded inside the carapace: 1) total body length (tip of rostrum to tip of telson); 2) carapace length (tip of rostrum to posterior margin of carapace); 3) abdomen length (anterior margin of the first to the posterior margin of the last abdominal segment; this excluded both the broad membrane between the abdomen and carapace, and the telson); and 4) telson length (anterior to posterior margin). These measurements were taken with Brown and Sharp digital callipers (Digit-Cal, Model No. 599-571-3) accurate to 0.01 mm. Trunk sections and claws were then preserved in 70% ethanol.

Calibrated drawings were made at magnifications from 60–310× using a *camera lucida* attached to a Wild M7S microscope. Claws from different sexes and sizes of shrimp were drawn in random order, to avoid unconscious bias. Prior to drawing, claws were placed on a bed of spherical beads and positioned so that the dactyl was 50 to 75% open, and the maximum projected area of the propus was as close as possible perpendicular to the viewing angle. Landmarks were identified while the claw and drawing were still superimposed, and were later digitized using a Summagraphics digitizing tablet (20 dots per mm resolution) and the digitizing program MacMeasureII (ver. 2.33; available from A.R.P.). Landmarks were selected to
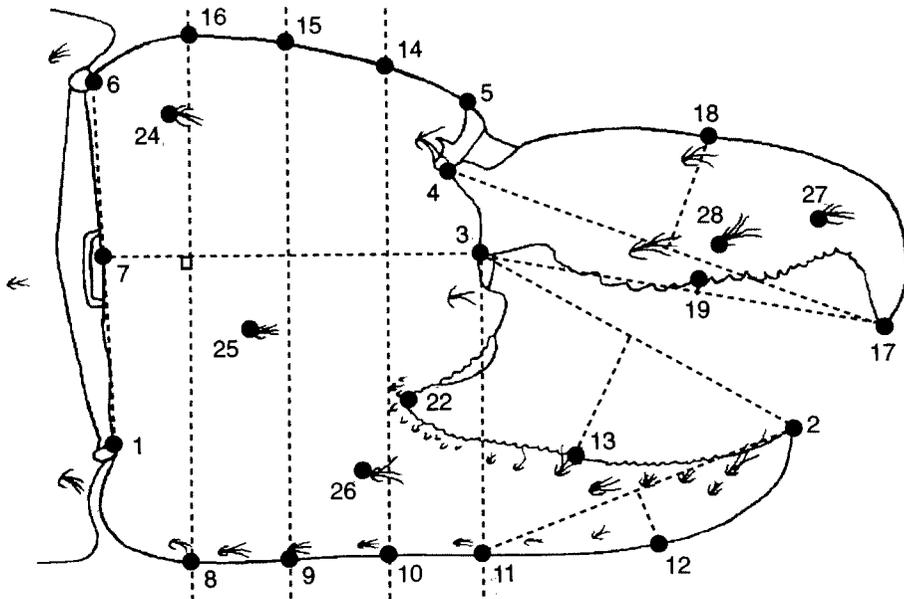
FIG. 1. Master claw of a mature male *Neotrypaea californiensis* (total body length 89 mm) illustrating the landmarks digitized on all claws. Most landmarks identified biologically well-defined (developmentally homologous) points, including hinge points (#1, #4, #6), intersections between the dactylar membrane and the propus margins (#3, #5), the tips of the propus and dactyl (#2, #17), the base of the propodal notch (#22), and the insertion points of several readily identifiable tufts of setae (#24–#28). Some were taken using others as a guide: landmark #7 is the midpoint between landmarks #1 and #6, landmarks #8 through #11 and #14 through #16 were defined by the intersection with the manus margin of lines drawn perpendicular to the midline of the manus (#3–#7) at 25% intervals, landmarks #12, #13, #18, and #19 were defined by the intersection with the manus or dactyl margin of lines drawn perpendicular to the midpoint of the lines connecting #2–#11, #2–#3, #3–#17, and #4–#17, respectively.

Claw dimensions were computed as Euclidean distances between pairs of landmarks: propus length (#1, #2), manus length (#3, #7), manus height (#9, #15), total dactyl length (#4, #17), dactyl lever length (#3, #4), mid-dactyl length (#4, #27; to avoid complications with curvature of the dactyl tip), mid-dactyl height (#18, #19), gape length (#2, #22). Angles were computed using three landmarks (the middle landmark was the vertex): propodal notch angle (#2, #22, #3), dactyl tip angle (#17, #27, #28). Mechanical advantage was computed as dactyl lever length/total dactyl length.

sample claw features as uniformly as possible, and claw dimensions used in subsequent analyses were computed from these landmarks (Fig. 1).

Statistical analyses

To estimate the combined error of drawing and digitizing, at least 10 master and minor claws of various sizes were drawn and digitized a second time. The average errors (S.D. of repeat measurements) were approximately 0.11 and 0.15 mm (generally < 2% for all but the smallest dimensions) for various dimensions of minor (N = 12) and master claws (N = 10), respectively. These values overestimate the measurement error of the remaining analyses because duplicate drawings were made of early, less reliable drawings. All subsequent analyses were conducted with the measurements from the more reliable duplicate drawings.

Allometric coefficients were computed as reduced major axis (RMA) regression coefficients from $\log_{10}$-transformed data. RMA slopes were calculated from ordinary least-squares linear regression slopes (OLS) by dividing the OLS slope by the correlation coefficient (LaBarbera, 1989). Allometric coefficients were

TABLE I

Incidence of right and left master claws in **Neotrypaea californiensis** and its dependence on sex or maturity. Maturity was assumed to occur at a total body length of 50 mm. All chi-square calculations were corrected for continuity (Sokal & Rohlf, 1981). The test for overall side bias was between observed and expected (24 right, 24 left)

	Side of master claw				
Sex/Maturity	Right	Left	Total	χ^2	P
Male					
Immature	9	7	16		
Mature	8	4	12	0.03	0.87
Total	17	11	28		
Female					
Immature	3	6	9		
Mature	8	3	11	1.76	0.19
Total	11	9	20		
Grand total	28	20	48		
		Male vs. Female		0.01	0.92
		Immature vs. Mature		1.49	0.22
		Overall Side Bias		1.02	0.31

compared between sexes and claw types with *t*-tests using standard errors of the OLS slopes. Where one or both OLS slopes were not significant statistically, however, valid P values could not be computed (McArdle, 1988). Statistical analyses were conducted with Statview II (ver. 1.03, Abacus Concepts), and landmark-morphometric analyses were conducted with Morphometrika (ver. 2.00, J. Walker).

Results

Heterochely frequencies

Males were more common in our samples than females, but we observed no significant difference in the frequencies of right or left master claws, either between the sexes, or between immature and mature individuals (Table I). In addition, although master claws occurred more commonly on the right side overall, this deviation from an expected frequency of 50 : 50 was not significant statistically.

Measures of overall body size

Even though the claws in *Neotrypaea californiensis* were sexually dimorphic (see below), we detected few differences between the sexes in measures of overall body size. Both carapace length and abdomen length increased isometrically with body length (regressions 1–4, **Appendix**). Although males exhibited a weak negative allometry for abdomen length (regression 3), this would not be significant statistically following a sequential Bonferroni adjustment for multiple tests (N = 4; Rice, 1989). Live weight exhibited a highly significant positive allometry relative to body length for males but not females, and the sexes differed significantly from each other (regressions 5, 6, **Appendix**). However, these differences were due entirely to the contribution of the claws, since trunk weight (live weight minus cheliped weight) varied isometrically with body length for both sexes (regressions 9, 10).

Although carapace length has often been used by others (Forbes, 1977; Felder & Lovett, 1989; Rowden & Jones, 1994), we used total body length to describe overall size in subsequent analyses for three reasons: 1) it varied isometrically relative to carapace length, abdomen length, telson length (data not shown), cephalothorax weight (with claws removed), and abdomen weight (regressions 1–10, **Appendix**), hence it provided as unbiased a measure of 'size' for subsequent analyses as any of these other traits; 2) it yielded a more precise prediction of live weight than did cephalothorax length ($r^2 = 0.992$ vs. 0.989; data not shown); and 3) it is an easier measure of 'size' to visualize than measures of weight or partial body length when presenting and interpreting results.

Variation in claw size

Allometry in claw weight differed markedly between claw types and between sexes (Fig. 2a; regressions 11–14, **Appendix**). Relative to body length, master claws were more positively allometric than minor claws for both sexes ($P < 0.001$ for both males and females), males were more positively allometric than females for both claw types ($P < 0.001$ for both master and minor claws), and all but female minor claws exhibited statistically significant positive allometry relative to body length. When expressed as a proportion of the body weight, however, only the master claws exhibited significant positive allometry (regressions 15–18, **Appendix**). As a consequence of their striking positive allometry, the master claw could contribute up to 25% of total body weight in large males (Fig. 2a). Master claw weights of males and females began to diverge most noticeably at 50–60 mm body length (carapace length of 12–14 mm), and above this size female master claws grow nearly isometrically with body length (i.e. the slope of the ratio is nearly zero).

Manus height of the master claws exhibited highly significant positive allometry relative to body length for both sexes (regressions 23, 25, **Appendix**), but minor claws did not differ from isometry (regressions 24, 26). Manus length, on the other hand, exhibited positive allometry only in males and a weak negative allometry in females (regressions 27–30). Only for male master claws, however, would this allometry be significant statistically following a sequential Bonferroni adjustment for multiple tests (N = 4).

Variation in claw shape

Claw shape also differed dramatically between claw types and between sexes. Master claws grew higher relative to their length than minor claws, and among mature shrimp, male master claws grew up to 30% higher than female master claws (Fig. 2b). As for claw weight, the difference between the sexes became most apparent at total body lengths greater than 60 mm. Dactyl shape in master claws exhibited a somewhat complex pattern of variation (Fig. 3a). Mid-dactyl height exhibited significant positive allometry relative to mid-dactyl length for both sexes (regressions 35 and 37, **Appendix**), but this allometry disappeared in males above 7 mm mid-dactyl length (regression 36). Hence, dactyls of master claws became proportionally higher in both sexes up to a total body length of 60 mm, but the allometry disappeared in males above this size, yielding more slender dactyls than would have been expected given their earlier pattern of growth. Finally, mechanical advantage increased with increasing size for master and minor claws, and was nearly 50% higher for master claws (Fig. 3b), but it did not differ between the sexes for either claw type (regressions 38–41).

Angles were more appropriate to quantify the acuteness of the propodal notch and the curvature of the dactyl tip. Both the angle formed by the propodal notch, and the angle formed at the tip of the dactyl became more acute with increasing size for all claws (Figs 4a, b), but these increases were
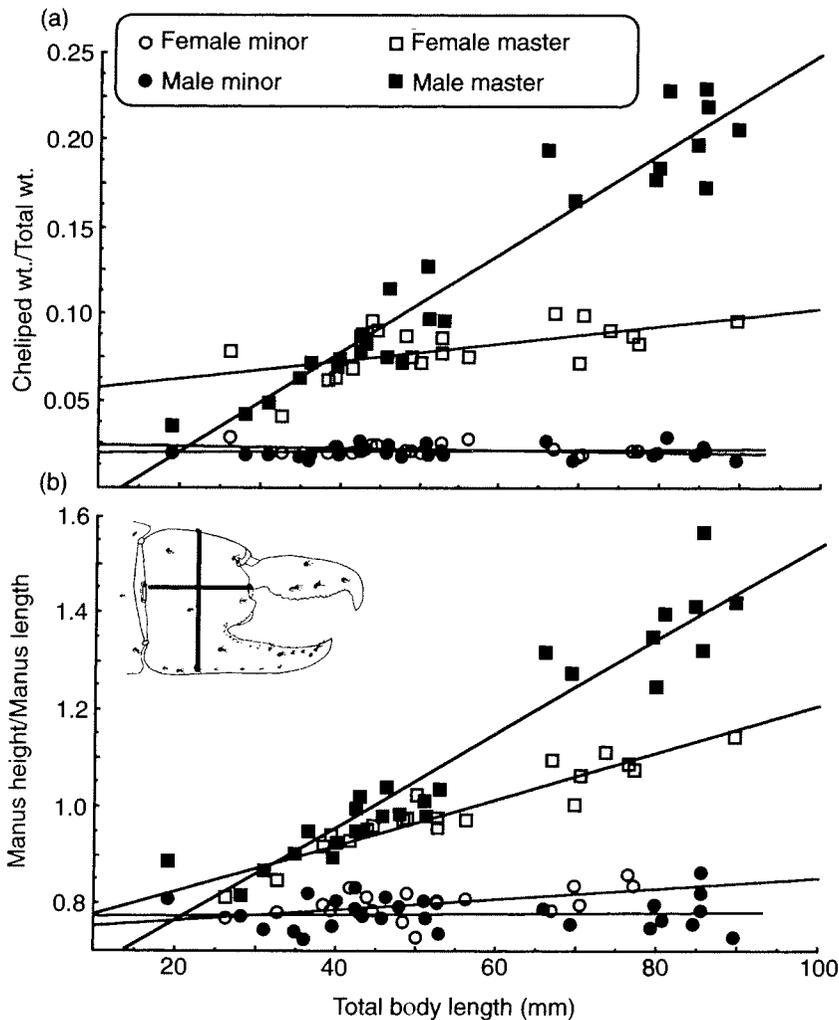
FIG. 2. Variation in relative cheliped weight (a) (weight of all limb segments/total body weight including chelipeds) and manus shape (b) (height/length) of master and minor claws as a function of total body length in *Neotrypaea californiensis*. Lines correspond to least-squares linear regressions (see **Appendix**, regression 15–22 for statistics). Note that the apparent lack of a difference between the slopes for minor claws in (a), even though the allometric coefficients clearly differ (regression 12 and 14), results in part from comparing claw weight against total weight, which includes the claws, and in part from plotting the cheliped wt./body wt. ratio against body length as opposed to log(body length).

only significant for master claws (regressions 42–49, **Appendix**). In addition, only the propodal notch angle differed between the sexes. Curiously, gape length (tip of fixed finger to base of propodal notch) varied isometrically with manus height in the master claws of both males and females (regressions 50 and 52), even though manus height exhibited a substantial positive allometry relative to body length (regressions 23 and 25). These three traits revealed the most about potential claw function.
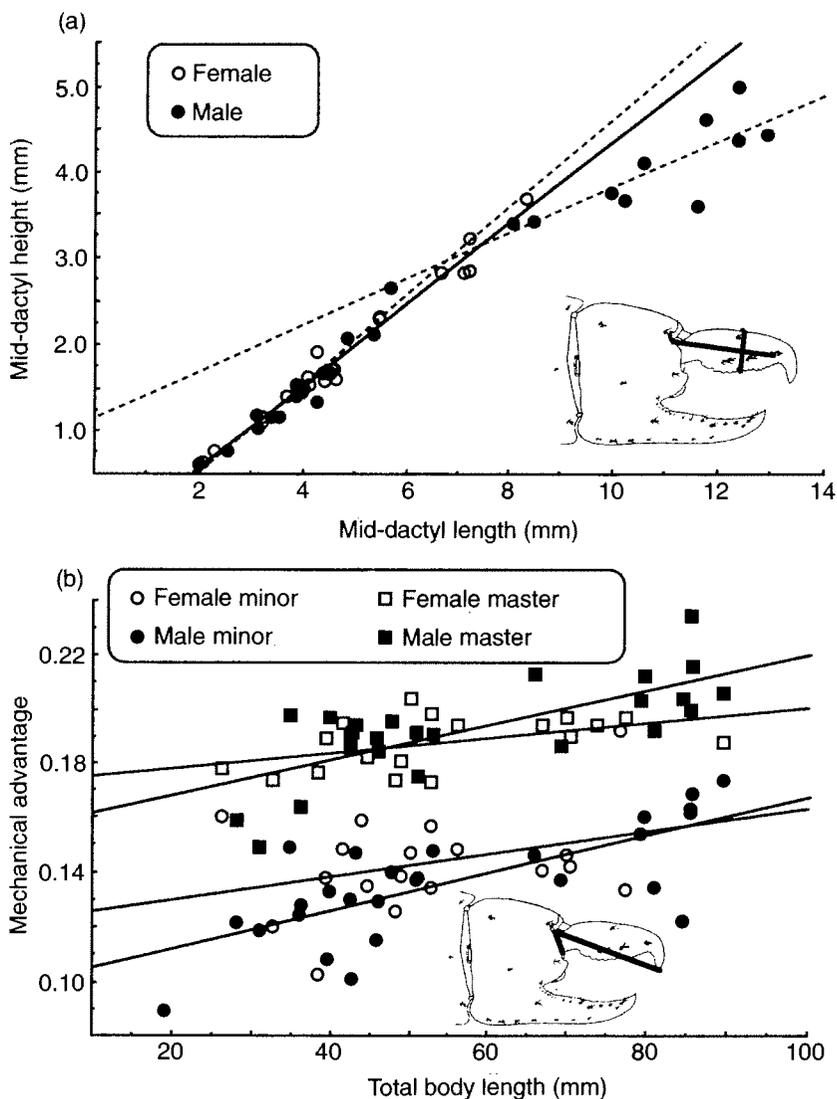
FIG. 3. Variation in mid-dactyl height as a function of mid-dactyl length of master claws (a) and mechanical advantage as a function of total body length of master and minor claws (b) in *Neotrypaea californiensis*. Lines correspond to least-squares linear regressions, and dashed lines indicate separate regressions for males smaller or larger than 7 mm mid-dactyl length (see Fig. 1 for dimensions measured and **Appendix**, regression 35–41 for statistics). Few females had dactyls this large or larger because females have relatively smaller master claws overall.

Master claws also differed between the sexes in other ways (Plate I). In addition to being significantly larger overall, the propodal notch in males was deeper and less acute at its base and exhibited more well-developed teeth along its dorsal margin, thus mature males exhibited a larger gape when claws were closed. Numerous fine teeth were also more well developed along the inner margins of the dactyl and fixed finger of males.
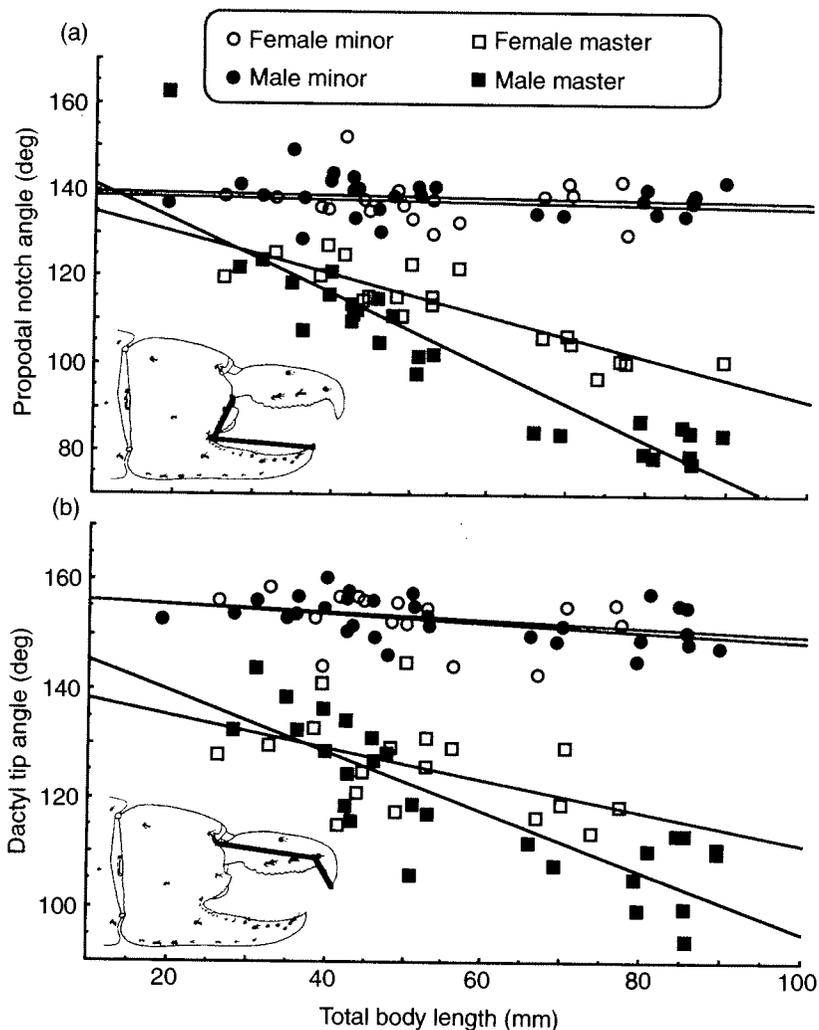
FIG. 4. Variation in propodal notch angle (a) and dactyl tip angle (b) as a function of total body length in *Neotrypaea californiensis*. Lines correspond to least-squares linear regressions (see Fig. 1 for dimensions measured and **Appendix**, regression 42–49 for statistics).

Discussion

Heterochely and claw function

Master claws of thalassinidean shrimp exhibit an impressive variety of sizes and shapes (e.g. see Edmondson, 1944; Biffar, 1971; Manning & Felder, 1991). Unlike upogebiid shrimp, where males and females are effectively homochelous (MacGinitie, 1934; Ngoc-Ho, 1977), most callianassid and ctenochelid shrimp are conspicuously heterochelous (Manning & Felder, 1991). The proportion of right master claws in *Neotrypaea californiensis* was approximately 0.5

(Table I), as also observed in most fiddler crabs (Crane, 1975), American lobsters (Herrick, 1895), and snapping shrimp (Darby, 1934). The sexual dimorphism observed in *N. californiensis* — males exhibited more well-developed claws than females — is also widespread among sexually-dimorphic brachyuran crabs (Vermeij, 1977). Thus, although it has certainly evolved independently, the prominent heterochely observed in *N. californiensis* shares much in common with other markedly heterochelous decapods.

The master claw in mature male *Neotrypaea californiensis* (Plate I) is unusual even by callianassid standards. Although some callianassid species have comparable-sized claws, only *Trypaea australiensis* exhibits a deeper propodal notch (Biffar, 1971; Manning & Felder, 1991). The peculiar shape of this hypertrophied master claw implies that male *N. californiensis* must use it in some form of highly stereotyped encounter whose outcome has a large impact on fitness.

Several lines of evidence suggest that *Neotrypaea californiensis* master claws are used to grapple with the master claws of similar-sized conspecifics during agonistic interactions or during mating. First, most thalassinidean shrimp are particle feeders and, although they may aid with burrowing, the claws appear to play only a minor role in feeding (Dworschak, 1987b). Second, the propodal notch makes little sense mechanically for a claw that would be used primarily for applying forces along the middle or distal portions of the fingers, as when biting or nipping. This notch, which becomes markedly deeper with increasing size (Fig. 4a), would localize such forces
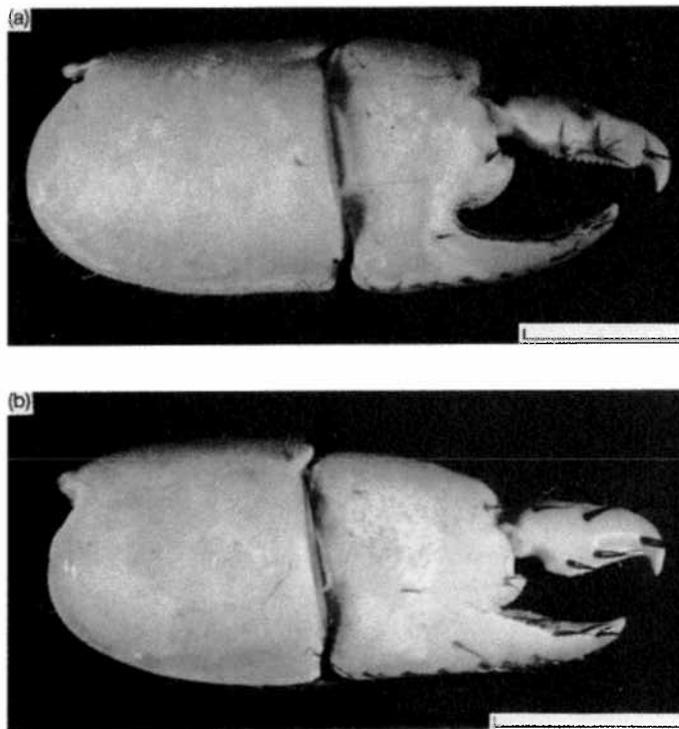
PLATE I. Master claws from mature male (a: 85.5 mm total body length) and female (b: 89.6 mm total body length) *Neotrypaea californiensis*. Scale bar is 10 mm.

at its base and thus increase the likelihood that the fixed finger would break off under load. Damaged master claws are, in fact, more common in *Lepidophthalmus louisianensis* during the breeding season (Felder & Lovett, 1989). Third, the shape of the gape in mature males is quite similar to that of the cross-section of the manus, both at the middle and base (Fig. 5). This would allow one individual to grasp another's master claw very precisely. Fourth, the length of this gape increases isometrically with manus height for both males and females (regressions 50 and 52, **Appendix**), even though manus height exhibits a marked positive allometry relative to manus length (Fig. 2b, regressions 23 and 25). As a consequence, the gape would be too large to grasp effectively the much smaller minor claws or even the master claws of much smaller individuals. Fifth, the sharply curved tip to the dactyl, which becomes quite hooked in mature animals (Fig. 4b, Plate I), seems much better suited to grappling than to biting or nipping. Sixth, the numerous fine, regularly shaped teeth that line the gape (Plate I) would appear to provide multiple points of contact for a firmer grip, and bear no resemblance to the coarser molariform or sharper cutting teeth of predatory crabs (Brown, Cassuto & Loos, 1979), or to the specialized solitary teeth of male fiddler crabs whose master claws are used for fighting (Crane, 1975). Finally, the mechanical advantage of master claws (0.18–0.22, Fig. 3b) is closer to that of 'fast' claws of other decapods (Warner & Jones, 1976; Brown *et al.*, 1979; Elner & Campbell, 1981), but it is substantially less than that observed in durophagous crabs (0.30–0.55; Vermeij, 1977). Thus, in spite of their large size, these claws do not appear to have been selected for increased strength.

Although the circumstantial evidence seems strong, direct behavioural observations will be required to confirm the inference that the peculiar form of *Neotrypaea californiensis* master claws has evolved for a specialized form of grappling between similar-sized conspecifics.

Claw growth and allometry

The master claws in male *Neotrypaea californiensis*, which can approach 25% of total body weight (Fig. 2a), are nearly as large as those observed in fiddler crabs (*Uca*), which can reach 40% of body weight (Neville, 1976). The prominent sexual dimorphism in the claws of callianassid shrimp has prompted several studies of the relationship between claw allometry and sexual maturity (reviewed in Felder & Lovett, 1989). As observed in *Lepidophthalmus louisianensis* (Felder & Lovett, 1989), the master claws of immature *N. californiensis* of both sexes exhibit a substantial positive allometry up to 45–50 mm total body length (Fig. 2a). Above this size, which presumably represents the onset of sexual maturity, the positive allometry continues in males, but virtually disappears in females (Fig. 2a). The change with increasing size in the allometric coefficients of dactyl shape in male *N. californiensis* (Fig. 3a) also suggests a pre-pubertal and post-pubertal form, at least in males. Unlike previously studied callianassid shrimp, however, *N. californiensis* also exhibited sexual dimorphism in the allometry of minor claw size, including claw weight (regressions 12, 14 **Appendix**), and manus and propus lengths (regressions 28, 30, 32, 34). Although no sexual dimorphism was observed in minor claw shape (regressions 20, 22, 39, 41, 43, 45, 47, 49, 51, 53), the presence of some sexual size dimorphism in minor claws suggests their growth is not completely independent of the factors that influence master claw size.

A landmark-morphometric analysis also yielded some insights into how claw shape differences arise developmentally in *Neotrypaea californiensis*. The prominent propodal notch could develop in one of two ways: a) via a uniform contraction along the entire length of the manus in the region of the notch; or b) via a localized differentiation of cuticle and loss of tissue only in the immediate vicinity of the notch. These two hypotheses can be distinguished by comparing the change in relative
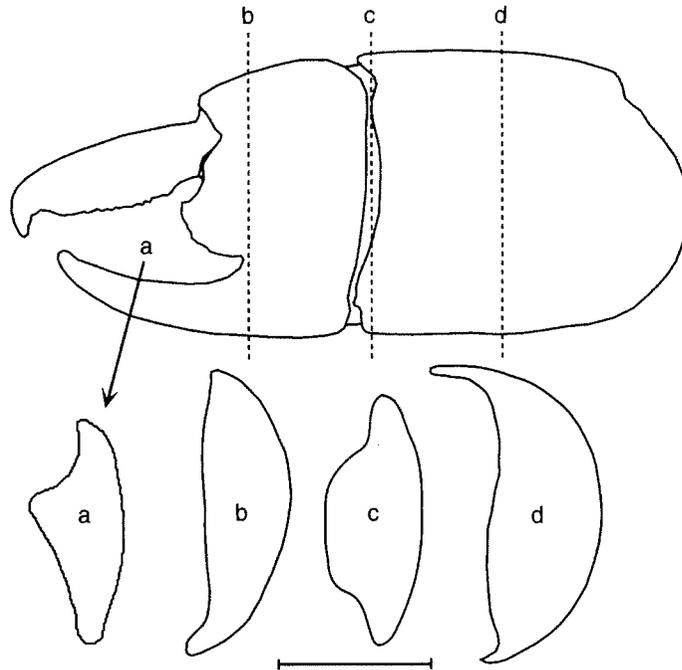
FIG. 5. (a) Outline of the gape in a mature male (85.5 mm total body length) master claw, compared to cross-sections from three regions of the same claw (b–d, marked by dashed lines) of *Neotrypaea californiensis*. In each cross-section, the outer surface is to the right. All drawings are to the same scale and from the same individual. Scale bar is 10 mm.

position of distinctive patches of setae on the manus surface (in particular landmarks #25 and #26, Fig. 1) using the analytical tools of landmark-morphometrics (Bookstein, 1992). This analysis provides strong evidence that the notch develops via the second mechanism (Fig. 6). Hence, substantial changes in claw shape appear to be achieved by very localized developmental mechanisms.

Sexual dimorphism and sexual selection

Although little is known about how they actually function, the notable sexual dimorphism in *Neotrypaea californiensis* master claws implies a more important role in males than females. First, master claws are disproportionately heavier (Fig. 2a), and higher relative to their length (Fig. 2b), in mature males compared to females. Second, in mature males the dactyl is distinctly more slender in the middle (Fig. 3a, Plate I), and the propodal notch angle and dactyl-tip angle are both more pronounced (Figs. 4a, b). As a consequence, the gape is substantially larger and closer in outline to a cross-section of the manus in males than in females (Plate I). Male master claws thus appear to be better suited for grappling.

Callianassid shrimp may thus represent another example of the widespread association between prominent sexual dimorphism in claws and male–male competition for females in other crustaceans (Warner, 1977). Indeed, in forced laboratory encounters, thalassinidean shrimp exhibit considerable aggression when they cannot escape from each other into burrows (Tunberg, 1986; Rowden & Jones, 1994). However, for obvious reasons, behavioural observations

of isolated individuals in laboratory fossaria (MacGinitie, 1934; Pohl, 1946; Torres *et al.*, 1977; Dworschak, 1987*a*) have yielded no information about mating behaviour or intra-burrow agonistic interactions (Felder & Lovett, 1989).

Implications for Thalassinidean claw evolution

Thalassinidean shrimp exhibit a remarkable variety of claw form, ranging from barely subchelate and effectively homochelous in some upogebiid species, through conspicuously

(a) Small -> Medium

(b) Medium -> Large
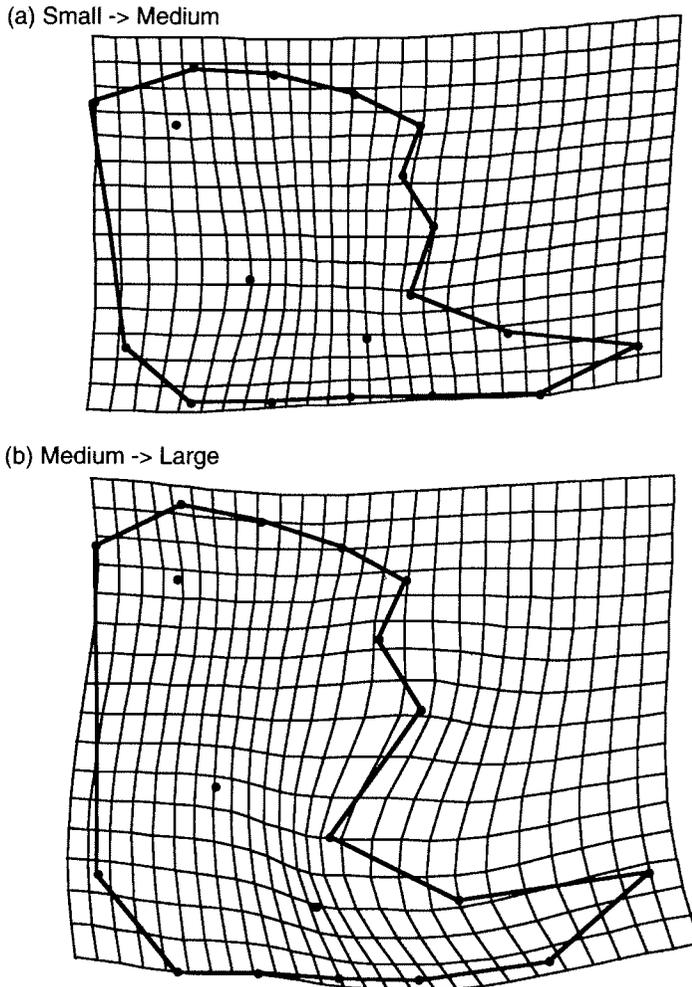
FIG. 6. Changes in propus shape with increasing size in master claws of male *Neotrypaea californiensis*: (a) claws of small shrimp (mean total body length = 33.2 mm, S.D. 3.58, N = 5) mapped on to those of medium-sized shrimp (mean total body length = 48.8, S.D. 3.16, N = 5); (b) claws of medium-sized shrimp mapped on to those of large shrimp (mean total body length = 85.1, S.D. 3.07, N = 5). Dots correspond to landmarks used in the analysis (see Fig. 1 for landmark locations). Gridlines represent total deformations (both uniform and non-uniform components) from the thin-plate spline analysis of Bookstein (1992), based on the mean landmark configuration of the five individuals in each size class.

hypertrophied and heterochelous forms in numerous ctenochelid and callianassid clades (Stevens, 1928; Biffar, 1971; Manning & Felder, 1991). Since their claws are rarely used for feeding, except among species that collect seagrass to decompose in their burrows (Dworschak, 1987*b*), some other factors must be driving claw evolution within the clade. As we have argued above, numerous lines of evidence suggest that the claws of *Neotrypaea californiensis* are used for sustained grappling with similar-sized conspecifics. One of the most striking features of *N. californiensis* claws is the pronounced propodal notch (Plate I), which may be diagnostic of their use for grappling.

A preliminary survey of the taxonomic distribution of propodal notches (Edmondson, 1944; Biffar, 1971; Manning & Felder, 1991) suggests they have evolved independently at least twice within the Callianassidae. First, propodal notches are weakly developed (Callianopsinae) or absent (Ctenochelinae) in the closely-related family, Ctenochelidae. Second, within the Callianassidae itself, their development varies quite considerably among subfamilies. Propodal notches are at best weakly developed in the Eucalliinae and appear to be lacking in the Cheraminae. Within the Callianassinae, other species of both *Neotrypaea* and *Trypaea* exhibit comparable or more pronounced propodal notches, yet such notches are either weak or non-existent in other callianassine genera (*Biffarius*, *Callianassa*). Similarly, within the Callichirinae propodal notches range from non-existent (*Glypturus*, some species of *Callichirus*), or weakly developed (*Corallianassa*, *Neocallichirus*) through to modest (*Lepidophthalmus*, some species of *Callichirus*).

The development of modest propodal notches within both the Callianassinae and the Callichirinae, each of which also includes taxa that lack such notches, and the lack of such notches in other callianassid subfamilies and in the related Ctenochelidae, all suggest that propodal notches have evolved at least twice, once within the Callianassinae and again in the Callichirinae. If such notches are diagnostic of a stereotyped intraspecific behaviour, then this behaviour too has presumably evolved twice. Needless to say, a formal comparative analysis based on a more rigorous phylogeny will be required to confirm this hypothesis.

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Appendix

Regression equations describing associations between traits in **Neotrypaea californiensis**. *Eq.—equation numbers referred to in the text; Fig.—figure in which data are presented; Sex: M—male, F—female; Claw: Mas—master, Min—minor, n.r.—not relevant; N—sample size; r^2—coefficient of determination; Slope ($\pm$S.E.)—slope of ordinary least-squares (OLS) regression; P—probability that OLS slope deviates from zero; Intercept ($\pm$S.E.)—intercept of OLS regression (S.E. of expected Y at mean X); RMA Slope—observed reduced major axis slope; Expect—RMA slope expected for isometry; P (RMA)—probability that observed RMA slope deviates from isometry (t-test); P (M v F)—probability that male and female RMA slopes differ from each other (t-test); n.s.—unable to conduct test on RMA slopes because one or more OLS slopes were not significant, McArdle, 1988). Trunk Weight—live wet weight excluding the weight of both claws. All linear dimensions are in mm, weights in g.*
See Fig. 1 for precise definitions of each linear dimension

Eq.	Fig.	X-variable	Y-variable	Sex	Claw	N	r^2	Slope ($\pm$S.E.)	P	Intercept ($\pm$S.E.)	RMA Slope	Expect	RMA P	M v F P
1		log(Body Length)	log(Carapace Len.)	M	n.r.	28	0.992	1.009 (0.0179)	< 0.001	−0.592 (0.0032)	1.013	1.0	0.463	0.195
2				F	n.r.	20	0.995	0.987 (0.0167)	< 0.001	−0.559 (0.0024)	0.990	1.0	0.542	
3			log(Abdomen Len.)	M	n.r.	20	0.994	0.964 (0.0151)	< 0.001	−0.150 (0.0027)	0.968	1.0	0.040	0.022
4				F	n.r.	20	0.998	1.000 (0.0118)	< 0.001	−0.205 (0.0017)	1.001	1.0	0.903	
5			log(Live Weight)	M	n.r.	28	0.994	3.193 (0.0471)	< 0.001	−5.039 (0.0083)	3.202	3.0	< 0.001	< 0.001
6				F	n.r.	20	0.996	3.006 (0.0447)	< 0.001	−4.766 (0.0064)	3.012	3.0	0.789	
7		Body Length	Carapace Length	M	n.r.	28	0.988	0.272 (0.0058)	< 0.001	−0.319 (0.1233)	0.273			0.031
8				F	n.r.	20	0.993	0.260 (0.0053)	< 0.001	0.145 (0.0918)	0.261			
9		log(Body Length)	log(Trunk Weight)	M	n.r.	28	0.993	3.011 (0.0492)	< 0.001	−4.795 (0.0087)	3.022	3.0	0.665	n.s.
10				F	n.r.	20	0.995	2.984 (0.0491)	< 0.001	−4.774 (0.0070)	2.991	3.0	0.861	
11		log(Body Length)	log(Claw Weight)	M	Mas	27	0.993	4.512 (0.0753)	< 0.001	−8.272 (0.0134)	4.528	3.0	< 0.001	< 0.001
12				M	Min	28	0.988	3.255 (0.0690)	< 0.001	−6.836 (0.0122)	3.274	3.0	< 0.001	< 0.001
13				F	Mas	20	0.978	3.390 (0.1213)	< 0.001	−6.532 (0.0173)	3.429	3.0	0.002	
14				F	Min	18	0.988	2.863 (0.0774)	< 0.001	−6.186 (0.0103)	2.879	3.0	0.137	
15	2A	Body Length	Claw Wt/Live Wt	M	Mas	27	0.922	0.003 (0.0002)	< 0.001	−0.037 (0.0036)	0.003			< 0.001
16	2A			M	Min	28	0.022	0.000 (0.0000)	0.449	0.019 (0.0006)	0.000			n.s.
17	2A			F	Mas	20	0.340	0.001 (0.0002)	0.007	0.052 (0.0029)	0.001			
18	2A			F	Min	18	0.108	0.000 (0.0001)	0.184	0.025 (0.0007)	0.000			
19	2B	Body Length	Manus Height/Length	M	Mas	27	0.911	0.010 (0.0006)	< 0.001	0.569 (0.0130)	0.010		< 0.001	< 0.001
20	2B			M	Min	28	0.002	0.000 (0.0003)	0.817	0.775 (0.0066)	0.002			n.s.
21	2B			F	Mas	20	0.881	0.005 (0.0004)	< 0.001	0.729 (0.0072)	0.005		< 0.001	
22	2B			F	Min	18	0.277	0.001 (0.0004)	0.025	0.742 (0.0068)	0.002			
23		log(Body Length)	log(Manus Height)	M	Mas	27	0.990	1.556 (0.0309)	< 0.001	−1.805 (0.0055)	1.564	1.0	< 0.001	< 0.001
24				M	Min	28	0.977	1.044 (0.0315)	< 0.001	−1.320 (0.0056)	1.057	1.0	0.084	0.024
25				F	Mas	20	0.967	1.197 (0.0518)	< 0.001	−1.256 (0.0074)	1.217	1.0	< 0.001	
26				F	Min	18	0.989	0.983 (0.0255)	< 0.001	−1.211 (0.0034)	0.988	1.0	0.653	
27		log(Body Length)	log(Manus Length)	M	Mas	27	0.983	1.126 (0.0298)	< 0.001	−1.105 (0.0053)	1.136	1.0	< 0.001	< 0.001
28				M	Min	28	0.989	1.042 (0.0216)	< 0.001	−1.207 (0.0038)	1.048	1.0	0.036	< 0.001
29				F	Mas	20	0.959	0.934 (0.0455)	< 0.001	−0.799 (0.0065)	0.954	1.0	0.323	
30				F	Min	18	0.984	0.919 (0.0292)	< 0.001	−1.004 (0.0039)	0.926	1.0	0.022	
31		log(Body Length)	log(Propus Length)	M	Mas	27	0.989	1.242 (0.0260)	< 0.001	−1.097 (0.0046)	1.248	1.0	< 0.001	< 0.001

Appendix (*cont.*)

Eq.	Fig.	X-variable	Y-variable	Sex	Claw	N	r²	Slope (± S.E.)	P	Intercept (± S.E.)	RMA Slope	Expect	RMA	M v F
32				M	Min	28	0.985	0.992 (0.0242)	< 0.001	−0.909 (0.0043)	1.000	1.0	0.991	< 0.001
33				F	Mas	20	0.959	0.974 (0.0473)	< 0.001	−0.671 (0.0067)	0.994	1.0	0.908	
34				F	Min	18	0.986	0.877 (0.0262)	< 0.001	−0.714 (0.0035)	0.883	1.0	< 0.001	
35	3A	log(Mid-Dact. Len.)	log(Mid-Dact. Ht.)	M*	Mas	16	0.956	1.348 (0.0777)	< 0.001	−0.640 (0.0093)	1.379	1.0	< 0.001	0.032
36	3A			M†	Mas	10	0.672	0.681 (0.1681)	0.037	−0.099 (0.0129)	0.831	1.0	0.341	
37	3A			F	Mas	20	0.980	1.226 (0.0417)	< 0.001	−0.564 (0.0068)	1.239	1.0	< 0.001	
38	3B			M	Mas	25	0.527	0.001 (0.0001)	< 0.001	0.155 (0.0027)	0.001			
39	3B	Body Length	Mechanical Advant.	M	Min	28	0.522	0.001 (0.0001)	< 0.001	0.098 (0.0028)	0.001			0.023
40	3B			F	Mas	18	0.237	0.000 (0.0001)	0.041	0.172 (0.0022)	0.001			n.s.
41	3B			F	Min	18	0.106	0.000 (0.0003)	0.188	0.121 (0.0046)	0.001			
42	4A			M	Mas	27	0.843	−0.844 (0.0730)	< 0.001	149.695 (1.5651)	−0.920			
43	4A	Body Length	Propus Notch Angle	M	Min	28	0.018	−0.027 (0.0391)	0.500	139.877 (0.8345)	−0.201			< 0.001
44	4A			F	Mas	20	0.760	−0.480 (0.0635)	< 0.001	139.552 (1.1061)	−0.550			n.s.
45	4A			F	Min	18	0.008	−0.030 (0.0848)	0.732	139.093 (1.3029)	−0.340			
46	4B			M	Mas	26	0.706	−0.554 (0.0730)	< 0.001	150.824 (1.5003)	−0.660			
47	4B	Body Length	Dactyl Tip Angle	M	Min	28	0.149	−0.071 (0.0334)	0.043	156.910 (0.7130)	−0.185			0.262
48	4B			F	Mas	19	0.290	−0.297 (0.1129)	0.018	141.162 (1.9329)	−0.552			n.s.
49	4B			F	Min	18	0.072	−0.083 (0.0749)	0.283	157.257 (1.1513)	−0.311			
50				M	Mas	27	0.989	0.994 (0.0206)	< 0.001	−0.138 (0.0057)	1.000	1.0	0.980	
51		log(Manus Ht.)	log(Gape Length)	M	Min	28	0.974	0.887 (0.0285)	< 0.001	0.003 (0.0053)	0.899	1.0	< 0.001	0.004
52				F	Mas	20	0.976	0.921 (0.0342)	< 0.001	−0.093 (0.0059)	0.932	1.0	0.062	n.s.
53				F	Min	18	0.963	0.825 (0.0401)	< 0.001	0.026 (0.0053)	0.840	1.0	< 0.001	

* For mid-dactyl lengths < 7 mm, corresponding to a total body length of approx. 60 mm in males
† For mid-dactyl lengths > 7 mm