

# Comparison of chela size and pincer force in scorpions; getting a first grip

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## Abstract

A key feature of the ancient body plan of scorpions is the pincer or chela. These multifunctional structures vary considerably in size and shape between different scorpion species. Here we provide the first comparative data on the pinching performance of the chelae of seven species of scorpions exemplifying the extremes of the shape range from slender to robust; *Leiurus quinquestriatus*, *Androctonus amoreuxi*, *Androctonus australis*, *Hadogenes* sp., *Pandinus imperator*, *Scorpio maurus* and *Pandinus cavimanus* (in the order of decreasing chela height to width ratio). Size-corrected chela height correlates highly with maximum pinch force. Independent contrasts suggest that the correlation of chela width, height and fixed finger length with maximum pinch force is independent of phylogeny, suggesting an adaptive component to the evolution of chela shape and performance.

## Introduction

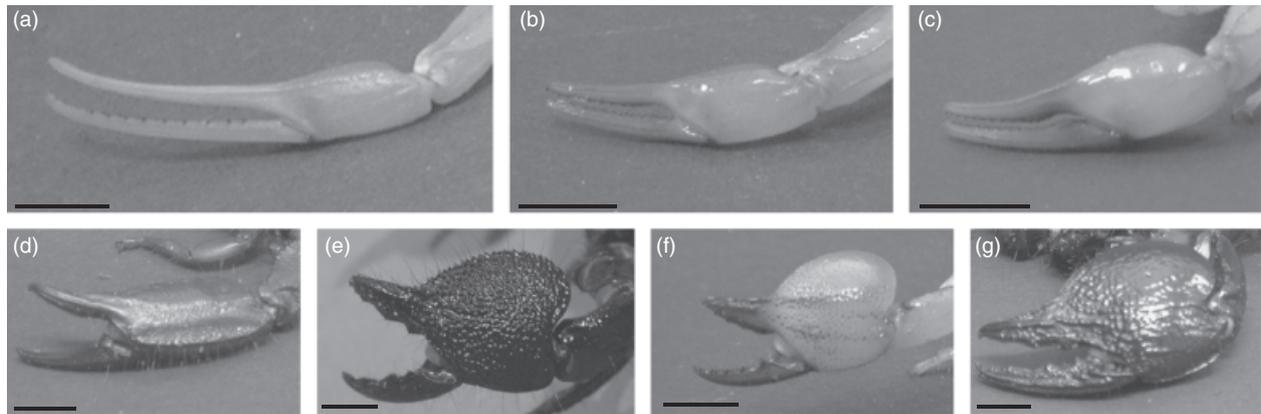
Scorpions are a highly successful group with over 1300 extant species inhabiting all continents except Antarctica (Fet *et al.*, 2000; Coddington *et al.*, 2004). Although their morphological variation is limited, they successfully inhabit both rainforest and deserts, and range from high mountains down to the littoral zone. Scorpions with a gross morphology similar to present-day forms are found in deposits from the late Silurian period (*c.* 418 Mya, Dunlop, Tetlie & Prendini, 2008). Despite the highly conserved, but apparently versatile body plan of scorpions, a striking amount of variation is present in the size and shape of the pincers or chelae as exemplified in Fig. 1.

The scorpion chela is formed by the last two segments of the pedipalp. The pedipalps are the second prosomal appendages, consisting of six segments. The tibia forms the immovable finger and the base of the chela, on which the movable finger or tarsus is placed. Although similar in appearance to the pincers of crustaceans and *Limulus* (Xiphosura), the chela of the scorpion lacks opening muscles and is opened by elastic recoil of the resilin-containing joint (Govindarajan & Rajulu, 1974; Sensenig & Shultz, 2004). The closing muscles are primarily situated in the tibia, and consist of three bundles. In *Leiurus*, two of these bundles

consist of longitudinal muscle fibres, and one has pinnate muscle fibres (Gilai & Parnas, 1970). Little information exists on the muscle arrangement in the chelae of other species. The patella also contains a small closer muscle that is connected to the tarsus by a long ligament (Snodgrass, 1952; Gilai & Parnas, 1970). The patellar closing muscle is usually very small relative to the muscles in the tibia, and therefore probably of little influence on the closing force of the chela.

Chela form varies greatly among scorpions and ranges from the tweezer-like slender chelae of species like *Leiurus quinquestriatus*, to the broad and powerful chelae of the emperor scorpion *Pandinus imperator*, which are reminiscent of the large claws of durophagous crabs (Fig. 1). In crustaceans, claw shape is highly correlated with diet (Yamada & Boulding, 1998), although other functions, such as in agonistic behaviour, signaling and grooming also influence the relative size and shape (Lee, 1995; Mariappan, Balasundaram & Schmitz, 2000).

Like crab chelae, scorpion chelae are used for several functions. Their most obvious uses are those of prey handling (Casper, 1985) and defence. Most scorpion species forage actively for insects and other small invertebrates. The pedipalps are densely covered with many sensory hairs and are held out during foraging as sensory arrays, serving a



**Figure 1** Chela profiles of species used in this study. (a) *Leiurus quinquestriatus*; (b) *Androctonus amoreuxi*; (c) *Androctonus australis*; (d) *Hadogenes* sp.; (e) *Pandinus imperator*; (f) *Scorpio maurus*; (g) *Pandinus cavimanus*. Scale bars are 5 mm.

function similar to the antennae of insects (Alexander, 1959; Fet *et al.*, 2003). Scorpions also use the chelae in burrowing (Harington, 1978). The pedipalps are usually the first part of the scorpion to come into contact with the prey, which is gripped immediately with the chelae. In many species, the prey is subsequently further immobilized by an injection of venom from the stinger or telson (Bub & Bowerman, 1979). In other species, however, the prey is subdued only with the chelae. Casper (1985) noted an ontogenetic change in *P. imperator*, where juveniles readily use their sting to subdue prey, whereas adults use only their chelae.

Most scorpion species are solitary and will avoid contact with conspecifics. Encounters can result in fights where both chelae and stinger are used to attempt to subdue the opponent. Both the sting and the chelae are also used in defence against predators. The chelae are used to pinch the attacker, but are also used as a shield for the more vulnerable body, or to seal off their burrows (Newlands, 1969). The chelae are also used for loosening the soil in digging. The loose soil is further transported with the walking legs. Finally, the chelae are used in mating, where the male grips the chelae of the female and walks around with her in search of a suitable substrate for spermatophore deposition (called the promenade-à-deux). Interestingly, it has been long noted that species with more potent venom possess relatively slender chelae and a broader metasoma (the scorpion 'tail', actually a continuation of the body). Chela form, in combination with metasoma size, is thus used as a rule of thumb to assess whether an unidentified scorpion could be dangerously poisonous (Newlands, 1969; Kleber *et al.*, 1999; Leeming, 2003).

Scorpion chelae can thus be considered as truly multi-functional structures, and are likely under divergent selective pressure for their many tasks. The capture of mobile, small prey may benefit from a slender pincer with long tibia and tarsus that allows for a fast grip with high precision. For defensive purposes, on the other hand, big, robust and strong pincers are advantageous. Given that the chela-closing muscles are primarily situated in the tibia, one would

expect a strong correlation between chela size and shape and the maximal pinch force an animal can exert.

Pinch force has proven a very informative character for both functional (Lee, 1993, 1995) as well as behavioural (Seed & Hughes, 1997) and ecological (Yamada & Boulding, 1998) studies in crustaceans. In this study, we provide the first dataset on the force-generating performance of scorpion chelae across a morphologically representative selection of species. Specifically, our goals were to (1) measure the pinch force in a morphologically diverse sample of scorpions; (2) correlate force production with morphology of the chelae.

## Materials and methods

### Species selection

Seven species were selected from three families to represent a broad range of scorpion chela morphologies (see Fig. 1), and based on their availability in the pet trade. The species *L. quinquestriatus* (Buthidae) and, to a lesser degree, *Androctonus amoreuxi* (Buthidae) and *Androctonus australis* (Buthidae) possess elongate, tweezer-like claws. The average ratio of length to height of the claw of these species is 6.0, 3.8 and 3.3, respectively. Short and powerful claws are represented by *P. imperator* (Scorpionidae), *Pandinus cavimanus* (Scorpionidae) and *Scorpio maurus* (Scorpionidae), with an average ratio of length to height of the claw of 1.6, 1.5 and 1.5, respectively. *Hadogenes* (Hemiscorpiidae) presents a special case, as the entire body of these scorpions is strongly flattened dorsoventrally, related to a life in rock crevices and under rocks. Only adults were used except for *P. imperator*, for which we included a range from medium-sized to adult specimens (Table 1). All animals were obtained from the pet trade and in good health upon acquisition and throughout the experimental period. All animals were maintained in captivity for at least 6 weeks, and at most 3 months, before the experiment started. Desert species (*L. quinquestriatus*, both *Androctonus* species and *S. maurus*) were kept in plastic

**Table 1** Scorpion species used in this study

Species (family)	Number of specimens	Size range, mean $\pm$ standard deviation (mm)	Maximum pinch force range, mean $\pm$ standard deviation (n)
<i>Pandinus imperator</i> (Scorpionidae)	14	65.6–130.9 92.6 $\pm$ 13.7	6.5–30.5 16.4 $\pm$ 6.8
<i>Pandinus cavimanus</i> (Scorpionidae)	6	79.3–93.1 87.7 $\pm$ 5.2	17.3–32.8 22.8 $\pm$ 5.9
<i>Hadogenes</i> sp. (Hemiscorpiidae)	5	77.5–112.0 93.1 $\pm$ 11.1	10.3–25.4 14.8 $\pm$ 3.6
<i>Scorpio maurus</i> (Scorpionidae)	4	43.1–55.1 48.8 $\pm$ 4.1	7.2–26.2 13.5 $\pm$ 5.6
<i>Androctonus australis</i> (Buthidae)	6	59.7–84.6 74.0 $\pm$ 8.3	1.2–2.9 1.8 $\pm$ 0.4
<i>Androctonus amoreuxi</i> (Buthidae)	7	50.0–54.9 52.4 $\pm$ 1.8	2.4–4.6 3.6 $\pm$ 0.8
<i>Leiurus quinquestriatus</i> (Buthidae)	6	77.8–86.6 83.6 $\pm$ 2.8	0.4–1.1 0.7 $\pm$ 0.2

Size range indicates the range of total lengths (not prosoma+mesosoma length) of the specimens used, not of the species.

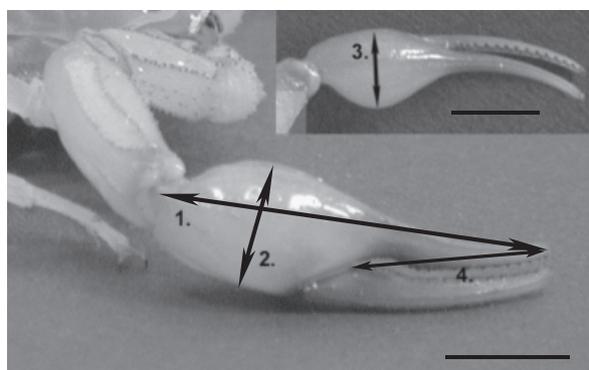
boxes on a layer of vermiculite substratum. Species requiring more humid circumstances (both *Pandinus* species, to a lesser extent *Hadogenes* sp.) were kept in large plastic boxes with humid substrate and with water available at all times. The plastic boxes that were used measured 123  $\times$  190  $\times$  80 mm. Large specimens (*Pandinus* and *Hadogenes*) were housed in boxes measuring 200  $\times$  230  $\times$  130 mm. All animals were fed with crickets *Acheta domestica* and cockroaches (*Blaberus* sp.) once every 1–2 weeks before and during the experiment. All specimens were in good health throughout the test period. All species were provided with a piece of polyethylene tubing as a hiding place, and kept at 24 °C.

### Chela size and shape

Morphometric data from the chelae were obtained using digital calipers (Mitutoyo, Kawasaki, Kanagawa, Japan;  $\pm$  0.01 mm). Chela length was defined as the distance from the tip of the fixed finger to the joint with the tibia. Height was measured as the maximum height in the plane of movement of the movable finger. Width was measured perpendicular to the height in the middle of the muscular part of the chela. The length of the fixed finger was measured from the tip of the fixed finger to the joint of the movable finger (Fig. 2). Manus length was calculated as the length of the chela minus the length of the fixed finger. Live animals were weighed on laboratory scales to the nearest 0.1 g. The length of the prosoma plus mesosoma (PML), as well as total body length (TL) were measured from digital photographs of live scorpions using the TPSdig digitizing program, version 2.10 (Rohlf, 2004).

### Force measurement

*In vivo* pinch forces were measured using a Kistler force transducer (type 9203, Kistler Inc., Winterthur, Switzerland) mounted on a purpose-built holder (see Herrel *et al.*,



**Figure 2** Length (1) and height (2) as measured on the chela. Width (3) of chela is shown in dorsal view in inset. Distance of fixed fingertip to joint of movable finger (4). Scale bars are 5 mm.

1999) and connected to a Kistler (model 5995) charge amplifier. Measurements were made in a climate-controlled room at 23–24 °C. During pinch-force measurements, scorpions were restrained between sponge pads in which a cutout was made to accommodate the body. Most specimens pinched readily, but some were stimulated to pinch by stroking the inside of the chela with the tip of a pair of tweezers. Five trials per claw were performed, each trial separated from the next by at least 1 day, and only the maximum force per claw was retained for further analyses.

### Analysis

Before analysis all morphometric values and force measurements were  $\log_{10}$  transformed. A paired *t*-test was performed in SPSS (SPSS Inc., Chicago, IL, USA) to determine differences between left and right chelae in maximum pinch force. For each specimen the maximum pinch force of the left and right chela were subsequently averaged

to represent a single maximum pinch force in the analysis. Linear measurements of the left and right chela were also averaged for each specimen. To correct for overall body size, the independent variables were  $\log_{10}$  transformed and regressed against the PML, and residuals were calculated. Correction for body size could not be done using PML as a covariate in an ANCOVA, as the requirement that the different groups should not differ significantly in the value of the covariate was violated by the species being different in size (Miller & Chapman, 2001). The  $R^2$ -values of the linear regressions are provided in Table 2. PML was used instead of TL as a measure of overall size because several of the species used in this study, especially *Hadogenes*, show considerable sexual dimorphism in the length of the metasoma. The residual maximum pinch force per specimen was regressed against the residual linear dimensions of the body and claw as independent variables (Table 3). Aspect ratios, defined as the ratio between chela length and height, as well as the ratio between chela length and the product of chela width and height, were also included in this analysis. Since

no data on muscle arrangement in all the different species were available, the area of an ellipse defined by the height (major axis) and width (minor axis) of the chelae was included as an estimate of cross-sectional area of the closer muscle. Likewise, the product of length, height and width was used as a proxy for claw volume.

Independent contrasts (ICs) (Felsenstein, 1985) were calculated with the Cactus program (Schwilk, 2000; Schwilk & Ackerly, 2001), using a phylogeny based on Coddington *et al.* (2004). Means for each species of the  $\log_{10}$ -transformed values were used. This resulted in five ICs for each character. The ICs of maximum pinch force were subsequently regressed against the ICs for chela length, height and width, fixed finger length, manus length, as well as PML (see Table 4). ICs were also calculated for the size-corrected variables, except PML. All regressions were forced through the origin for analyses on ICs.

## Results

The slopes of the regressions of the linear measurements show that chela length is not isometric with PML (slope = 8.33,  $R^2 = 0.716$ ). Chela width and height show even lower correlations with overall body size across species (see Table 2 and Fig. 3). Pinch force has a very weak correlation with PML (slope = 0.117,  $R^2 = 0.375$ ).

Multiple regression of the size-corrected residuals of the linear measurements of the chela showed chela height to have the highest correlation with pinch force ( $R^2 = 0.837$ , see Table 3). The aspect ratio (the ratio of height to length of the chela) correlates even better with maximum pinch force ( $R^2 = 0.896$ , see Fig. 4).

ICs analysis of non-size corrected variables showed both chela height and chela width to be correlated with maximum pinch force. The significance values of some of these regressions were, however, slightly above 0.05 because of the small number of species included in the analysis (see Table 4). Also in the independent contrast analysis of non-size corrected

**Table 2** Linear regressions of  $\log_{10}$ -transformed dimensions across all seven species of scorpion

Independent variable	$R^2$	$P$	Slope
Mass	0.728	<0.001	3.22
Chela length	0.716	<0.001	0.833
Chela height	0.472	<0.001	0.264
Chela width	0.397	<0.001	0.427
Chela fixed finger length	0.442	<0.001	0.130
Chela manus length	0.667	<0.001	0.765
Ellipse surface of chela cross-section	0.453	<0.001	0.167
Maximum pinch force	0.375	<0.001	0.117
Aspect ratio (length/height)	0.191	0.002	-0.205
Aspect ratio (length/(height × width))	0.284	<0.001	-0.153

Independent variable is  $\log_{10}$ -transformed prosoma+mesosoma length.

**Table 3** Linear regressions and correlations of size-corrected (residual)  $\log_{10}$ -transformed dimensions across all included species and the associated ANOVA  $P$ -values

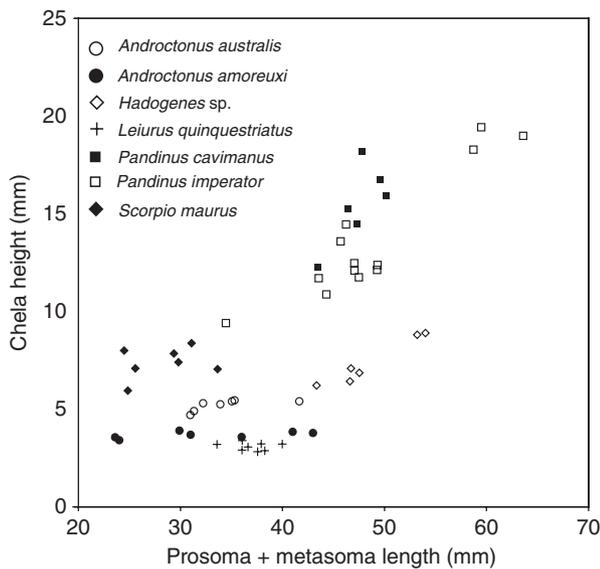
Independent variable	Regression			Correlation	
	$R^2$	$P$	Slope	Pearson's correlation coefficient	Significance (one-tailed)
Mass	0.208	0.001	0.691	0.456	<0.001
Chela length	0.075	0.060	0.406	0.247	0.030
Chela height	0.837	<0.001	0.995	0.915	<0.001
Chela width	0.777	<0.001	0.897	0.881	<0.001
Manus length	0.247	<0.001	3.80	0.497	<0.001
Fixed finger length	0.485	<0.001	-3.21	-0.697	<0.001
Ellipse surface of chela cross-section	0.820	<0.001	0.968	0.906	<0.001
Aspect ratio (length/height)	0.896	<0.001	0.831	0.947	<0.001
Aspect ratio [(length/(height × width))]	0.890	<0.001	0.881	0.943	<0.001
Length × height × width	0.708	<0.001	1.013	0.841	<0.001

Independent variable is size-corrected (residual)  $\log_{10}$ -transformed maximum pinch force. The Pearson correlation coefficient and its significance were calculated additionally.

**Table 4** Linear regressions of independent contrasts

Independent variable	Not size corrected		Size corrected	
	$R^2$	$P$	$R^2$	$P$
PML	0.040	0.703	–	–
Chela length	0.000	0.971	0.615	0.065
Chela height	0.654	0.051	0.753	0.025
Chela width	0.692	0.040	0.771	0.021
Fixed finger length	0.094	0.555	0.867	0.007
Manus length	0.221	0.347	0.229	0.336
Aspect ratio (length/height)	0.700	0.038	0.838	0.010

Independent variable is maximum pinch force.  
 P-values are derived from an ANOVA.  
 PML, prosoma plus mesosoma length.

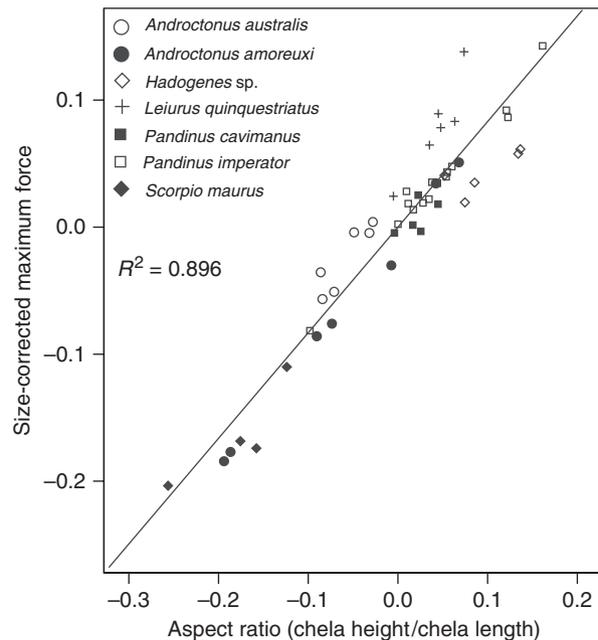
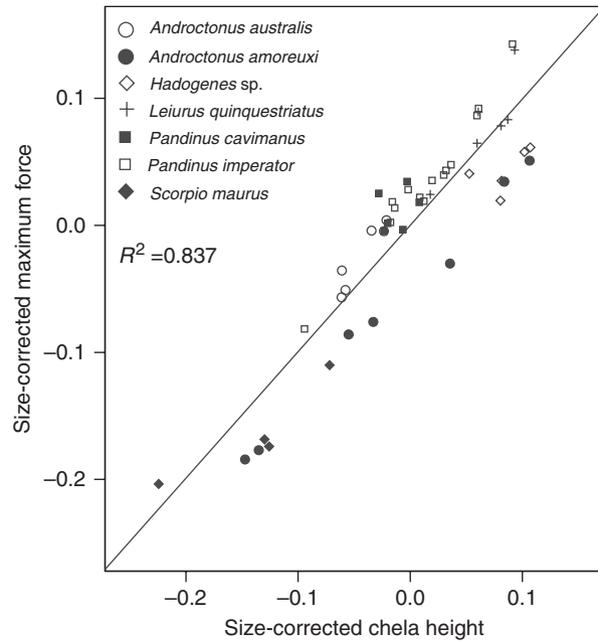


**Figure 3** Averaged chela height against prosoma and metasoma length (PML) showing the variation of relative chela size among the species included in this study. Note that for some species, the PML does not seem to correlate with chela height. In these species, the variability in PML is primarily due to feeding state.

variables, the aspect ratio of the chela (length/height) shows a high correlation with pinch force. The independent contrast analysis of the size-corrected variables shows a strong correlation between pinch force and both the aspect ratio of the chela, as well as the length of the fixed finger.

### Discussion

We found chela height to have the highest correlation with maximum pinch force of all the size-corrected linear measurements (see Table 3). This agrees with the finding of Lee (1993) that in the crab species *Carcinus maenas*, chela height is a good indicator of chela strength. However, without substantial variation in size the relationship may not be evident. Sneddon *et al.* (2000), working on a narrower size range in the same crab species found no such relationship.



**Figure 4** Size-corrected maximum pinch force plotted against size-corrected average chela height (top) and aspect ratio (bottom) of the left and right chela. These figures show the high correlation between pinch force and chela height, and between pinch force and the aspect ratio of the chela.

Across the seven scorpion species examined in this study, chela height is a very good indicator for maximum pinch force, while the ratio of the chela length to the chela height was even more highly correlated with size-corrected maximum pinch force (Fig. 4). The latter can be interpreted as an effect of the higher mechanical advantage caused by a

shorter out-lever (the moving finger of the chela) relative to the in-lever (constrained by the height of the chela manus). This interpretation is further confirmed by the high correlation between maximum pinch force and fixed finger length in the independent contrast analysis of the size-corrected variables (Table 4). Apart from the chelae of *Hadogenes*, which are restricted in height owing to the constraints imposed by living in narrow rock crevices, species that have evolved long, rather than high chelae, suggest selection for an aspect of chela performance other than maximum force.

Although adaptation to other functions cannot be excluded based on the present data, we propose that the gripping system of scorpions with slender chelae is another illustration of a leverage system optimized for speed rather than for force. Whereas predatory brachyuran crabs feed primarily on molluscs and other hard and slow-moving prey, scorpions generally feed on much faster and soft-bodied prey such as insects and spiders. If diet is the main factor determining chela shape in scorpions, as it is in many crabs, we would expect scorpions to have fast rather than strong chelae, on average. High closing speed can be achieved at the expense of the force generation by reducing the mechanical advantage of the lever system. Different levels of mechanical advantage have been shown for the major and minor claw of the blue crab *Callinectes sapidus* (Seed & Hughes, 1997), where the major claw is optimized for force, and the minor for closing speed and shearing (Hughes, 2000). Optimization for high closing speed would manifest as an elongation of the 'fingers' of the chela, as well as a shorter distance between the fulcrum and the point of muscle attachment of the movable finger. Long, slender chelae, such as those of *Leiurus*, are 'faster' designs than the robust chelae of *Pandinus*, and may reflect different abilities for capture of elusive prey.

It is also possible that slender and robust chela morphologies, as in some crab species, are indicative of differences in prey availability and/or selection of prey of different hardness. We were unable to test whether pinch force is correlated with durophagy, as diet data are not available for a sufficient number of scorpion species included in this study (McCormick & Polis, 1990). Additionally, long and slender chelae would be more apt for extracting prey from small crevices.

In defence against predators and in interspecific competition, stronger rather than fast chelae are probably more advantageous (as in Sneddon *et al.*, 2000; but see Levinton & Allen, 2005). Species possessing large chelae are considered to be mildly venomous for humans and vertebrates in general. This rule of thumb seems to hold for the few species for which LD50 values have been established. In species with large chelae, the defensive power of venom that is effective against predators seems to be replaced by the possibility to them delivering a stronger pinch. LD50 values are established using vertebrates such as mice, and therefore are more likely an indicator of the potential of the scorpion venom against predators than against prey items, which are usually small invertebrates. If low LD50 values (highly effective venom) only indicate toxicity against vertebrates

(predators), and are inversely related to the venom's effectiveness against invertebrate prey, it would suggest that large claws are important for defence. Although data exist on the presence of single arthropod- and mammal-specific compounds in the venom for some species, these data are insufficient for the species studied here.

Many species of crabs show a strong dimorphism in claw form (heterochelic), whereas scorpions do not. Durophagous crabs will possess a large and strong claw for crushing prey, and a smaller one for manipulating food items (Hughes, 2000). Newlands (1969) suggested that scorpionids may use one chela as a shield, while using the other to pinch the attacker. Such behaviour would pose different functional demands on the 'shield' and the 'weapon'. However, we found no systematic difference in the force-generating performance of the left and right chela over all specimens included in this study. This does not exclude the possibility that scorpions show a preference for the use of one chela on an individual basis. The absence of morphologically heterochelic species of scorpions could be the result of a lack of conflicting selection on claw performance, or a developmental constraint.

Similarly, chela size and shape is highly sexually dimorphic in some crab species. Some scorpion species also show some sexual dimorphism in chela shape. Males in the family Bothriuridae have a different dentition on the inside of the fingers, which is assumed to be an adaptation for holding the female's chelae during mating (Maury, 1975). Also, *P. cavimanus* males differ from females in having a concave section on their chelae, and males of *Opisththalmus* species have more elongate chelae than females (Kovářík, 2009). This shows that there is some developmental plasticity within a species. Echoing another selective pressure in crabs, if chela performance is important for male-male combat, we would expect males to have substantially larger chelae than females. This is not the case in most scorpions, and we suppose that the importance of intra-specific competition as a selective force for chela performance is limited.

The above hypotheses for possible selective forces on scorpion chela form and performance remain to be tested. Clearly, more experimentation will be necessary to explain why some scorpion chelae seem to be optimized for speed, and others for force. Additionally, scorpion chelae and venom functionally overlap in defence and subjugation of prey, and therefore provide an excellent but mostly unexplored system for the study of functional trade-offs.

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## References

- Alexander, A. (1959). A survey of the biology of scorpions of South Africa. *Afr. Wildl.* **13**, 99–106.
- Bub, K. & Bowerman, R.F. (1979). Prey capture by the scorpion *Hadrurus arizonensis* Ewing (Scorpiones, Vaejovidae). *J. Arachnol.* **7**, 243–253.
- Casper, G.S. (1985). Prey capture and stinging behavior in the emperor scorpion, *Pandinus imperator* (Koch) (Scorpiones, scorpionidae). *J. Arachnol.* **13**, 277–283.
- Coddington, J.A., Giribet, G., Harvey, M.S., Prendini, L. & Walter, D.E. (2004). Arachnida. In *Assembling the tree of life*: 296–318. Cracraft, J. & Donoghue, M. (Eds). Oxford: Oxford University Press.
- Dunlop, J.A., Tetlie, O.E. & Prendini, L. (2008). Reinterpretation of the Silurian scorpion *Proscorpius osborni* (Whitfield): integrating data from paleozoic and recent scorpions. *Palaeontology* **51**, 303–320.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.
- Fet, E.V., Neff, D., Graham, M.R. & Fet, V. (2003). Metasoma of *Orthochirus* (Scorpiones, Buthidae): are scorpions evolving a new sensory organ? *Rév. Ibérica Arachnol.* **8**, 69–72.
- Fet, V., Sissom, W.D., Lowe, G. & Braunwalder, M.E. (2000). *Catalog of the scorpions of the world (1758–1998)*. New York: New York Entomological Society.
- Gilai, A. & Parnas, I. (1970). Neuromuscular physiology of the closer muscles in the pedipalp of the scorpion *Leiurus quinquestriatus*. *J. Exp. Biol.* **52** (2), 325–344.
- Govindarajan, S. & Rajulu, G.S. (1974). Presence of resilin in a scorpion *Palamnaeus swammerdami* and its role in the food-capturing and sound-producing mechanisms. *Experientia* **30**, 908–909.
- Harrington, A. (1978). Burrowing biology of the scorpion *Cheloctonus jonesii* Pocock (Scorpionida, Scorpionidae). *J. Arachnol.* **5**, 243–249.
- Herrel, A., Spithoven, L., Van Damme, R. & De Vree, F. (1999). Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analysis. *Funct. Ecol.* **13**, 289–297.
- Hughes, R.N. (2000). Crab claws as tools and weapons. In *Biomechanics in animal behaviour*: 195–206. Domenici, P. & Blake, R.W. (Eds). Oxford: BIOS Scientific Publishers.
- Kleber, J.J., Wagner, P., Felgenhauer, N., Kunze, M. & Zilker, T. (1999). Vergiftung durch Skorpionstiche. *Deutsches Ärzteblatt* **96**, A1711–A1715.
- Kovařík, F. (2009). *Illustrated catalog of scorpions. Part I*. Slavikova, Prague: Clarion Productions.
- Lee, S.Y. (1993). Chela height is an acceptable indicator of chela strength in *Carcinus maenas* (Linnaeus, 1758) (Decapoda, Brachyura). *Crustaceana* **65**, 115–116.
- Lee, S.Y. (1995). Cheliped size and structure: the evolution of a multifunctional decapod organ. *J. Mar. Biol. Ecol.* **193**, 161–167.
- Leeming, J. (2003). *Scorpions of Southern Africa*. Cape Town: Struik Publishers.
- Levinton, J.S. & Allen, B.J. (2005). The paradox of the weakening combatant: trade-off between closing force and gripping speed in a sexually selected combat structure. *Funct. Ecol.* **19**, 159–165.
- Mariappan, P., Balasundaram, C. & Schmitz, B. (2000). Decapod crustacean chelipeds: an overview. *J. Biosci.* **25**, 301–313.
- Maury, E.A. (1975). Sobre el dimorfismo sexual de la pinza de los pedipalpos en los escorpiones Bothriuridae. *Bull. mus. nat. hist. nat. (Paris) Sér. 3* **305**, 765–771.
- McCormick, S.J. & Polis, G.A. (1990). Prey, predators and parasites. In *Biology of scorpions*: 294–320. Polis, G. (Ed.). Stanford: Stanford University Press.
- Miller, G.A. & Chapman, J.P. (2001). Misunderstanding analysis of covariance. *J. Abnorm. Psychol.* **110**, 40–48.
- Newlands, G. (1969). Scorpion defensive behaviour. *Afr. Wildl.* **23**, 147–153.
- Rohlf, F.J. (2004). *tpsDig, digitize landmarks and outlines, version 2.0*. Stony Brook: Department of Ecology and Evolution, State University of New York.
- Schwilk, D.W. (2000). CACTUS: comparative analysis of continuous traits using statistics, v.1.12. Available at <http://www.pricklysoft.org/software/cactus.html>
- Schwilk, D.W. & Ackerly, D.D. (2001). Flammability and serotiny as strategies: correlated evolution in pines. *Oikos* **94**, 326–336.
- Seed, R. & Hughes, R.N. (1997). Chelal characteristics and foraging behavior of the blue crab *Callinectes sapidus* Rathbun. *Estuar. Coast. Shelf Sci.* **44**, 221–229.
- Sensenig, A.T. & Shultz, J.W. (2004). Elastic energy storage in the pedipalpal joints of scorpions and sun-spiders (Arachnida, Scorpiones, Solifugae). *J. Arachnol.* **32**, 1–10.
- Sneddon, L.U., Huntingford, F.A., Taylor, A.C. & Orr, J.F. (2000). Weapon strength and competitive success in the fights of shore crabs (*Carcinus maenas*). *J. Zool. (Lond.)* **250**, 397–403.
- Snodgrass, R.E. (1952). *A textbook of arthropod anatomy*. Ithaca, NY: Cornell University Press.
- Yamada, S.B. & Boulding, E.G. (1998). Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. *J. Exp. Mar. Biol. Ecol.* **220**, 191–211.