

# Maximum force production: why are crabs so strong?

Graeme M. Taylor

Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9 (gmtaylor@odum.biology.ualberta.ca)

Durophagous crabs successfully hunt hard-shelled prey by subjecting them to extremely strong biting forces using their claws. Here I show that, for a given body mass, six species of *Cancer* crabs (*Cancer antennarius*, *Cancer branneri*, *Cancer gracilis*, *Cancer magister*, *Cancer oregonensis* and *Cancer productus*) were able to exert mean maximum biting forces greater than the forces exerted in any other activity by most other animals. These strong biting forces were in part a result of the high stresses (740–1350 kN m<sup>-2</sup>) generated by the claw closer muscle. Furthermore, the maximum muscle stress increased with increasing mean resting sarcomere length (10–18 µm) for the closer muscle of the claws of these six *Cancer* species. A more extensive analysis incorporating published data on muscle stresses in other animal groups revealed that stress scales isometrically with the resting sarcomere length among species, as predicted by the sliding filament model of muscle contraction. Therefore, muscle or filament traits other than a very long mean sarcomere length need not be invoked in explaining the high stresses generated by crustacean claws.

**Keywords:** Uniramia; Crustacea; Decapoda; brachyurans; muscle tension; muscle stress

## 1. INTRODUCTION

Selection for strong biting forces has probably been a key feature in the evolution of clawed crustaceans because hard-shelled prey are a ubiquitous food resource for these benthic predators (Vermeij 1977, 1987; West *et al.* 1991; Smith & Palmer 1994). Many estimates of decapod claw biting forces have been reported and the functional and evolutionary importance of these forces in feeding on hard-shelled prey is significant (Elner 1978; Brown *et al.* 1979; Elner & Campbell 1981; Warner *et al.* 1982; Boulding 1984; Boulding & LaBarbera 1986; Smith & Palmer 1994; Freire *et al.* 1996; Preston *et al.* 1996). Crab claws appear to produce some of the strongest mechanical forces reported for any group of animals; their biting forces having been estimated to be as high as 800 N (Vermeij 1987; Blundon 1988). The exceptionally strong claw biting forces are the product of a single closer muscle acting on the first lever arm of the dactyl (i.e. moveable finger). This closer muscle produces some of the highest maximum muscle stresses (force per unit area of muscle) ever recorded for any muscle type in any animal group; forces of up to 2000 kN m<sup>-2</sup> have been reported for the claw closer muscle of the stone crab (*Menippe mercenaria*) (Blundon 1988). Can the extremely high muscle stresses of crab claws be explained by traditional models of muscle contraction or do we need to invoke a novel mechanism in accounting for these observations?

The sliding filament model of muscle contraction makes a simple prediction: when other factors are equivalent, the maximum muscle stress should increase isometrically with the resting sarcomere length (Gordon *et al.* 1966). It should increase because the force is proportional to the number of myosin–actin cross-bridge sites that can form within each half sarcomere and additional active myosin heads are assumed with increasing filament length. The increase should be isometric with changes in the sarcomere length because stress changes linearly with an overlap of the thick and thin filaments (Gordon *et al.*

1966) and the structural distance between myosin heads is uniform along the thick-filament backbone (Wray 1979). Although the sliding filament model has been widely accepted because it portrays the dependence of active tension on changing sarcomere length with contraction (Gordon *et al.* 1966; Cooke 1997), empirical evidence for the dependence of the maximum muscle stress on the resting sarcomere length among species has remained elusive.

Huxley & Niedergerke (1954) predicted that muscle stress (force per unit area) should increase with increasing resting sarcomere length nearly 50 years ago. This prediction has not been tested rigorously among species because studies have tended to focus on vertebrate or insect flight skeletal muscles, which exhibit little variation in their resting sarcomere length. Unlike vertebrate and insect flight muscles, which yield stresses of 100–300 kN m<sup>-2</sup>, the muscle in decapod crustacean claws can generate stresses of 400–2000 kN m<sup>-2</sup>. Whether the higher stresses reported for this group result from simple differences in the resting sarcomere length or from other differences in the contractile machinery such as filament geometry and kinetics remains unresolved (Jahromi & Atwood 1969; West *et al.* 1992).

## 2. METHODS

### (a) *Experimental animals*

Six north-eastern Pacific *Cancer* species (*Cancer antennarius*, *Cancer branneri*, *Cancer gracilis*, *Cancer magister*, *Cancer oregonensis* and *Cancer productus*) were collected from various shallow-water sites in the vicinity of the Bamfield Marine Station, Bamfield, British Columbia, Canada. In order to measure their claw biting forces, several mid-intermoult crabs of each species were selected based on their estimated claw wear (claw index 2 as described in Taylor *et al.* (2000)). The crabs were housed individually in plastic mesh containers (200 mm × 140 mm × 90 mm) which were submerged in large fibreglass aquaria supplied with running seawater (salinity 32‰ at 10–12 °C). Their biting forces

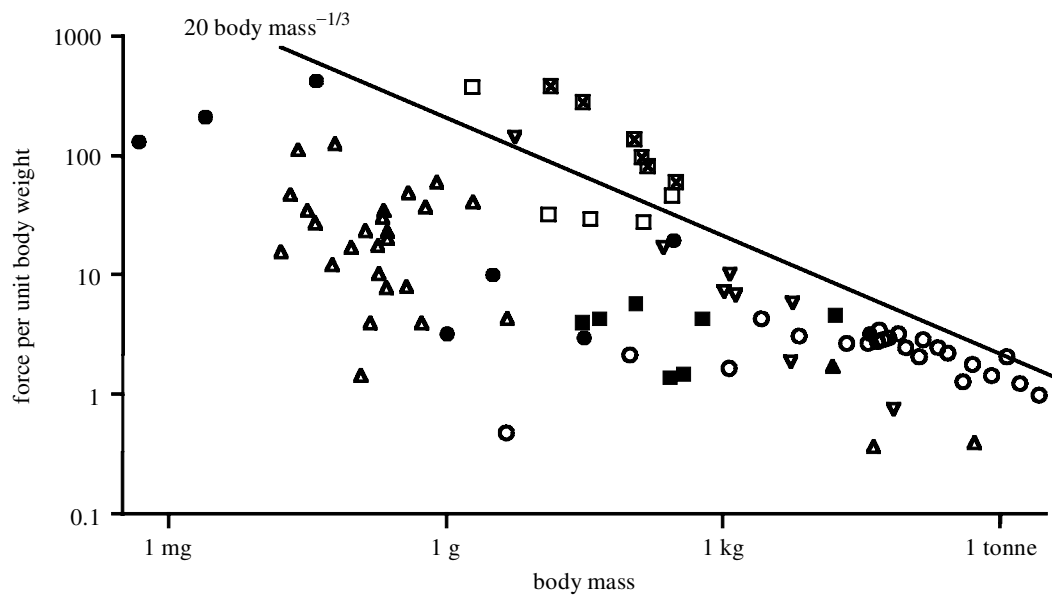


Figure 1. Regression of the maximum force per unit body weight against body mass for several animal species engaged in various activities. Each point represents a single species. Most values are from Alexander's (1985) figure 1. The mean maximum forces exerted by the claw bite forces of the six species of *Cancer* crabs are from this study. In addition, values on arthropod running and pushing were compiled from Evans & Forsythe (1984) and from Full *et al.* (1995), thereby providing a more complete description of the forces exerted around the 1 mg–1 g body mass range. The activities are as follows: running (open circles), jumping (filled circles), pushing and pulling (upwardly pointing open triangles), swimming (filled squares), flight (upwardly pointing filled triangles), nipping (open squares), nipping-*Cancer* spp. (referred to as biting in the text) (open squares containing cross) and biting (downwardly pointing open triangles). The solid line,  $20 \text{ body mass}^{-1/3}$  (body mass in kilograms), represents an upper limit to most of the maximum forces exerted by animals, as suggested by Alexander (1985).

Table 1. *Maximum biting force of claws from six Cancer species assuming an ideal mechanical advantage (i.e. MA = 1)*

species	bite force (N) mean ( $\pm$ s.e.)	range	<i>n</i>	mean body mass (g)
<i>C. antennarius</i>	154.0 (10.2)	63.1–273.8	27	112.4
<i>C. branneri</i>	84.8 (4.3)	65.6–116.6	13	30.5
<i>C. gracilis</i>	128.5 (7.8)	91.1–189.0	14	155.9
<i>C. magister</i>	182.4 (10.9)	116.9–271.0	21	309.5
<i>C. oregonensis</i>	52.9 (2.2)	31.1–76.9	30	13.9
<i>C. productus</i>	132.1 (10.6)	41.9–264.4	30	135.6

were measured within seven days of collection because their maximum force and consistency tended to decline with time in the laboratory (Taylor *et al.* 2000).

### (b) Claw biting force measurements

This was performed as described previously (Smith & Palmer 1994) with minor modifications and the actual bite-force values are reported elsewhere (Taylor *et al.* 2000). In brief, individual crabs were removed from the water and encouraged to grasp a strain gauge apparatus forcefully (Smith & Palmer 1994), which was adjusted to 60% of the maximum gape for each claw. The contact position of the dactyl and pollex with two rings that were mounted on the strain gauge apparatus during the biting force measurements was between the tip and the first tooth along the occlusive surface. The apparatus was calibrated before and after each session with known weights, which covered the range of possible biting forces. The average of these two calibration curves was used to digitize the biting forces (in

newtons) from the original chart recordings. Each session included bite measurements from both the right and left claws in succession of seven to ten crabs. No more than two biting force measurements were obtained for a single claw on any given day and the mean number of bites used to assess the mean biting force of a claw for a single individual was in the range 6.9–8.2.

### (c) Muscle stress calculations

After the biting force measurements were obtained, the claws were autotomized from the crabs and drawn via a camera lucida attached to a dissecting microscope in a view perpendicular to the plane of the dactyl rotation. All linear measurements, such as the manus height and lever lengths 1 and 2 of the dactyl, were digitized from individual claw drawings. The apodemes were dissected and their surface areas measured by digitizing the projected outlines. Muscle stress was then calculated using the formula  $S = F/A \sin 2Q$ , where  $F$  is the force applied to the base of the dactyl by the closer muscle,  $A$  is the area of one side of the apodeme and  $Q$  is the mean angle of pinnation of the fibres (Govind & Blundon 1985). Angle of pinnation measurements were taken from other similar-sized individuals of each *Cancer* species. To ensure representative angles of pinnation of those claws used in the biting force measurements, the claws were fixed (10% buffered formalin) at *ca.* 60% of the maximum claw gape. The angles of six to eight fibres were measured from the mid-section of the closer muscle for each claw. The average ( $\pm$  s.e.) angles of pinnation were as follows: *C. antennarius*  $36.7 \pm 0.71^\circ$  ( $n = 27$ ), *C. branneri*  $36.6 \pm 0.91^\circ$  ( $n = 14$ ), *C. gracilis*  $34.6 \pm 0.82^\circ$  ( $n = 16$ ), *C. magister*  $33.6 \pm 0.96^\circ$  ( $n = 16$ ), *C. oregonensis*  $37.0 \pm 0.92^\circ$  ( $n = 14$ ), and *C. productus*  $31.5 \pm 0.70^\circ$  ( $n = 22$ ).

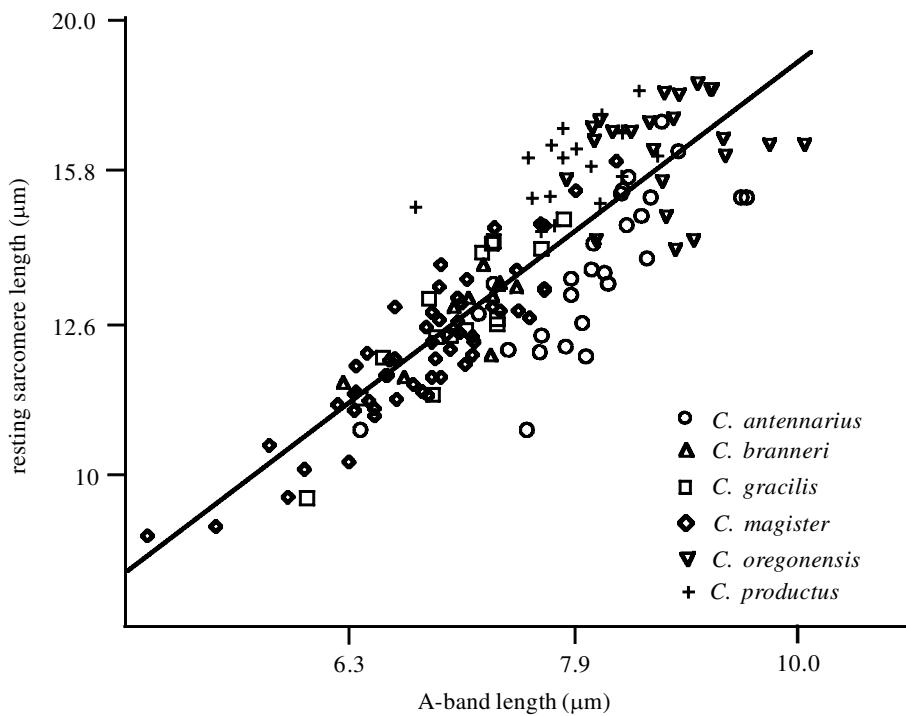


Figure 2. Correlation of the mean claw resting sarcomere length and A-band length for *Cancer* spp. ( $y = 1.119x + 0.151$ ,  $r^2 = 0.747$  and  $p < 0.001$ ). Each point corresponds to a mean value for a single claw closer muscle and the axes are logarithmic.

Table 2. Maximum closer muscle stress of claws from six *Cancer* species

	stress ( $\text{kN m}^{-2}$ ) mean ( $\pm$ s.e.)	range	$n$	mean claw height (mm)
<i>C. antennarius</i>	865.7 (34.8)	551.0–1182.0	24	20.7
<i>C. branneri</i>	1031.5 (61.9)	713.4–1535.7	12	12.5
<i>C. gracilis</i>	525.5 (28.7)	382.8–742.6	14	21.7
<i>C. magister</i>	756.0 (28.2)	519.4–962.9	20	20.8
<i>C. oregonensis</i>	1006.7 (30.2)	816.7–1345.8	21	12.1
<i>C. productus</i>	792.1 (60.0)	421.4–1223.9	15	19.2

Table 3. Sarcomere lengths of the closer muscle of claws from six *Cancer* species

	sarcomere length ( $\mu\text{m}$ ) mean ( $\pm$ s.e.)	range	$n$	mean claw height (mm)
<i>C. antennarius</i>	13.7 (0.32)	10.7–17.1	27	22.9
<i>C. branneri</i>	12.7 (0.27)	11.5–13.7	9	13.2
<i>C. gracilis</i>	12.7 (0.36)	9.6–14.7	15	20.3
<i>C. magister</i>	12.2 (0.26)	10.0–15.3	26	20.7
<i>C. oregonensis</i>	16.5 (0.36)	14.2–17.1	9	10.7
<i>C. productus</i>	16.1 (0.26)	14.4–17.8	13	20.8

#### (d) Measurement of filament lengths

Sarcomere and A-band length measurements were obtained from other crabs of similar size to those used for the biting forces measurements. The claw closer muscles were fixed as described in Govind & Blundon (1985). The sampling of the fibres from the closer muscle of each claw was restricted to a section that ran dorsal–ventral mid-way along the manus. Histochemical analysis supported a restricted sampling regime because the closer muscles of three species (*C. productus*, *C. oregonensis* and juvenile *C. magister*) stained at a uniform intensity over their lengths for both myofibrillar ATPase and NADH diaphorase (G. M. Taylor, unpublished data). The mid-section was divided into four smaller regions, which were defined by exoskeletal carinae running in a proximo-distal direction along the manus. Exoskeletal carinae are homologous structures in *Cancer* (Nations 1975) and, therefore, the sites sampled were consistent between species. Ten fibres were teased apart at random from each of these four regions from wet mount preparations. A single resting sarcomere length from a fibre and its A-band length were measured with a phase-contrast microscope (magnification  $\times 500$ ) via a camera lucida and a digitizing tablet. Therefore, a mean sarcomere length for a given claw was the average of 40 randomly sampled sarcomeres within four predetermined regions.

#### (e) Determination of the scaling coefficient of allometry

Data from the literature were compiled, plotted and analysed in order to define the scaling relationship (see electronic Appendix A, which can be found at The Royal Society Web site, for the plotted data and their sources). I restricted my survey on Vertebrata to a review (Josephson 1993) except for three stress values calculated indirectly for three human muscles (Thorpe *et al.* 1998). Sarcomere lengths were not reported by Thorpe *et al.* (1998), so an average sarcomere length ( $2.7 \mu\text{m}$ ) was assumed based on reported values for mammalian muscle (Josephson 1993). In spite of the considerable variation in sarcomere length displayed by the Uniramia (Hoyle 1983), muscle performance data in the literature were sparse ( $n = 8$ ). All uniramian stress values were from insect flight muscle, which were also reported in Josephson (1993), except for a single high stress value of  $705 \text{ kN m}^{-2}$  for the hind leg tibia extensor of *Schistocerca gregaria* (Bennet-Clark 1975).

### 3. RESULTS AND DISCUSSION

*Cancer* crabs exerted maximum forces using their claws greater than those exerted in any other activity by any

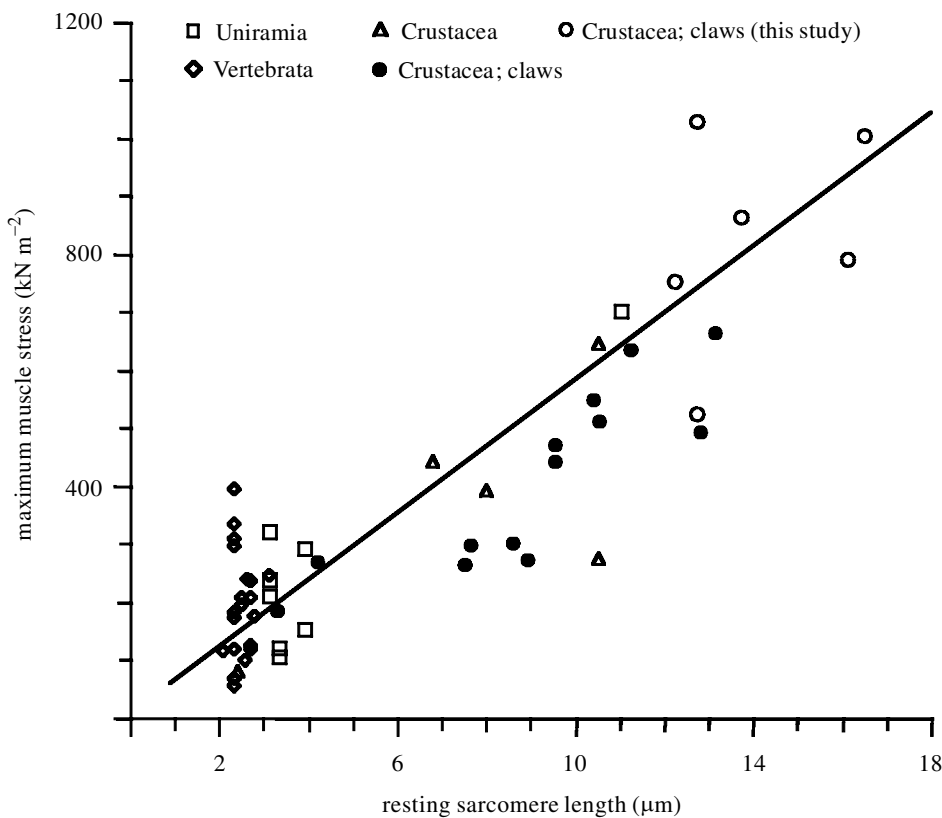


Figure 3. Regression of the muscle resting sarcomere length against the mean maximum stress for data compiled from the literature representing three subphyla (Vertebrata, Uniramia and Crustacea). The slope of the reduced major axis model ( $\beta = 1.134$ ) ( $r = 0.889$ ) did not differ significantly from an expected slope of 1.0 ( $p < 0.05$ ). The axes are linear, while the regression analysis was performed on  $\log_{10}$ -transformed data.

other animal for a given body mass (figure 1 and table 1). Most forces exerted by animals lie below an expected line of  $20 \text{ body mass}^{-1/3}$  (body mass in kilograms) (Alexander 1985) while the biting forces of clawed crustaceans lie close to or above this line. Among animals, the variation in force per unit body weight arises from differences in either mechanical advantage, the muscle allometry relative to body mass, the muscle's angle of pinnation or the stresses the muscle can produce (Alexander 1968, 1985). Durophagous crab claws appear to be selected for maximizing all such traits responsible for increased force production (Taylor 2001). Here, I focus on muscle stress as determined by sarcomere length as the primary agent driving the relatively high biting forces of crabs.

The sarcomere length increased with the A-band length within all six species of *Cancer* crabs examined (figure 2). Therefore, the resting sarcomere lengths reported here were not significantly confounded by differential contraction of the muscles and provide a reliable estimate of the size of the fundamental contractile unit. The A-bands correspond to thick filaments and, thus, provide a more reliable measure of the size of the contractile unit (i.e. the number of potential myosin-actin cross-bridge sites), but most studies have tended to report on sarcomere lengths because, although they will vary depending on the state of the muscle contraction, they are easier to measure.

The maximum muscle stress tended to increase with increasing sarcomere length among species of *Cancer* crabs (figure 3, open circles, and see tables 2 and 3). This same relation was observed when published values for claws from other crustaceans were included (figure 3, solid symbols). Significantly, when all crustaceans were considered together, the slope of this relationship did not differ

from isometry (figure 3). Therefore, for crustacean claws, the maximum muscle stress and, as a consequence, the maximum biting force both increased with sarcomere length as predicted by the sliding filament model. This increased maximum biting force therefore not only evolved via increases in the relative claw size and mechanical advantage (Vermeij 1977, 1978), but also via changes in the muscle properties.

It is well-known that crustaceans are able to generate higher maximum muscle stresses than vertebrates and most insects (Josephson 1993). However, the physiological basis of this difference has remained unresolved: are the higher stresses due simply to increases in the resting sarcomere length or is it necessary to invoke other fibre-associated traits such as the density of the myosin filaments (Jahromi & Atwood 1969; West *et al.* 1992), arthropod 'catch-like' effects (Günzel & Rathmayer 1994), the myofibrillar bundle diameter (Hilber & Galler 1998), differences in the actin-myosin filament ratios (Jahromi & Atwood 1969; West *et al.* 1992) and potential differences in the actin-myosin cross-bridge duty factors (Cooke 1997)? Because of the heterogeneous nature of crustacean muscle (Atwood 1973) and because of the vast diversity of muscle types within the animal kingdom (Hoyle 1983), some have suggested that the sliding filament model offers little more than a general qualitative description of the relation between the structural features of muscle and performance (Jahromi & Atwood 1969; Hoyle 1983). However, examination of the values of muscle stress for crustacean claws along with those for vertebrates and insects revealed that, within and among all three subphyla, 83% of the variation in the muscle stress can be explained by the resting sarcomere length (table 4).

Table 4. *Effects of the subphylum and sarcomere length on the maximum muscle stress*

(MMP, method of muscle preparation (i.e. either whole or isolated fibre(s)); SL, sarcomere length.)

source	d.f.	MS	<i>p</i>
(a) ANCOVA: log maximum stress (dependent)			
subphylum	2	61.7	0.148
log SL	1	142.4	< 0.001
error	48	3.1	—
(b) ANCOVA: log maximum stress (dependent)			
subphyla	1	11.3	0.061
MMP	1	6.1	0.164
MMP × subphyla	1	1.4	0.501
log SL	1	94.5	< 0.001
error	39	—	—

When the differences in the method of muscle preparation were accounted for and the effects of the sarcomere length on muscle stress were removed, there was an almost significant difference in muscle performance between vertebrates and crustaceans (table 4) (limited data on uniramous muscle stress prevented this group from being entered into this analysis). Contrary to expectation, vertebrates tended to produce greater stresses than crustaceans for a given sarcomere length (adjusted least-squares means ( $\pm$  s.e.) of  $383.7 \pm 11.4$  and  $225.6 \pm 11.9$  kN m<sup>-2</sup>, respectively). The majority of the stress values reported for vertebrates are from isolated fibre preparations under isometric conditions and, as such, higher stress values are expected for two reasons: (i) because of the higher densities of the contractile units within a given cross-sectional area for a fibre versus a whole-muscle preparation (Josephson 1993), and (ii) because of the researchers' ability to produce pure isometric contractions of isolated fibres (Thorpe *et al.* 1998). A closer analysis did reveal that the stresses produced by single-fibre preparations were consistently higher than those produced by whole-muscle preparations for crustaceans and vertebrates (adjusted least-squares means (s.e.), crustacean whole muscle =  $211.8 \pm 12.0$  kN m<sup>-2</sup> ( $n = 18$ ), crustacean single fibre =  $240.3 \pm 11.8$  kN m<sup>-2</sup> ( $n = 6$ ), vertebrate whole muscle =  $326.6 \pm 12.3$  kN m<sup>-2</sup> ( $n = 6$ ) and vertebrate single fibre =  $450.7 \pm 12.1$  kN m<sup>-2</sup> ( $n = 14$ )). In addition, the interaction between the subphylum and method of muscle preparation was not significant so, regardless of muscle preparation, vertebrates tended to produce higher stresses for a given sarcomere length (table 4).

Clearly, the higher muscle stresses reported here and elsewhere (Warner & Jones 1976; Elner & Campbell 1981; Warner *et al.* 1982; Govind & Blundon 1985; Blundon 1988) for crustacean claws result almost entirely from differences in the resting sarcomere length and other differences in the muscle characteristics need not be invoked.

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