Probing the evolutionary biomechanics of elastic energy storage in mantis shrimp

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Abstract

Structural and biomechanical variation in elastic energy storage mechanisms is fundamental to the rich evolutionary diversity of fast movements. Mantis shrimp (Crustacea: Stomatopoda) power their fast and powerful predatory appendages with an exoskeletal compressive spring. Here we compare the mineralization patterns of the spring and elastic energy storage mechanics across 10 species of mantis shrimp, including species with hammer-like, spear-like and intermediate raptorial appendage forms. Using computed tomography to visualize mineralization patterns, we found that the primary spring is conserved across all species, but its size, length and articulations vary considerably. A materials testing machine was used to measure the maximum compression force of the spring and the spring constant. We found that spring constants were nearly overlapping across species, even with a 200-fold range in body mass; however, body size scaling relationships varied across taxa. For example, three taxa exhibited no correlation between spring mechanics and body size while *Gonodactylaceus falcatus* exhibited a significant positive correlation between body size and maximum compression force and a non-significant association with spring constant, and *Gonodactylus chiragra* showed no correlation between body size and maximum force and a significant negative correlation with spring constant. This variation in spring form and mechanical behavior suggests that different prey capture strategies may indeed be associated with evolutionary variation in the underlying power-amplifying springs.

Introduction

Mantis shrimp use raptorial appendages (Fig. 1) to generate extremely fast and powerful strikes. [1, 2, 3, 4] Combining a latch system with an exoskeletal spring allows them to store substantial elastic potential energy prior to releasing the strike. [4, 5] Spring mechanics and mineralization have been characterized previously in *Gonodactylaceus falcatus* and *Odontodactylus scyllarus*, which use their raptorial appendages as hammers (i.e., "smashers"). They store elastic energy in a mineralized "tape spring", called the ventral bar, which extends from the meral-V along the ventral limits of the merus segment (Fig. 2). *G. falcatus*' spring was found to act as a linear, Hookean spring where $F=kx$, such that F is maximum force, x is displacement and k is the spring constant. [4] We focused on two primary questions in this study:

1) Do the mechanical properties and mineralization of appendages across stomatopods indicate that the spring is present in all species?

2) What are the differences in the mechanical properties of the spring system across appendage types?

Methods

• Ten species were tested, including both smashers and spearers.

• Specimens from each species were scanned using Computed Tomography (micro-CT) to determine the mineralization patterns of the appendage.

• A materials testing machine was used to measure the force produced while compressing the exoskeletal spring (Fig. 3).

• We calculated average maximum compression force, spring constant, and resilience.

Table 1. Sample sizes, appendage sizes and species tested. Smasher species are denoted in blue.

Species	Number of Individuals (Appendages)	Merus Length Range (mm)
Gonodactylus chiragra	10 (11)	15.55 – 23.20
Gonodactylus smithii	11 (14)	15.54 – 20.86
Hemisquilla californiensis	11 (11)	18.35 – 44.33
Lysiosquillina maculata	5 (5)	28.67 – 53.76
Lysiosquillina sulcata	3 (3)	23.41 - 32.01
Neogonodactylus bredini	1 (1)	12.08
Neogonodactylus festae	1 (1)	11.23
Neogonodactylus oerstedii	6 (8)	12.53 – 17.79
Neogonodactylus wennerae	2 (3)	14.29 – 17.70
Pseudosquilla ciliata	4 (6)	11.97 – 12.93
Gonodactylaceus falcatus	8 (8)	9.33-15.96

Figure 1. The California mantis shrimp, *Hemisquilla californiensis*, has large raptorial appendages, which it uses to dislodge and break molluscs. Image by Roy Caldwell.
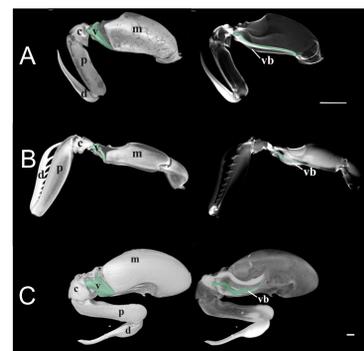

Figure 2. Three representative micro-CT scans illustrate the variation in mineralization patterns across an undifferentiated raptorial appendage (A, *Hemisquilla californiensis*), a spearer (B, *Lysiosquillina maculata*), and a smasher (C, *Gonodactylaceus falcatus*). The component segments are labeled as: merus (m), meral-V (v), carpus (c), propodus (p), dactyl (d), and the ventral bars (vb).
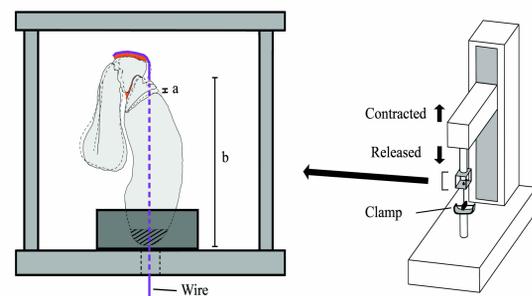

Figure 3. The spring parameters were measured by compressing and releasing the spring with a materials testing machine. The machine pulled on a wire, running through the merus, to compress the appendage a distance represented by "a." The compression distance and the force required to contract the appendage were recorded at 500 Hz and used to analyze the spring properties of the appendage. Distance "a" represents the maximum contraction distance. Distance "b" is the merus length measured in Table 1.

Results

Figure 4. A phylogeny of stomatopods with the taxa sampled indicated in red. [6] Note that all *P. ciliata* specimens failed during mechanical spring tests and thus were not included in the results.
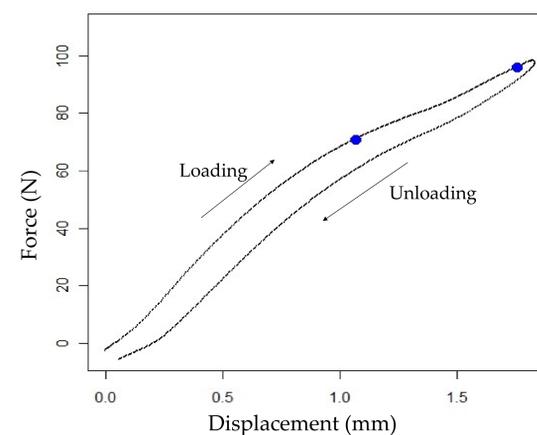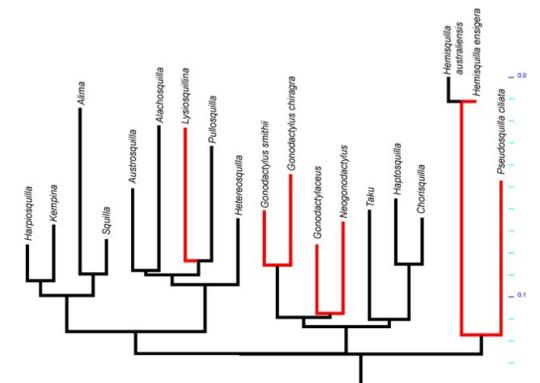

Figure 5. A representative force-displacement curve. Maximum force was calculated as the peak force of the loading curve. The spring constant was calculated as the slope of a linear regression line applied to the linear region, 60%-95%, of the loading curve, denoted by the blue points. Resilience was calculated by dividing the area under the unloading curve by the area under the loading curve.
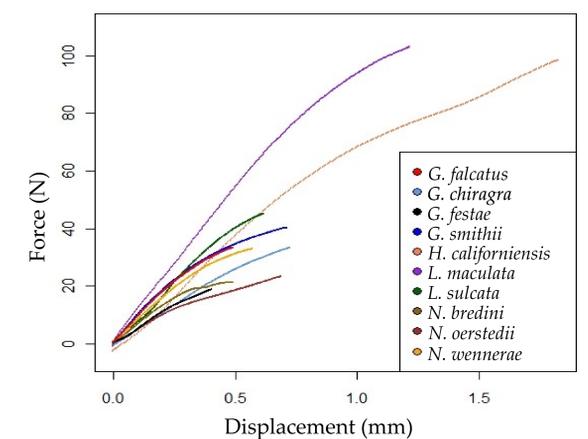

Figure 6. Representative loading curves showing the linear increase in force with displacement and the variation in maximum force across species.
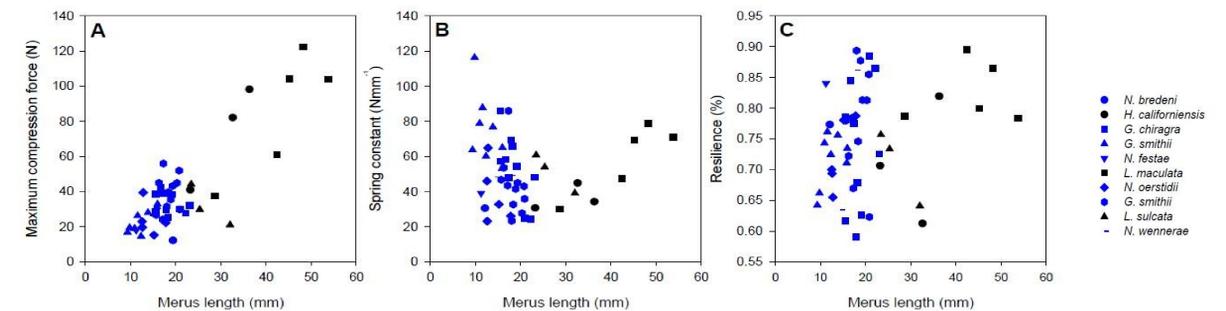

Figure 7. Scaling of spring mechanics within and across species. Each species is indicated with a unique symbol; smasher species are indicated in blue, spearers are in black. Within *G. falcatus* and across species, maximum compression force increased with increasing merus size (A; Least squares linear regression, ANOVA, p<0.05; phylogenetically independent contrasts (PIC) yielded a significant positive relationship if df were not reduced due to a polytomy). B. Spring constant was negatively correlated within some smasher species and positively correlated with some spearer species; however, across species, using both species data and PIC, the spring constant was not significantly correlated with merus length. C. Resilience was not correlated with merus length within or across species.

Discussion

The spring that powers the mantis shrimp strike is conserved across species, despite a spectrum of feeding ecologies that range from smashing to spearing prey. For all species studied, the ventral bars are areas of high mineralization and thus are likely the primary location of the spring, as in *G. falcatus*. [5] The spring in most species can be characterized as Hookean and have overlapping spring constants.

Although all species showed similarities in spring location and spring constant, there was variation in the structure of the spring and some of the spring mechanics. For instance, the maximum compression force was greater in larger animals, which in this study were species with spearer and intermediate appendage morphologies. Furthermore, a smasher and a spearer species showed different scaling relationships between the spring constant and merus length. These variations in spring structure and mechanics may be important correlates with the evolution of different feeding ecologies.

Acknowledgements

References

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