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Evolution of mantis shrimp telson armour and its role in ritualized fighting

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Mantis shrimp possess both formidable weapons and impact-resistant armour that clash during ritualized combat. The telson is one of few biological structures known to withstand the repeated high impact forces of smashing mantis shrimp strikes, and it is hypothesized that this pairing of armour and weapon is associated with the evolution of telson sparring. We carried out a comparative analysis of telson impact mechanics across 15 mantis shrimp species to assess if the telsons of sparring species (i) are consistently specialized for impact-resistance, (ii) are more impact-resistant than those of non-sparring species, and (iii) have impact parameters that correlate with body size, and thereby useful for assessment. Our data from ball drop tests show that the telsons of all species function like a stiff spring that dissipates most of the impact energy, but none of the measured impact parameters are correlated with the occurrence of sparring behaviour. Impact parameters were correlated with body mass for only some species, suggesting that it is not broadly useful for size assessment during ritualized fighting. Contrary to expectation, sparring mantis shrimp do not appear to have coevolved telson armour that is more robust to impact than non-sparring species. Rather, telson structure is inherently impact-resistant.

1. Background

Animals that possess potent weapons largely participate in ritualized fighting to resolve conflicts over resources without serious injury or fatality [1]. When ritualized behaviour escalates from displays to physical combat, the availability of adequate protective armour could be indispensable. For animals such as red deer, which physically interlock their antlers during ritualized combat, the antlers function effectively as both weapon and impact-resistant armour [2,3]. Such multifunctional structures are beneficial because the costs of developing specialized or elaborate weaponry can limit the development of other morphological traits [4], making it potentially difficult for animals to evolve both robust weapons and armour. Examples of distinct armour for ritualized fighting are rare, but mantis shrimp present an interesting case in which their unique form of ritualized combat, termed telson sparring [5], may have coevolved with specialized morphological armour. During telson sparring, mantis shrimp take turns firing their ballistic weapons (i.e. raptorial appendages) against the telson, or tailplate, of their opponent. Individuals direct nearly every strike to the telson, and this is facilitated by the recipient assuming a coiled position referred to as a 'telson coil' [5,6]. This behaviour imparts the telson with a fundamental role in ritualized combat, for which it must be mechanically robust to the repeated strikes of conspecifics.

Fascination with the raptorial weapon and its prospects for bioinspiration have led to extensive study of the appendage and strike mechanics [7–13], greatly overshadowing the nature and potential of telson armour. Using a spring-loaded system, smashing mantis shrimp unfurl their raptorial appendages with extreme accelerations that cause cavitation and produce impact forces as great as 1500 N [8]. Predatory strikes produce enough force to break hard mollusc shells, but may require anywhere from a single strike to hundreds
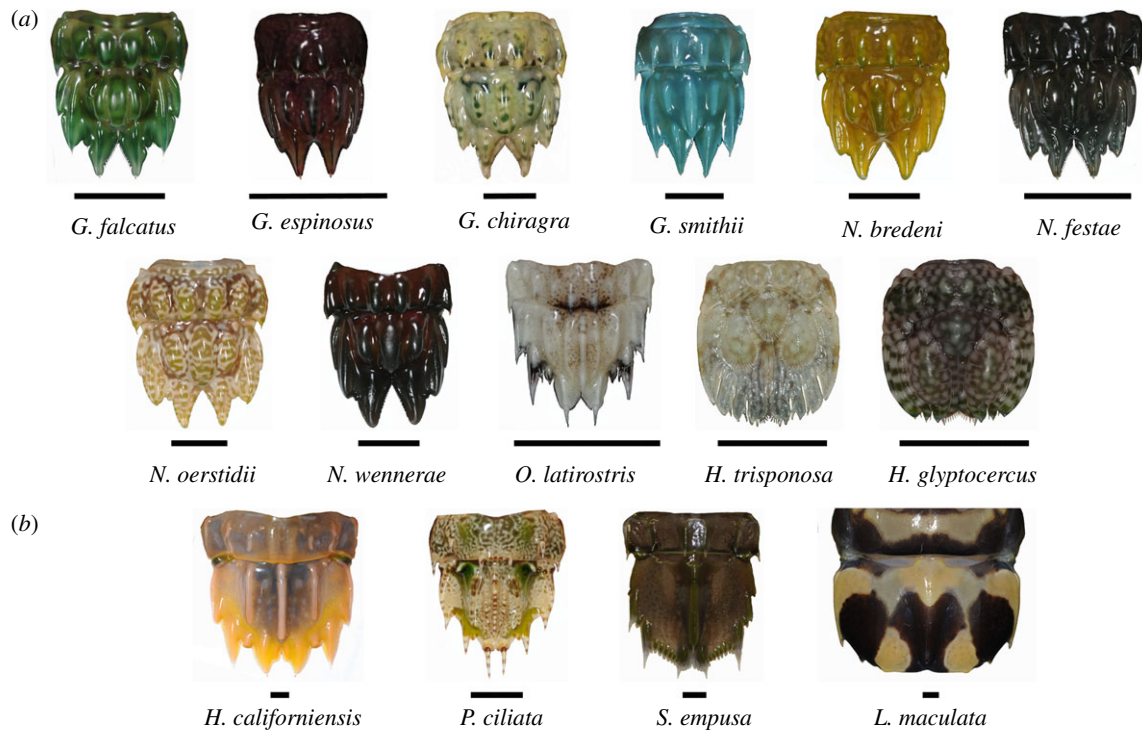
Figure 1. Telson diversity of mantis shrimp species used in this study. (*a*) Upper two rows are sparring species. (*b*) Bottom row is non-sparring species. Scale bar, 10 mm. All telson images, except that of *S. empusa*, modified from and courtesy of Claverie & Patek [20]. (Online version in colour.)

of strikes to do so [14]. Sparring strikes contain more energy than predatory ones [15], yet the telson withstands multiple strikes during a single sparring match and likely numerous strikes from conspecifics during the long intermoult period (over three months [16]). Intraspecific fighting is common because burrows and cavities are used for shelter and mating, but are often a limited resource that mantis shrimp aggressively defend [17], and telson sparring is a critical element in this defence. It is essential for mantis shrimp to maintain the structural integrity of both weapon and armour. Damaged or lost appendages, and even moulting, causes mantis shrimp to concede contests more readily [6,18,19]. A damaged telson may likewise reduce an animal's ability to defend its burrow, placing selective pressure on impact-resistance.

Telson morphology is unsurprisingly diverse among the more than 500 species of mantis shrimp [20,21], though there are some generally consistent features. Most telsons, for instance, are dome-shaped with 1 to 3 carinae, which are raised protuberances of relatively thick and heavily calcified cuticle (figure 1). When multiple carinae are present, their spacing leaves insufficient width for the dactyl heel to contact the cuticle between them, thereby restricting strikes to the carinae. Just as the dactyl heel must be sufficiently hard to resist penetration during impact, so must be the carinae of the telson. In *Neogonodactylus wennerae*, the carinae are heavily calcified, but the surrounding cuticle is generally thinner and less calcified, imparting flexibility to the telson [22]. Thus the telson as a structure functions like engineered impact resistant armour, where the hard carinae resist penetration and the surrounding cuticle deforms to allow energy dissipation.

The impact response of the telson defines its ability to withstand strikes, but it may also provide size- or performance-based information to both individuals during sparring. Energy exchange occurs during each impact and several parameters have the potential for assessment by opponents. Impact parameters such as the coefficient of restitution (COR), impulse, and duration of contact all correlated with body size in the smasher *N. wennerae* [22]. Any of these parameters could indicate an animal's mechanical potency, thereby providing relevant information on aggression or endurance, which are valuable for assessment. Body size is generally a good predictor of contest winners [5,23], so information extracted from telson impacts may be especially helpful when one individual remains obscured within the burrow entrance. If so, the morphology of the telson may contribute to ritualized fighting in multiple ways, as armour and a source of information for assessment.

Telson sparring is described as common among mantis shrimp with smasher type appendages (Gonodactylidae), but is not known to occur in species with spearer appendages [17,24]. Spearer appendages are distinct from those of smashers in morphology (the dactyls are armed with spines rather than a bulbous heel), strike kinematics (they achieve lower accelerations and impact forces) [25], and function (they are primarily used to capture fast-moving or soft-bodied prey) [17]. Despite these differences, spearing appendages are still deadly and spearer species will either strike other mantis shrimp with a closed dactyl to limit damage or simply impale them, causing significant injury [17]. Telson sparring has not been observed in any spearer species, but if it were present, their reduced impact forces may not require as robust impact-resistant armour as smasher species. Superficially, telsons appear to be more robust in smashers that participate in telson sparring and it has therefore been hypothesized that telson armour coevolved with ritualized fighting [17].

The morphological variation in mantis shrimp telsons and the confined presence of telson sparring behaviour to smasher species posit interesting possibilities about its development as both impact-resistant armour and an

Table 1. Information on the species used in this study. Species with smasher appendages are grouped as sparring species (white rows). Species with spearer and unusual smasher appendages were grouped as non-sparring species (grey rows). N is the number of individuals (female, male).

family	genus	species	appendage	N	mass range (g)	collection location
Gonodactylidae	Gonodactylaceus	falcatus	smasher	5 (1,4)	0.24–0.93	Oahu, Hawaii
Gonodactylidae	Gonodactylellus	espinosus[a]	smasher	5 (4,1)	0.24–0.40	Lizard Island, Australia
Gonodactylidae	Gonodactylus	chiragra	smasher	7 (3,4)	2.98–5.93	Lizard Island, Australia
Gonodactylidae	Gonodactylus	smithii	smasher	5 (2,3)	3.89–6.15	Lizard Island, Australia
Gonodactylidae	Neogonodactylus	bredini	smasher	5 (3,2)	0.54–1.29	Isla Galeta, Panama
Gonodactylidae	Neogonodactylus	festae	smasher	9 (4,5)	0.62–1.26	Isla Naos, Panama
Gonodactylidae	Neogonodactylus	oerstedii[a]	smasher	5 (4,1)	1.41–4.68	Isla Galeta, Panama
Gonodactylidae	Neogonodactylus	wennerae	smasher	17 (9,8)	0.47–4.60	Tampa Bay, Florida
Odontodactylidae	Odontodactylus	latirostris[a]	smasher	4 (5,0)	1.04–1.73	Lizard Island, Australia
Protosquillidae	Haptosquilla	glyptocercus	smasher	5 (4,1)	0.44–0.72	Lizard Island, Australia
Protosquillidae	Haptosquilla	trispinosa[a]	smasher	5 (2,3)	0.24–0.81	Lizard Island, Australia
Hemisquillidae	Hemisquilla	californiensis	unusual smasher	5 (1,4)	24.3–106	Santa Catalina Island, California
Lysiosquillidae	Lysiosquillina	maculata	spearer	4 (0,4)	36.5–192	Lizard Island, Australia
Pseudosquillidae	Pseudosquilla	ciliata	spearer	5 (4,1)	3.30–4.64	Oahu, Hawaii
Squillidae	Squilla	empusa	spearer	5 (5,0)	7.61–11.2	Panacea, Florida

[a]Smasher species with no documentation of sparring (unknown).

assessment tool, and ultimately its role in the evolution of ritualized fighting. We examined these possibilities by testing the hypotheses that the telsons of sparring species (i) are consistently specialized for impact-resistance, (ii) are more impact-resistant than those of non-sparring species, and (iii) have impact parameters that correlate with body size. Meaningful assessment of impact mechanics in biological systems is challenging, and we took the approach of using collision energetics as established in previous work on the mantis shrimp telson impact response [22]. The exchange of kinetic energy during impact is defined by the structures involved and is informative of their mechanical behaviour under realistic interactions. Ball drop tests were used to measure and compare the telson impact mechanics of 15 species of mantis shrimp, encompassing smashers, spearers, and an undifferentiated form [9]. Key aspects were mapped onto a phylogeny for evolutionary context and detailed analysis of telson morphology and mechanical properties of a smasher and a spearer species provided further structural insights.

2. Material and methods

2.1. Animal acquisition and maintenance

A total of 91 individuals from the 15 chosen mantis shrimp species (Crustacea: Stomatopoda) were either collected from the field or purchased from commercial suppliers (table 1). Telson morphology is diverse among these species (figure 1). The large species, *Hemisquilla californiensis* and *Lysiosquillina maculata*, were kept in individual 20 l tanks filled with recirculating artificial seawater (salinity: 32–36 ppt, 22°C). All other species were kept in individual 2 l plastic cups filled with artificial seawater that was changed twice weekly (salinity: 32–36 ppt, 22°C). Animals were fed both fresh and frozen grass shrimp twice weekly.

Body mass and sex were determined for each animal prior to testing. Animals were checked for moult stage by examining a pleopod under the microscope [16]. Only intermoult animals were used for this study. Males and females were combined for analyses due to limited availability of animals and the fact that both sexes are known to participate in telson sparring. None of the impact response parameters differed between sexes for *G. chiragra* and *N. festae* (T-tests; all $p \geq 0.43$), or for *N. wennerae* from a previous study [22]. Immediately prior to each impact test, individuals were anaesthetized and euthanized by placement in a −20°C freezer until dead but not frozen. Data for *Neogonodactylus wennerae* were gleaned from a previous study [22].

2.2. Impact tests

The impact response of the mantis shrimp telson was determined through impact tests, as described in detail in a previous study [22]. Whole mantis shrimp were positioned horizontally and secured on top of a 2.5 cm thick steel countertop slab. The telson rested on a small 3.0 mm thick Plexiglass strip glued to the slab, which allowed positioning for a direct, collinear impact. To prevent dislodgement of the animal at impact, a small drop of cyanoacrylate glue was placed on the tip and base of each uropod, and at the base of both sides of the fourth abdominal tergite. A small 440C stainless steel ball (6.33 mm diameter; 1.022 g; Rockwell C: 58-65; Small Parts, Miramar, FL, USA) was dropped through the air, without spin, from an electromagnet (model E-66-100-34, Magnetic Sensor Systems, Van Nuys, CA, USA) that was attached to a ring stand. The electromagnet was positioned approximately 100 mm above each animal, giving an impact velocity of 1.67 m s^{-1}. The kinetic energy of this collision was calculated using

$$\frac{1}{2}mv^2,$$

where m is ball mass and v is velocity at impact, and was determined to be equivalent to a smasher mantis shrimp (body mass of 1.0 g) striking at 15 m s^{-1}. This energy is thus comparable either to a small animal striking with high velocity or to a large animal striking with low velocity, which is reflective of the negative scaling of strike velocity with body mass across species of

smashing and spearing mantis shrimp [12]. To facilitate comparison among species, we used the same impact energy for all drop tests. It is important to acknowledge that our tests do not encompass the range of strike velocities observed in different mantis shrimp species, which limits the scope of our results because the COR is sensitive to impact velocity [26].

For each animal, the ball was dropped 10 times onto each of two targets: the centre carina of the telson and the centre of the fifth abdominal tergite (see [22]). The order of testing on either the telson or abdomen was randomized to control for test order. For the two large species, *H. californiensis* and *L. maculata*, additional ball drop tests were performed in between or adjacent to the carinae. Animals were covered by a seawater-soaked paper towel in between ball drops to prevent dehydration.

Each ball drop test was recorded with a high-speed digital video camera (APX-RS, Photron, San Diego, CA, USA or Phantom Miro 310, Vision Research, Wayne, NJ, USA) at 15 000 frames s^{-1}, 0.067 ms shutter duration, and 256 × 512 pixel resolution. A 10 mm × 10 mm grid was placed in the camera's field of view for calibration in addition to the ball.

A coarse examination of impact strength and failure using ball drop tests was performed on two species: a smasher, *Neogonodactylus bredeni* ($N = 5$, mass = 0.95 ± 0.63 g), and a spearer, *Pseudosquilla ciliata* ($N = 5$, mass = 3.12 ± 1.7 g). For these tests, animals were prepared and tests were performed as described above, but drop tests were conducted with a series of four steel balls in order of increasing size: (i) 6.33 mm diameter, 1.022 g, (ii) 9.53 mm diameter, 3.466 g, (iii) 15.89 mm diameter, 15.09 g, and (iv) 19.05 mm diameter, 27.85 g. All balls were 440C and of the same Rockwell C hardness (58–65; Small Parts, Miramar, FL, USA). This series of ball drops produced impact energies estimated to be equivalent to: (i) a 1.0 g animal striking at 15 m s^{-1}, (ii) a 2.0 g animal striking at 20 m s^{-1}, (iii) a 5.0 g animal striking at 20 m s^{-1}, and (iv) a 25 g animal striking at 15 m s^{-1}. Each ball was dropped on the telson once, in order of increasing size. After each impact the telson was examined for cracks and tests were ended once cracks were detected. Impact strength was estimated as the greatest impact energy that did not induce any visible cracks.

2.3. Impact parameters

The COR was calculated by measuring the velocity before and after ball impact, using the 10 frames preceding contact and the 10 frames following separation, respectively. The first and last frames in which the ball was in contact with the specimen were determined (Irfanview v. 4.20, Irfan Skiljan, Austria) and then ball displacement over 10 frames was measured (SigmaScan Pro 5.00, SPSS, Chicago, IL, USA). From these distances and changes in time, impact and separation velocities were determined and used to calculate the coefficient of restitution, *e*:

$$e = \frac{v_f}{v_i},$$

where v_f is the velocity at separation and v_i is the velocity at impact [26,27]. The amount of energy lost during impact is calculated as

$$1 - e^2,$$

where *e* is the coefficient of restitution [28,29].

Impact was also modelled as a collision between two springs, and spring stiffness, *k*, was calculated using

$$k = m\frac{\pi^2}{t^2},$$

where *m* is ball mass and *t* is impact duration [28,30].

Impact duration was calculated as the time between first contact and separation. Deformation was estimated as the displacement of the ball during the compression phase of impact. Finally, impulse, *I*, was calculated using the change in momentum

$$I = m\Delta v,$$

where *m* is ball mass and Δv is the change in ball velocity (i.e. $v_i + v_f$).

Impact parameters were calculated for each drop test and then averaged for each animal.

2.4. Hardness tests

Materials testing was conducted on the telson of one smasher species, *Neogonodactylus bredeni* ($N = 8$), and one spearer species, *Squilla empusa* ($N = 8$). Telsons were excised from the animals and cleaned of internal tissue. Dissection scissors were used to carefully cut around the base of the central carina and then the ventral surface of the carina was sanded with sandpaper until flat. The ventral side of the prepared carina was then secured to an aluminium block with cyanoacrylate, exposing the dorsal surface of the carina for indentation. A series of five indents were made along the midline of the carina, penetrating the epicuticle layer, using a nanoindentation materials testing machine (Nano Hardness Tester, Nanovea, Irvine, CA, USA) equipped with a Berkovich diamond indenter tip. Indents were carried out with a load of 40 mN and loading and unloading rates of 80 mN min^{-1}. This load limited penetration to the outer region of the cuticle (epi- and exocuticle layers). Hardness and stiffness values of indentations were averaged for each specimen.

2.5. Morphology

Telsons from one *Neogonodactylus bredeni* and one *Squilla empusa* were examined using scanning electron microscopy (SEM). The telsons were excised, cleaned, and cut transversely across the dorsal surface. Samples were placed in a critical point drier (AutoSamdri 815 Series A, Tousimis, Rockville, MD, USA), secured to a double 90° SEM mount revealing the cross section, and sputter coated with iridium. Cross sections were examined with an ultra-high resolution SEM equipped with energy dispersive X-ray (EDX) (XL30 SFEG, FEI, Hillsboro, OR, USA; Oxford X-MAX 80 EDS detector, Concord, MA, USA) at a 20 kV acceleration voltage. EDX elemental mapping was carried out at 10 kV and used to visualize the distribution and density of key elements (Ca, Mg, and P) in the dorsal region of the carinae.

2.6. Phylogeny

The sampling of Stomatopoda for this study arguably spans the known phylogeny of the group [31]. To assess possible covariation of telson armour with ritualized fighting, a phylogeny was constructed for the 15 mantis shrimp species used in this study. DNA sequences for mitochondrial cytochrome oxidase subunit I (COI), 12S rRNA (12S) and 16S rRNA (16S) and nuclear 28S rRNA (28S) and 18S rRNA (18S) were sourced from GenBank for 14 of the terminals and new sequences were generated for *Neogonodactylus festae* (table 2). The COI sequences were aligned using MUSCLE [32], while rDNA sequences (12S, 16S, 18S and 28S) were separately aligned using MAFFT [33], with the Q-INS-I option and default gap open and extension parameters. The third codon positions of COI were excluded based on the evidence of saturation found by Van der Wal *et al.* [31]. The five gene partitions were concatenated and analysed using RAxML 8 [34] using the GTR+G model separately for each partition. Clade support was assessed via 100 bootstrap pseudoreplicates using the same model. The tree was rooted using *Hemisquilla californiensis*, based on a previous phylogenetic study of Stomatopoda [31].

Table 2. Stomatopod terminals used in this study with GenBank accession numbers. Dash (—) indicates missing sequence. *Hemisquilla californiensis* was used as the outgroup based on previous studies.

terminal	CO1	16S	12S	18S	28S (D2–D7)	28S (D9–D10)
Gonodactylaceus falcatus	HM138786	HM138827	—	HM138871	HM180015	HM180059
Gonodactylellus espinosus	HM138782	HM138822	—	HM138866	HM180010	HM180054
Gonodactylus chiragra	HM138785	HM138826	AF107594	HM138870	HM180014	HM180058
Gonodactylus smithii	HM138788	HM138829	AF107595	HM138873	HM180017	HM180061
Hemisquilla californiensis	HM138791	HM138832	—	HM138876	HM180020	HM180064
Haptosquilla glyptocercus	HM138789	HM138830	AF107599	HM138874	HM180018	HM180062
Haptosquilla trispinosa	HM138790	HM138831	—	HM138875	HM180019	HM180063
Lysiosquillina maculata	HM138793	HM138834	AF107603	HM138878	HM180022	HM180066
Neogonodactylus bredini	HM138795	HM138837	—	HM138866	HM180025	HM180069
Neogonodactylus festae	a	—	—	a	a	a
Neogonodactylus oerstedii	HM138796	HM138838	AF107596	HM138882	HM180026	HM180070
Neogonodactylus wennerae	KT001541	KT001544	—	KT001547	KT001550	—
Odontodactylus latirostris	HM138797	HM138841	—	HM138885	HM180029	HM180073
Pseudosquilla ciliata	HM138800	HM138844	AY947836	HM138888	HM180032	HM180076
Squilla empusa	HM138809	HM138853	AF107605	HM138897	HM180041	HM180085

[a]*Neogonodactylus festae* was newly sequenced for this study and provided by M. Porter.

2.7. Analysis

Impact parameters were compared between the telson and the abdomen of each species using either paired *t*-tests or Mann–Whitney and were correlated with body mass using least-squares linear regression. To facilitate comparisons across species, those known to spar were coded as a binary character, 'Sparring'; those with smashing appendages and known to spar were coded as sparrers, while those with spearer appendages were coded as 'non-sparring' (= *L. maculata*, *P. ciliata* and *S. empusa*). Smasher species with no documentation of sparring behaviour were coded as 'unknown'. The undifferentiated form, *H. californiensis*, does not telson spar and was coded as a 'non-sparring' species. Impact parameters were compared across species using ANCOVA with body mass as a covariate followed by *post hoc* Tukey tests when appropriate. Tukey adjusted *p*-values were used to account for multiple pairwise comparisons (105 tests) and are reported as ranges of *p*-values. All statistics were performed using R (v3.0.2). Results are represented as mean ± s.d.

To consider the evolution of telson impact features within the phylogeny, the mean COR and spring stiffness for each species were mapped as continuous characters onto the maximum-likelihood phylogeny after being scored in Mesquite 3.6 [35]. Transformations were estimated using maximum parsimony. The transformation for Sparring was then mirrored against transformations for COR and spring stiffness to visually assess any possible covariability.

3. Results

The maximum-likelihood phylogenetic analysis gave the best tree (figure 2) (log-likelihood = −18784.2) that was largely congruent, given the taxon sampling, with previous results [31]. The main exception was the placement of the gonodactyloid *Haptosquilla*, which did not group with other members of this taxon. This *Haptosquilla* clade showed a relatively long branch compared to other stomatopods. Also, *Pseudosquilla* formed a clade with *Squilla* rather than with other gonodactyloids. There was overall low bootstrap support for these

relationships, as is also apparent in Van der Wal *et al.* [31] and it would appear that much more data is required to properly infer stomatopod phylogeny. The transformations for sparring evolution, spring stiffness and COR are shown in figure 3 on the maximum-likelihood topology. The placement of *Haptosquilla* means that sparring either evolved twice or that the *Pseudosquilla*/*Squilla* clade has lost sparring. Both spring stiffness and COR showed marked homoplasy and neither showed any obvious patterns relative to the occurrence of sparring behaviour (figure 3).

3.1. Impact parameters

The COR of the telson was significantly lower than that of the abdominal tergite for only three species of smashers (*N. bredeni*, *N. wennerae*, and *H. glyptocercus*) and the primitive smasher *H. californiensis* (table 3). All other species had similar CORs for both telson and abdominal tergite (table 3). All but two species had the same telson COR (ANCOVA, $F_{14,60} = 10.03$, $p \ll 0.001$) and there was no effect of mass ($F_{14,60} = 2.73$, $p = 0.10$) or interaction between species and mass ($F_{14,60} = 2.73$, $p = 0.14$) (figure 4a). The species that differed were *H. californiensis*, which had a COR lower than all species (adj $p \ll 0.001$ to 0.007) except *S. empusa* (adj $p = 0.21$) and *S. empusa*, which had a COR lower than seven other species (adj $p \ll 0.001$ to 0.02). The telson COR does not reveal any evolutionary pattern related to sparring and non-sparring behaviour among species (figure 3a).

Spring stiffness of the telson was consistently greater than that of the abdomen for all smasher species (table 3) and was only statistically greater than the abdomen for one species of spearer (*L. maculata*). In alignment with the spring constant, most telsons experienced significantly less deformation during impact than the abdomens, at least for the smasher species (table 3). All species, regardless of sparring behaviour and body mass, had the same telson spring stiffness (ANCOVA, $F_{14,60} = 1.28$, $p = 0.25$; mass covariate $F_{14,60} = 0.67$, $p = 0.42$)
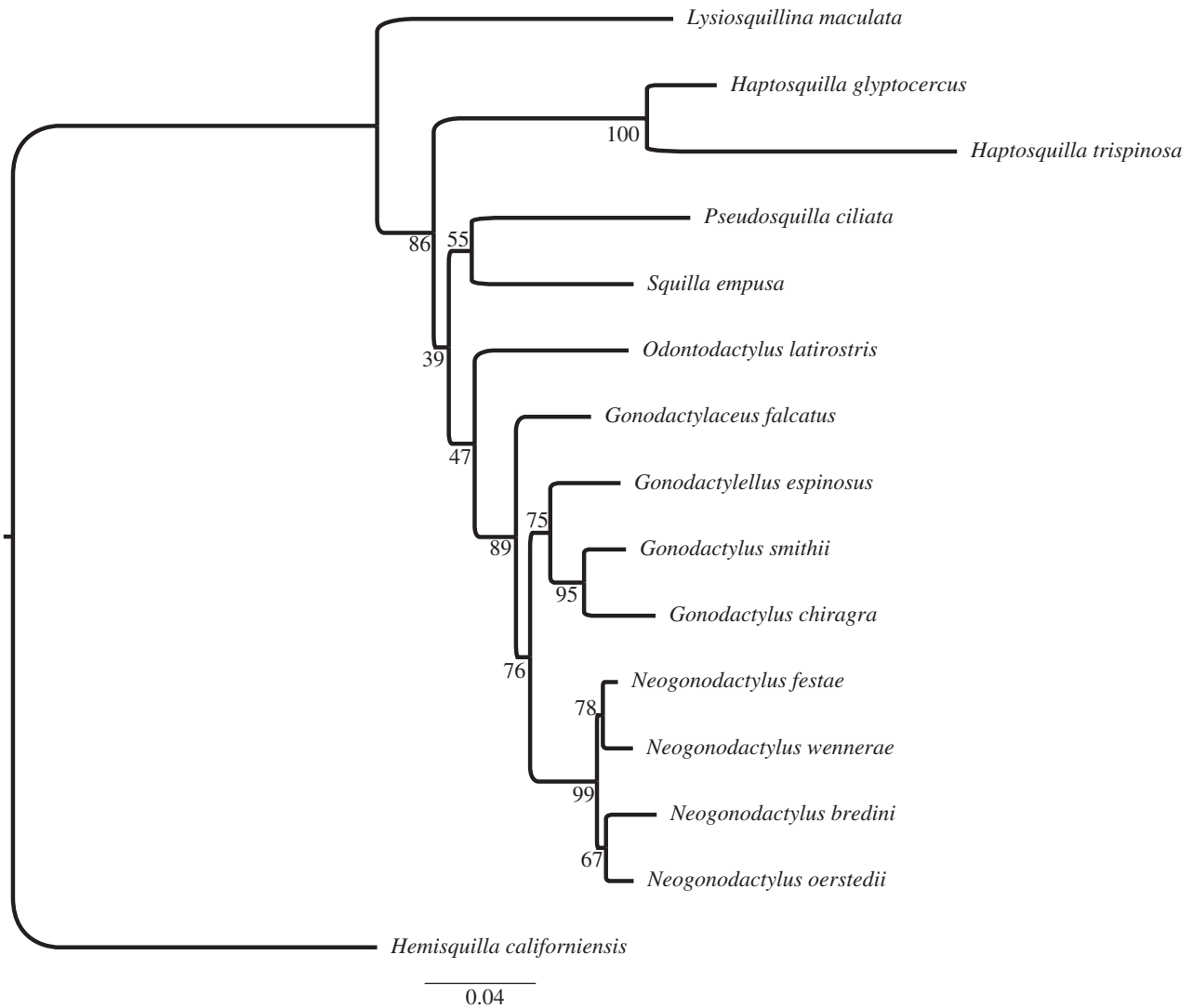
Figure 2. Maximum-likelihood tree from the concatenated 5 gene (COI, 12S, 16S, 18S and 28S) dataset. The tree is rooted with the unusual smashing mantis shrimp *H. californiensis* based on previous studies. Bootstrap scores are at the nodes.

(figure 4*b*). Telson deformation differed between some species (ANCOVA, $F_{14,60} = 10.80$, $p \ll 0.001$) with no effect of mass ($F_{14,60} = 3.25$, $p = 0.08$), but an interaction between species and mass ($F_{14,60} = 3.59$, $p \ll 0.001$). Only three species differed in telson deformation: *H. trisponosa* and *O. latirostris* each had significantly greater telson deformation than 10 other species (adj $p \ll 0.001$–0.01), while *G. espinosus* had significantly less telson deformation than 5 other species (adj $p \ll 0.001$–0.03).

Duration of impact was significantly less in the telson than the abdominal tergite for the majority of smashers and one of the spearer species (*S. empusa*) (table 3). Telson impact duration was only significantly different between *O. latirostris* and *G. chiragra* (ANCOVA, $F_{14,60} = 3.40$, adj $p = 0.04$) and between *O. latirostris* and *G. smithii* (adj $p = 0.04$). All other species had the same impact duration regardless of sparring behaviour (table 3). The impulses experienced by the telson and the abdominal tergite were the same for most species, except *N. festae*, *N. oerstidii*, and *H. glyptocercus* (table 3). There was a significant difference in telson impulse between species (ANCOVA, $F_{14,60} = 14.35$, $p \ll 0.001$), with no effect of mass ($F_{14,60} = 2.27$, $p = 0.14$) or interaction between species and mass ($F_{14,60} = 1.53$, $p = 0.13$). *Hemisquilla californiensis* had a significantly lower telson impulse than 12 of the other species (adj $p \ll 0.001$–0.008), *S. empusa* had a lower impulse than nine of the species (adj $p \ll 0.001$–0.04), and *N. festae* had a lower

impulse than 10 other species (adj $p \ll 0.001$–0.008). Other than these few species, mantis shrimp had the same telson impulse regardless of sparring behaviour (table 3).

For *H. californiensis* (unusual smasher), the COR of the region adjacent to the carina was 0.37 ± 0.03, which was not statistically different from that of the abdomen (paired *t*-test, $t = 1.257$, $N = 3$, $p = 0.34$). On the other hand, in *L. maculata*, the COR of the region adjacent to the carina was 0.66 ± 0.07 and significantly higher than that of the abdomen (paired *t*-test, $t = -4.581$, $N = 4$, $p = 0.02$).

3.2. Impact failure

The telsons of both *N. bredeni* and *P. ciliata* exhibited similar failure behaviour. Cracks formed in the thinner cuticle regions surrounding the carinae, which showed no visible damage. During impacts from ball 2, the telsons compressed nearly completely and sprung back to the original state, demonstrating significant elasticity and no visible damage. Three of the five telsons from each species incurred cracks, some major, with impacts from ball 3 and not all returned fully to their original state. Remaining telsons from *N. bredeni* failed catastrophically during impacts with ball 4, whereas those of *P. ciliata* suffered major cracks and permanent deformation. Interestingly, impacts from ball 4 produce an impact energy of 0.04 J, which is
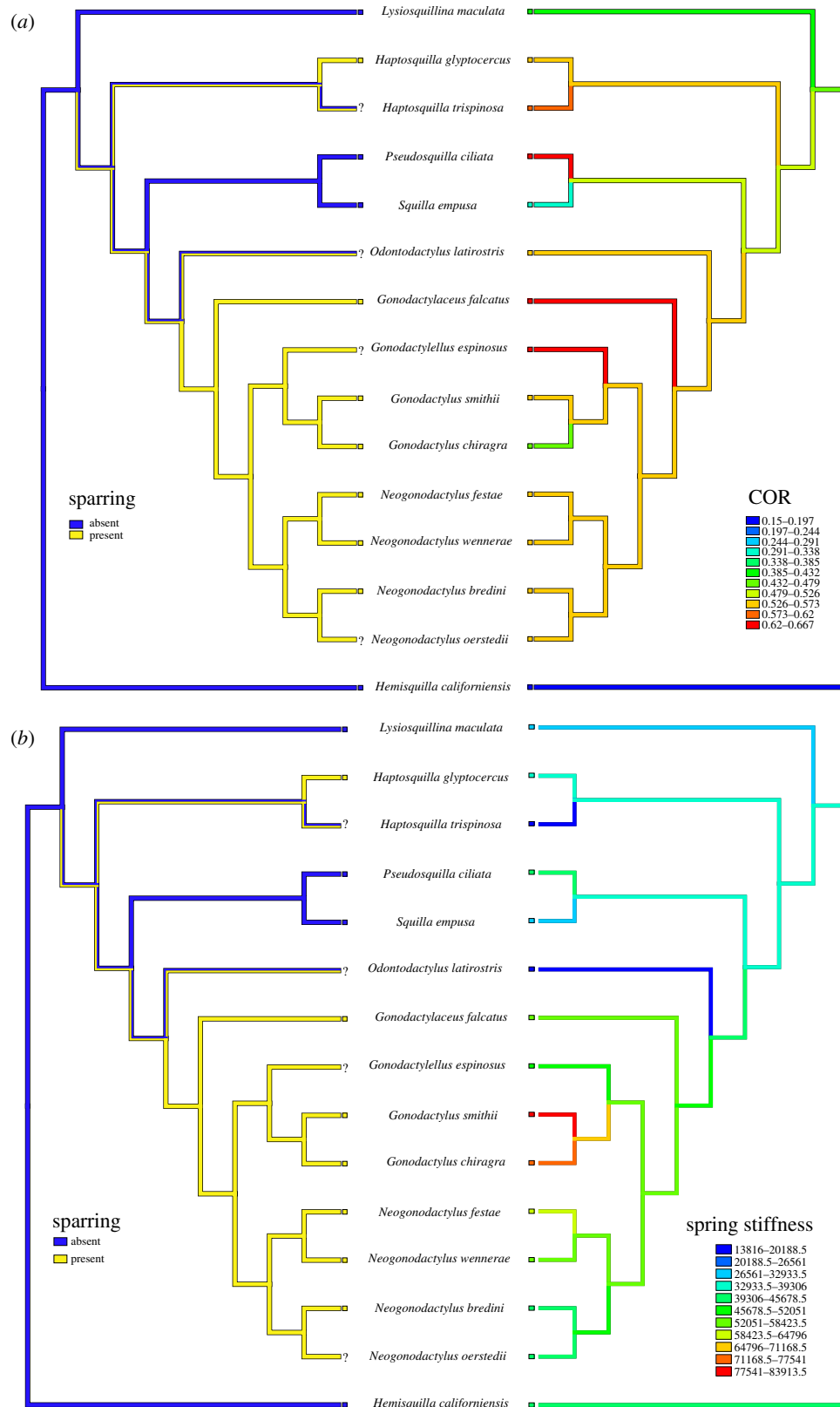
Figure 3. Most parsimonious reconstructions on the maximum-likelihood topology for the character 'Sparring' mirrored against continuous characters (*a*) COR and (*b*) spring stiffness. (Online version in colour.)

above the average strike energy of *N. bredeni*, but within their range as reported by Green *et al.* [15].

3.3. Scaling of impact parameters

Telson impact parameters generally showed no correlation with body mass among the species measured (table 4), though small sample sizes resulted in low statistical power for some species. Yet, correlations were detected for some of the parameters in smasher and spearer species. These include the COR for *N. wennerae* and *G. smithii*; spring constant for *N. wennerae, H. californiensis, P. ciliata, S. empusa*; impulse for *N. wennerae*; and impact duration for *N. wennerae, H. californiensis*, and *S. empusa*.

Table 3. Impact parameters of telson and abdomen for all species used in this study. Sparring species = white rows. Non-sparring species = grey rows. Data are presented as mean (s.d.). Bold indicates significant difference between telson and abdomen.

species	N	COR		spring constant (×10^4 kg m^{-2})		impulse (mNs)		impact duration (ms)		deformation (mm)	
		telson	abdomen	telson	abdomen	telson	abdomen	telson	abdomen	telson	abdomen
G. falcatus	5	0.71 (0.20)	0.61 (0.21)	**5.8 (2.9)**	2.6 (2.1)	2.7 (0.33)	2.3 (0.33)	**0.44 (0.16)**	0.71 (0.19)	**0.15 (0.06)**	0.27 (0.08)
G. espinosus[a]	5	0.63 (0.04)	0.65 (0.07)	**4.7 (2.2)**	1.9 (1.0)	2.7 (0.11)	2.7 (0.13)	**0.52 (0.18)**	0.82 (0.23)	**0.03 (0.02)**	0.34 (0.10)
G. chiragra	7	0.50 (0.15)	0.48 (0.16)	**7.3 (5.5)**	2.4 (1.1)	2.4 (0.24)	2.4 (0.26)	**0.47 (0.14)**	0.71 (0.18)	**0.12 (0.06)**	0.20 (0.11)
G. smithii	5	0.54 (0.07)	0.53 (0.08)	**7.8 (0.2)**	4.0 (0.9)	2.4 (0.12)	2.4 (0.10)	0.43 (0.12)	0.52 (0.06)	**0.13 (0.03)**	0.19 (0.03)
N. bredini	5	**0.52 (0.09)**	0.60 (0.08)	**4.5 (2.8)**	1.1 (0.6)	2.3 (0.25)	2.3 (0.23)	0.51 (0.17)	1.19 (0.81)	0.13 (0.10)	0.35 (0.33)
N. festae	9	0.56 (0.15)	0.49 (0.11)	**6.4 (7.6)**	0.9 (0.3)	**2.0 (0.02)**	2.2 (0.02)	**0.53 (0.16)**	1.07 (0.21)	**0.12 (0.11)**	0.22 (0.17)
N. oerstedii[a]	5	0.53 (0.17)	0.37 (0.24)	**4.4 (4.0)**	0.8 (1.4)	**2.6 (0.00)**	2.0 (0.50)	**0.73 (0.50)**	2.12 (1.14)	**0.08 (0.07)**	0.42 (0.16)
N. wennerae	17	**0.56 (0.08)**	0.67 (0.05)	**7.1 (4.4)**	5.3 (4.4)	2.5 (0.14)	2.7 (0.08)	0.54 (0.16)	0.62 (0.15)	**0.16 (0.03)**	0.26 (0.05)
O. latirostris[a]	4	0.53 (0.12)	0.59 (0.09)	**1.4 (0.9)**	0.3 (0.2)	2.5 (0.19)	2.6 (0.16)	**0.99 (0.36)**	2.16 (1.08)	**0.35 (0.17)**	0.90 (0.42)
H. glyptocercus	5	**0.57 (0.03)**	0.62 (0.03)	**3.7 (1.2)**	0.3 (0.09)	**2.5 (0.02)**	2.6 (0.06)	**0.54 (0.08)**	1.97 (0.35)	**0.21 (0.03)**	0.88 (0.16)
H. trispinosa[a]	5	0.61 (0.06)	0.54 (0.08)	**1.7 (1.2)**	0.2 (0.1)	2.6 (0.12)	2.5 (0.13)	0.86 (0.25)	2.38 (0.95)	0.36 (0.11)	1.03 (0.36)
H. californiensis	5	**0.15 (0.05)**	0.40 (0.18)	4.5 (2.8)	2.8 (1.9)	1.8 (0.11)	2.2 (0.26)	0.56 (0.22)	0.67 (0.18)	0.13 (0.07)	0.50 (0.57)
L. maculata	4	0.42 (0.11)	0.43 (0.06)	**3.2 (0.5)**	0.09 (0.04)	2.3 (0.21)	2.3 (0.07)	**0.57 (0.05)**	3.50 (0.66)	**0.22 (0.05)**	1.19 (0.24)
P. ciliata	5	0.62 (0.04)	0.50 (0.17)	4.0 (2.5)	1.7 (0.6)	2.6 (0.07)	2.4 (0.29)	0.55 (0.13)	0.81 (0.16)	0.20 (0.07)	0.29 (0.02)
S. empusa	5	0.33 (0.06)	0.44 (0.22)	2.7 (1.7)	1.1 (1.0)	2.0 (0.17)	2.2 (0.36)	0.86 (0.49)	1.38 (0.83)	0.19 (0.04)	0.35 (0.15)

[a]Smasher species without documented sparring (unknown).
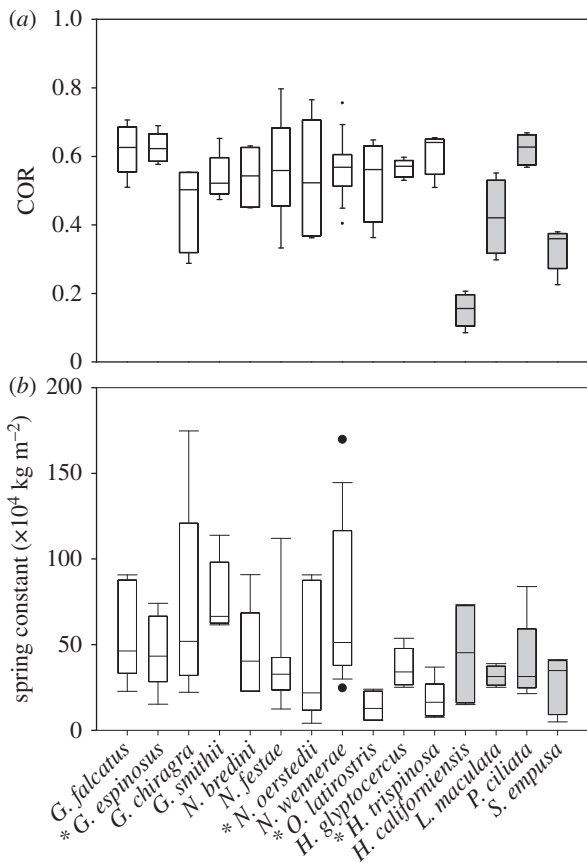
Figure 4. Telson impact properties. (*a*) Mean COR does not differ between sparring (white) and non-sparring (grey) species. (*b*) Mean spring constant does not differ between sparring (white) and non-sparring (grey) species. Smasher species with 'unknown' sparring denoted with asterisk. Box boundaries: 25th and 75th percentile; error bars: 10th and 90th percentile; solid line: median.

3.4. Telson morphology and mechanical properties

The smasher *N. bredeni* has three carinae on the telson compared to the spearer *S. empusa* that has only one (figure 1). The carinae of both species have the same bulbous shape with thickened cuticle. Cuticle thickness of the carina is 0.32 mm in *N. bredeni* and 0.35 mm in *S. empusa*, meaning that the smaller *N. bredeni* has a thicker carina relative to body size. The adjacent cuticle is also similar: 0.19 mm and 0.21 mm, respectively. Both species have relatively uniform distributions of Ca and Mg across the cuticle. Phosphorus also occurs throughout, with greater density in the exocuticle region (figure 5).

The mean hardness of the contact surface of the carina of *N. bredeni* (0.63 ± 0.38 GPa) was not statistically different from that of *S. empusa* (hardness: 0.56 ± 0.21 GPa) (*t*-test, $t = 0.442$, $N = 8$, $p = 0.67$) (figure 6). Neither was carina stiffness different between the two species (*N. bredeni*: 14.05 ± 9.68 GPa; *S. empusa*: 20.19 ± 16.43 GPa) (*t*-test, $t = -0.911$, $N = 8$, $p = 0.38$) (figure 6). Whereas the hardness of *N. bredeni*'s carina decreased with increased body mass (LSR, slope $= -0.66$, d.f. $= 6$, $R^2 = 0.69$, $F = 13.2$, $p = 0.01$), stiffness did not (LSR, slope $= -5.41$, d.f. $= 6$, $R^2 = 0.07$, $F = 0.48$, $p = 0.52$). Neither hardness (LSR, slope $= 2.1 \times 10^{-4}$, d.f. $= 6$, $R^2 = 4.0 \times 10^{-5}$, $F = 2.4 \times 10^{-4}$, $p = 0.99$) nor stiffness (LSR, slope $= -0.26$, d.f. $= 6$, $R^2 = 0.01$, $F = 0.07$, $p = 0.81$) correlated with body mass for *S. empusa*.

4. Discussion

Evolving impact-resistant armour is essential if sparring mantis shrimp are to withstand the forceful strikes of conspecifics during telson sparring. The telson is undoubtedly an effective shield against impacts, but our data do not support the hypothesis that sparring mantis shrimp evolved telsons that are mechanically more robust to impact than non-sparring species. Neither energy dissipation (low COR) nor spring stiffness are correlated with the occurrence of sparring within the phylogeny (figure 3). All of the species examined in this study have telsons that exhibit similar impact behaviour, regardless of appendage type and telson morphology. The telson is a relatively stiff spring that dissipates most of the impact energy. Furthermore, telson impact parameters tend not to be correlated with body size, rendering its broad use for size assessment during combat limited. Telson armour, as characterized by impact response, does not appear to have coevolved with ritualized fighting in mantis shrimp.

4.1. Telson armour

From a simplified point of view, crustacean cuticle is akin to bicycle helmets, and other engineered impact-resistant armour, that use a hard outer shell and a compliant inner liner to effectively reduce peak accelerations and minimize internal damage [36]. The heavily calcified outer layers of the cuticle (epicuticle and exocuticle) generally provide hardness while the inner layer (endocuticle) confers toughness [37,38]. The composite nature and layered, helicoidal organization of fibres provide multiple mechanisms to control crack propagation, and imbue the cuticle with toughness against impact that surpasses that of model tough materials, such as abalone shells [39]. While this is a general feature of crustacean cuticle, fine-tuning of composition and arrangement at multiple levels of organization can yield enhanced impact resistance. The dactyl heel is a striking example of this specialization; it has a modified structure and composition that prevents significant wear and damage from frequent forceful impacts [11,40]. Specifically, the dactyl heel is enhanced by thickened cuticle with distinct regions that vary in fibre organization and the amount, orientation, and crystallinity of key minerals (Ca, Mg and P) [11]. Increased calcium phosphate in the relatively thick impact region raises hardness and stiffness, which facilitates the transfer of kinetic energy to prey or conspecifics, whereas inner regions provide fracture toughness to minimize damage [11,40]. It is logical to expect that the telson would share some similar modifications to withstand impact.

The carina of the telson, which is struck by the dactyl heel during telson sparring, imitates the structure of the dactyl heel to some extent. In both of the two species examined for morphology, *N. bredeni* and *S. empusa*, the telson carinae are also rounded in cross section and characterized by thickened cuticle, with an outer impact region (epi- and exocuticle layers) that accounts for approximately 21 and 30% of total cuticle thickness, respectively, and is comparable to the estimated 29% for the dactyl heel [11] and unspecialized crustacean cuticle [41]. Based on EDX maps, Ca and Mg are relatively uniform across the cuticle, but P appears to be in higher density in the outer impact region, which may serve to harden the contact surface similarly to the dactyl heel. Despite the similarities in

Table 4. Scaling of impact parameters of telson and abdomen for all species used in this study. Regression slopes, R^2, and p-values calculated from OLS. Bold indicates slope significantly different from zero. Sparring species = white rows. Non-sparring species = grey rows.

species	COR			spring constant (×10⁴ kg m⁻²)			impulse (×10⁴ mNs)			impact duration (ms)			deformation (mm)		
	slope	R^2	p-value	slope	R^2	p-value	slope	R^2	p-value	slope	R^2	p-value	slope	R^2	p-value
G. falcatus	0.09	0.28	0.35	0.96	0.02	0.81	5.00	0.50	0.18	0.00	0.21	0.44	−0.12	0.78	0.05
G. espinosus[a]	−0.54	0.50	0.18	−21.5	0.32	0.32	10.00	0.36	0.28	0.00	0.11	0.58	−0.01	0.00	0.95
G. chiragra	0.01	0.01	0.88	−0.72	0.02	0.77	0.30	0.01	0.80	0.00	0.06	0.59	0.04	0.46	0.09
G. smithii	−0.08	0.94	**0.006**	−1.30	0.26	0.38	1.00	0.74	0.06	0.00	0.15	0.51	0.02	0.26	0.38
N. bredini	0.05	0.04	0.73	4.50	0.33	0.31	50.00	0.44	0.22	0.00	0.20	0.45	−0.19	0.45	0.21
N. festae	0.17	0.08	0.47	15.8	0.25	0.18	3.00	0.11	0.40	0.00	0.02	0.69	−0.30	0.38	0.08
N. oerstedii[a]	−0.09	0.49	0.19	1.58	0.26	0.38	−0.02	0.17	0.49	0.00	0.04	0.74	0.03	0.34	0.31
N. wennerae	−0.05	0.56	**0.0009**	−2.40	0.41	**0.01**	−0.90	0.51	**0.002**	0.00	0.50	**0.002**	0.01	0.06	0.38
O. latirostris[a]	0.16	0.16	0.61	2.50	0.65	0.19	20.00	0.14	0.63	0.00	0.75	0.14	−0.47	0.65	0.19
H. glyptocercus	−0.02	0.00	0.92	−0.28	0.00	0.97	−0.20	0.01	0.91	0.00	0.00	0.98	−0.06	0.05	0.73
H. trispinosa[a]	−0.03	0.01	0.86	3.40	0.43	0.23	−1.00	0.05	0.72	0.00	0.30	0.34	−0.30	0.35	0.29
H. californiensis	0.00	0.08	0.65	0.07	0.99	**0.0004**	−0.02	0.45	0.21	0.00	0.98	**0.001**	0.00	0.75	0.06
L. maculata	0.00	0.61	0.22	0.01	0.32	0.44	−0.02	0.28	0.47	0.00	0.34	0.42	0.00	0.37	0.39
P. ciliata	−0.02	0.03	0.79	4.60	0.78	0.05	0.60	0.13	**0.00**	0.00	0.62	0.11	−0.10	0.51	0.18
S. empusa	0.00	0.00	0.94	−1.10	0.85	**0.03**	−0.30	0.07	0.66	0.00	0.82	**0.03**	0.01	0.30	0.34

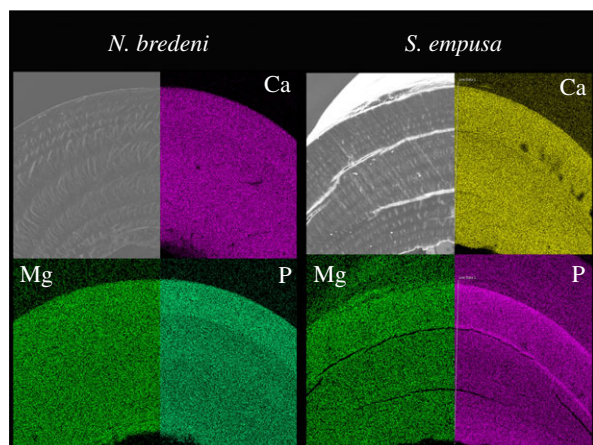[a]Smasher species without documented sparring (unknown).

Figure 5. Elemental mapping of key elements in a smasher (*N. bredeni*) and a spearer (*S. empusa*) carinae cuticle using EDX. Ca and Mg are uniformly distributed, but P shows greater density in the outer exocuticle layer. (Online version in colour.)
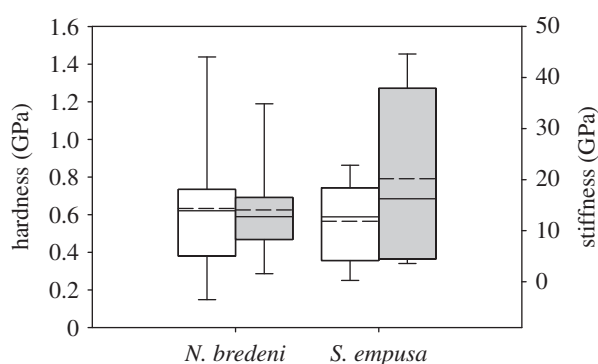

Figure 6. Mechanical properties of telson carinae in a smasher (*N. bredeni*) and a spearer (*S. empusa*) species. Neither hardness (white) nor stiffness (grey) differed between the species. Box boundaries: 25th and 75th percentile; error bars: 10th and 90th percentile; solid line: median; dashed line: mean.

morphology though, the impact surface of the telson carina has approximately 6× lower hardness and 4× lower stiffness than the impact region of the dactyl heel [11]. These differences in mechanical properties between the dactyl heel and telson result in greater impact energy being transferred to the telson during a sparring strike.

Telsons accommodate significant impact energy through their macroscale structure as well. In a departure from the specialized dactyl heel and the non-specialized abdominal tergites, the telson combines both stiff and compliant regions of cuticle that together prevent penetration, spread the impact force, and dissipate energy. Rather than a uniformly hard and stiff structure that would increase brittleness and incur more costs to construct and carry, hard material is restricted to the carinae, which are surrounded by compliant cuticle. Impacts produce consistent behaviour among diverse telsons, where the carinae do not deform but the compliant region permits compression of the entire dome-like dorsal surface. As a whole, telsons generally have greater spring stiffness compared to non-specialized abdominal tergites, resulting in less deformation and shorter contact times. This would be expected to increase the impact force and potential damage by focusing the impact energy over a shorter time scale, a strategy avoided in engineered designs, such as vehicles

that use crumpling to absorb energy and minimize damage. However, in live interactions this is mitigated by the telson coil position that allows significant abdominal flexion and displacement of the telson. Under our testing conditions, collisions with the telson and abdomen have similar COR values for most species, meaning that on average 71% of the energy gets dissipated during impact. The main difference between these segments is that the abdomen dissipates energy through significant deformation, which may be damaging to internal tissues.

4.2. Armoured sparring or not

Telson impact mechanics are generally consistent among species, regardless of their appendage type and sparring behaviour. Contrary to our predictions that sparring mantis shrimp would have telsons with enhanced impact resistance, none of the impact parameters significantly differed between sparring and non-sparring species. In particular, we expected that sparring species evolved low CORs and high spring constants because these measures reflect greater energy dissipation and stiffness during impacts, and because they characterized a smasher species from a previous study [22]. Yet, when these parameters were analysed against the phylogeny, neither measure was correlated with the presence of telson sparring. Our data do not support the hypothesis that sparring species coevolved more robust telson armour. While a larger assortment of species studied could yield a broader pattern between armour and behaviour, our data show clearly that several sparring and non-sparring species are not distinguishable in their telson response to impact forces. This inspires the question of whether the generalization of impact-resistant telson armour reflects an adaptive value for non-sparring species or is simply an inherent feature of telson structure.

Telson structure, particularly the carinae, varies not only between sparring and non-sparring mantis shrimp, but also extensively within each of these groups. Among the smashers used in this study, telsons typically possess three carinae, but their shapes are highly variable (figure 1). The *Neogonodactylus* species tend to have broad, bulbous carinae, but others have narrow carinae (*O. latirostris*) or even flat, rounded carinae (*H. glyptocercus* and *H. trisponosa*). Of the spearers, both *L. maculata* and *S. empusa* have one wide carina in the middle, but *P. ciliata* is similar to the smasher *O. latirostris* that has three narrow carinae. Concomitant with these variations in structure are variations in the proportions of stiff and compliant elements, but these differences, and the differences in carina shape, do not emerge in the structural responses of telsons to biologically relevant impact energies. It appears that impact-resistance is inherent across a range of telson structural templates.

Consistent impact behaviour across diverse telsons poses interesting questions about the integration across scale (from chemical to structural) for impact resistance, and also about the function of the telson. Telson carinae and other attributes, such as spines, may be important for ecological factors other than ritualized fighting. For example, telsons are sometimes used to physically block burrow entrances and species will attempt to overtake burrows by striking the telson of the inhabitant in a non-ritualized manner [17,42]. In this scenario, impact resistance could be of importance for non-sparring species that might engage with interspecific

aggressors. Mantis shrimp also use their telsons in other aggressive ways, such as to stab or push an opponent [17,43], actions that also require a stiff structure. There are thus a variety of behaviours other than sparring that may pose selective pressures on telson morphology.

Our approach to characterizing the impact-resistance of telsons using ball drop tests and energy dynamics has the advantage of observing responses under biologically relevant conditions, but does not address all possible factors that may be important. For example, species may differ in telson strength and mode of failure, which could be correlated with the impact forces that they generate during a strike. When spearers strike, they do so with significantly lower accelerations and impact forces than smashers [25]. Our coarse comparison of the telson impact strength and mode of failure between the sparring *N. bredeni* and the non-sparring *P. ciliata* revealed that both failed in the same manner and withstood similar impact forces despite having different carina structure. Both species withstood impact energies estimated to be comparable to that of a medium-sized smasher's (2.0 g) strike at 20 m s^{-1}, but failed at impact energies comparable to a larger animal (5.0 g) striking at that same impact velocity and even some of the higher energy strikes of *N. bredeni* [15]. We did not test impact strength broadly enough to determine if it is a potential factor evolutionarily correlated with sparring behaviour, but it is evident that this parameter is similar among at least some spearer and smasher species.

For our analysis, we linked the occurrence of telson sparring with appendage type and grouped all smashers known to spar as sparring species and smasher species not documented as sparring as 'unknown'. This approach was used because multiple previous studies have declared that sparring is only carried out by smasher species [17,24]. Spearers, in contrast, tend to strike other parts of the body during conflicts, but can modulate the damage inflicted by striking with either a closed or open dactyl [17]. Within the smashing gonodactylids, and even within populations of species, there is a range in levels of aggressiveness and the likelihood of telson sparring [17]. If telson armour is correlated with sparring behaviour, then it would be expected that telson armour varies within the smashers based on fighting proclivity. Aggression levels during sparring are not available for most species in our study, so it is not possible to test for correlations between species aggression and telson impact properties. Yet, the similar telson impact properties of *N. bredeni*, which is known to be an aggressive sparrer [17], and *G. chiragra*, which is less likely to spar [6], lessens the likelihood that telson impact response correlates with species aggression. Our cumulative data showing consistent impact response across multiple smasher species further diminish this assertion.

4.3. Assessment from telson impacts

Body size is generally a good indicator of winners in contests and opportunities for size assessment arise from multiple displays that comprise ritualized fighting. Physical contact during telson sparring can provide an honest signal for assessment by both participants because each individual experiences the energy dynamics of an impact, which are governed by the laws of physics. How much energy is imparted, dissipated, and returned depends greatly on the properties of each of the colliding structures, and there are several components of an impact that may correlate with body size. A previous study on *N. wennerae* found that the COR, impulse, and impact duration all correlated with body mass [22]. Yet in this study, the relationships between impact parameters and body size were diffuse, with only some species displaying correlations and with generally only one parameter. Based on our data, different telson templates can confer size-based information during sparring, but its broad utility as a size assessment tool appears to be limited. We cannot reject the possibility, however, that different scaling relationships may emerge at higher or lower impact energies relevant to species-specific strikes.

Once ritualized fighting has escalated to combat, other indicators of fighting ability, such as animal condition, aggression, or endurance, become more important to assess than body size. In contests between the mantis shrimp *N. bredeni*, winners are determined by the number of strikes rather than strike force [5], implicating that endurance is an important signal to assess. Both physiological and mechanical endurance can be qualified through telson impacts, either by fatigue in strike force or telson structure. Mechanical fatigue in the telson may emerge in some impact parameters over multiple strikes and yield information about telson condition. For example, plastic deformation of the contact area and residual stresses due to repeated impacts can cause changes to the COR [44]. Telsons are not as hard as dactyl heels and are thus more likely to experience fatigue, which could be communicated through changes in the COR and acted upon by either individual in their decision to continue the fight or concede. We know from a previous study that *N. wennerae* exhibited no fatigue in telson COR over 100 sequential impacts [22]. This is far more impacts than the typical number of strikes exchanged during a sparring interaction, but it is reasonable that higher energy impacts would induce material fatigue at a faster rate and that fatigue may manifest in other impact parameters like spring constant.

5. Conclusion

We conducted a comparative study of telson impact mechanics among smasher and spearer mantis shrimp species and found no evidence that smasher telsons are more robust to impact than spearers, nor that telson armour is correlated with the occurrence and evolution of telson sparring. Rather, it appears that telsons are mechanically similar over a range of morphologies due to the fundamental integration of stiff and compliant material and structure. This architecture makes telsons uniquely resistant to high impact forces and a source for bioinspiration. Our unique and integrative approach to studying impacts in biological systems has helped to define the limited functional role that the telson played in the evolution of ritualized fighting in mantis shrimp and more generally in the coevolution of specialized weapons and armour.

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