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The snapping shrimp dactyl plunger: a thermomechanical damage-tolerant sandwich composite

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ABSTRACT

The dactyl plunger of *Alpheus* sp. was found to be a layered composite, with mineral-rich outer and inner layers and a chitin-rich middle layer of high porosity. The chitin-rich middle layer is itself composed of several porous chitin laminae. Modelling heat conduction through the plunger cross-section revealed that the chitin-rich layer is able to insulate heat and retard its progress through the material. Heat accumulates in the plunger after a series of successive snaps and as such, its thermally resistant design can be considered most useful under the conditions of successive snapping. The plunger has a concurrent mechanical damage-tolerant design with biogenic mineral layers, viscous (chitin–mineral) interfaces, energy-dissipating porous chitin, and sidewalls composed of ordered, layered aragonite. The snapping shrimp plunger has a design that may protect it and internal soft tissues from thermomechanical damage during plunger–socket compression prior to cavitation bubble release.

1. Introduction

Snapping shrimps comprise a specialised family (Alpheidea) of arthropods with asymmetrical chelae (Fig. 1), the larger of which produces a highly audible and explosive snapping sound. Though earlier reports hypothesised that the explosive sound is a result of physical impact between the finger and thumb of the chela (Johnson et al., 1947), it is now understood that the sound is due to the collapse of a cavitation bubble outside the chela. This bubble is formed by compression of air between a plunger and socket within the chela (Fig. 2) and exits the chela at a velocity of 7–32 m/s (Herberholz and Schmitz, 1999; Versluis et al., 2000), collapsing a few millimetres from the tip of the chela (Versluis et al., 2000) and releasing an explosive acoustic sound of approximately 190 dB (Fergusson and Cleary, 2001). The immediate external pressure drop, after the bubble exits, is in the order of ca. 0.1–0.3 MPa (Versluis et al., 2000; Kim et al., 2010; Hess et al., 2013). The sound intensity of the cavitation bubble collapse is close to that of the mono-pulsed sperm whale click, which has been recorded at ca. 236 dB (Mohl et al., 2003), making the snapping shrimp one of the loudest extant marine animals. Sonoluminescence is produced alongside extreme heat as the cavitation bubble collapses. The temperature approaches the surface temperature of the sun (Downer, 2002) at around 5000 K, presumably due to high compression in the final stages of the cavitation bubble collapse (McNamara et al., 1999). Acoustic pressure pulses that arise through cavitation bubble collapse are typically in the order of 700 kPa (Lohse et al., 2001). Several factors will affect the bubble sizes and velocities. Amongst the more prominently mentioned in the literature are: chela shape (Kim et al., 2010), the rate and style of snapping closure (Ritzmann, 1974; Mellon and Stephens, 1979; Mellon, 1981), and the gender of the shrimp − males of similar size to females generate bubbles with higher velocity (Herberholz and Schmitz, 1999) whilst also possessing stouter chelae than similar-sized females.

While there are several researchers who have considered the acoustics of snapping (Everest et al., 1948; Au and Banks, 1997; Legg et al., 2007) and the physics associated with cavitation bubble collapse

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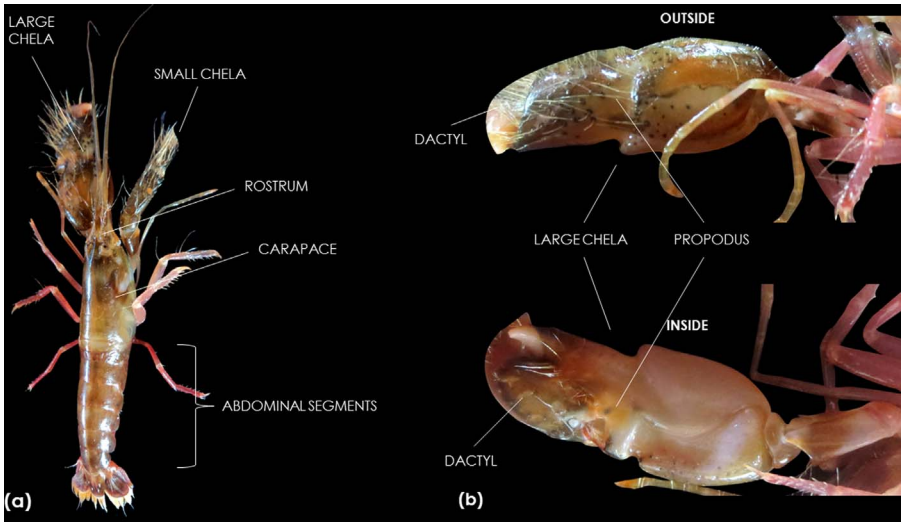

Fig. 1. (a) Snapping shrimp external morphology from the dorsal view; (b) enlarged view of the large chela as observed from both the inside (ventral) and outside (dorsal) view.

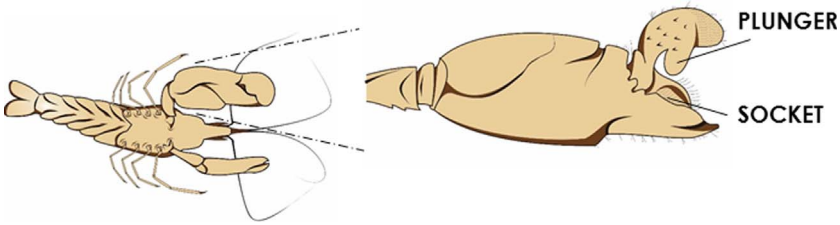

Fig. 2. Schematic drawing showing the plunger–socket system of the snapping shrimp.

(Versluis et al., 2000; Chitre et al., 2003), neither the compressive pressures nor the heat energy *within* the socket during plunger compaction have been reported in the literature. To date, very little has been reported on the snapping shrimp dactyl plunger. Johnson et al. (1947) noted high levels of calcification at the tips of the chela. Beyond this, we find no reports on either the material or the architectural characterisation of the enlarged chela of the snapping shrimp. Yet, plunger–socket compressive pressures, heat generation due to the compression, and the shock waves resulting from 'snapping' are all potential sources of damage to the materials of the chela, most prominently in the area of the plunger–socket system. For the plunger–-socket system to survive repeated pressurisation and the resultant temperatures and shock waves, it logically requires a material design that can withstand coupled thermomechanical energies.

Here, we hypothesise that special architectures imparting damage tolerance will exist in the snapping shrimp dactyl plunger. In particular, we posit that these architectures will exhibit a design able to withstand high heat and mechanical forces. Our objectives for this paper are to characterise the microarchitecture of the plunger both physically and chemically. We consider the plunger to be the most logical starting-point since it is directly involved with compression and cavitation bubble creation, and is thus exposed to both mechanical and thermal energies during the process of 'snapping'.

2. Materials and methods

2.1. Bioprospecting and capture of snapping shrimps

Nocturnally active snapping shrimp were collected overnight at Pantai Drini, Gunug Kidul, Java, Indonesia (8.1385° S, 110.5775° E) during November 2014 and a second time during January 2016. Shrimps were killed by indirect icing, which was subsequently followed by freezing, by which means the shrimps were also preserved. The treatment and killing of shrimps followed guidelines from both the European Union Financial Instrument for Fisheries Guidance (FIFG) and the NIH Guide for Care and Use of Laboratory Animals. Ten shrimps were captured in total over the two separate expeditions.

2.2. Genetic and morphological identification of the shrimps

Two loci of the pistol shrimp mitochondrial genome were amplified using universal COI and 16S primers according to Folmer et al. (1994) and Hultgren and Stachowicz (2008), respectively (Table 1). DNA was isolated from the limb tissues of the shrimp and extracted using Chelex 10%. The extraction was conducted at a temperature of 95 °C for 30–45 min, and followed by sodium acetate and alcohol precipitation. High-fidelity polymerase (KOD Xtreme polymerase; Millipore) was used for DNA amplification. The polymerase chain reaction (PCR) cycle and temperature were consecutively set at 30 s pre-denaturation (96 °C); 40 cycles of 30 s denaturation (94 °C), 30 s annealing (49 °C for COI and 50–58.5 °C for 16S), and 60 s elongation (68 °C); it ended with 90 s final extension (72 °C). The results produced included sequences of 680 bp (COI) and 420 bp (16S), which were sequenced using the Turku Centre for Biotechnology (Finland) sequencing service. The sequences were BLASTed into the GenBank database in order to find their relevant adjacent homology. MUSCLE alignment was needed to construct a phylogenetic tree using a neighbour-joining statistical method in MEGA6 (Saitou and Nei, 1987; Edgar, 2004; Tamura et al., 2004, 2013).

Table 1
Primers for DNA barcoding.

16S (Hultgren and Stachowicz, 2008)	Forward: (5'-TATT TTGA CCGT GCAA AGGT AG-3')
	Reverse: (5'-ATTT AAAG GTCG AACA GACC CT-3')
COI (universal) (Folmer et al., 1994)	LCO1490: (5'- GGTCAACAAATCATAAAGATATTGG-3')
	HCO2198: (5′-TAAACTTCAGGGTGACCAAAAAATCA-3′)