



Raman spectroscopic analysis of the composition of the clam-shrimp carapace (Branchiopoda: Laevicaudata, Spinicaudata, Cyclestherida): a dual calcium phosphate-calcium carbonate composition

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ABSTRACT

Clam shrimps constitute a paraphyletic group of bivalved branchiopod crustaceans that includes orders Laevicaudata, Spinicaudata, and Cyclestherida. The unique mineral content of the carapace, formed by molt retention in Spinicaudata and Cyclestherida, has been variously ascribed to calcium carbonate or calcium phosphate. We analyzed the composition of modern carapaces from one laevicaudatan species, thirteen spinicaudatan species (including cyzicids, leptestheriids, and limnadiids), one cyclestherid species, and two species of the notostracan *Triops* Schrank, 1803 (as an outgroup comparison within Branchiopoda) via Raman spectroscopy. The results were surprisingly variable. The outgroup *Triops* species varied in either having no mineral content to having a slight amount of calcium phosphate. The laevicaudatans likewise had a minor calcium phosphate peak; the leptestheriid spinicaudatan had strong calcium phosphate and calcium carbonate peaks; the limnadiid spinicaudatans were variable, varying from no mineral content to strong dual calcium carbonate and calcium phosphate peaks; the cyzicid spinicaudatans tended to have strong calcium phosphate peaks with some amount of calcium carbonate; and the cyclestherid had no mineral content. The results support the conclusion that spinicaudatans primitively have a dual mineralization system in their carapace that utilizes both calcium phosphate and calcium carbonate, with the calcium phosphate ability being basal. This suggestion of a dual mineralization system is novel in branchiopods and warrants study from material scientists. Better understanding of the distribution of phosphate *versus* carbonate among modern spinicaudatans will help us understand the evolution of biomineralization in the group. This, in turn, will shed light on the fossilization potential of different fossil clam-shrimp lineages.

Key Words: biomineralization, exoskeleton

INTRODUCTION

Raman spectroscopy is a technique that utilizes the inelastic scattering of light off of a sample to determine the molecular structure and/or mineralogy of the material. This is done by producing a spectrum of the inelastically (or Raman) scattered light, which can be thought of as a material fingerprint. These analyses allow for relatively easy identification without destructive sample analysis or preparation. Raman analysis is employed in a wide variety of fields like chemistry, Precambrian paleontology, astrophysics, pharmacology, and forensics, but it has only recently been

employed to identify the mineral content of modern and fossil invertebrates (Vrazo *et al.*, 2018).

Branchiopods are small, predominantly freshwater crustaceans that specialize in seasonally astatic aquatic habitats. All, except the fairy shrimp (Anostraca), have some sort of carapace (Rogers, 2009). What exactly the carapace is made of is a contentious question. Clam shrimps (Spinicaudata in particular) have been proposed to have several different compositions to the mineral portion of their chitinous carapaces. Clam shrimps constitute a group of bivalved branchiopod crustaceans included

in order Diplostraca (Schwentner *et al.*, 2018). The Diplostraca and their sister clade Notostraca (tadpole shrimps) make up the Phyllozoa. Within Diplostraca, clam shrimps are paraphyletic with respect to Cladocera (Schwentner *et al.*, 2018). Specifically, the Diplostraca clade consists of two clades: Laevicaudata (smooth clam shrimps) and Onychocaudata. Onychocaudata in turn, consists of Spinicaudata and Cladoceraomorpha. Cladoceraomorpha consists of Cyclestherida (tropical clam shrimps) and Cladocera (water fleas). The Cladocera are not considered here.

Early workers (summarized in Dudich, 1931) identified calcium carbonate (CaCO_3) or “calcifications” in clam shrimps, but the methods by which they made this discovery are unclear (possibly the acid test used by workers studying the mineral content of cladoceran carapaces; see Klunzinger, 1864). Dudich (1931) used a variety of microscopic and chemical techniques to assess the mineral composition of various branchiopod species. He found that the species of notostracans he studied lacked mineral content (i.e., aachalicodermie). The species of spinicaudatan clam shrimps that he studied varied from lacking mineral content to having some amorphous calcium carbonate (i.e., amorphochalcosite). In one species of clam shrimp (*Cyzicus bucheti* (Daday, 1913)), Dudich (1931) identified crystalline calcium carbonate (i.e., morphochalcosite). Dudich (1931) found that laevicaudatans lacked any carapace mineral content. Cladocerans, according to Dudich (1931), mostly lacked mineral content, but a few rare species were reported to contain either amorphous calcium carbonate or calcium phosphate ($\text{Ca}_3(\text{PO}_4)_2$) (Gicklhorn, 1925). Tasch (1969: p. R143) merely stated that clam shrimp in general were “. . . never strongly calcified,” following Mathias (1937). Rieder (1972), in his study of the histology of the carapace of clam shrimps, made no mention of the mineral content. Stigall *et al.* (2008: 350) cited the ambiguous statement of Tasch (1969) to support the claim that clam shrimp have calcium phosphate in their carapaces. Stigall *et al.* (2008) performed EDX analysis of the carapace of fossil clam shrimps and determined that they contained calcium phosphate. Subsequent workers have confirmed Stigall’s analysis (Astrop *et al.*, 2015; Hu *et al.*, 2020; Monferran

et al., 2018), which has led to a situation where an EDX analysis of the carapaces of clam shrimps indicating an absence of phosphate was then interpreted as evidence of diagenetic replacement by calcium carbonate (Stigall *et al.*, 2017).

Though no one has proposed a dual mineral system for the carapaces of clam shrimps, it is actually consistent with previous analyses. Both calcium phosphate and calcium carbonate will react with HCl (though only weakly in the case of calcium phosphate), thus the acid tests of Klunzinger (1864) and others could indicate either calcium phosphate or calcium carbonate. The EDX analysis of Stigall *et al.* (2008) certainly detected the presence of calcium and phosphate (and interpreted the presence of calcium phosphate). The EDX analysis, however, was unable to detect elements as light as carbon, thus the peak in calcium could also indicate the presence of calcium carbonate. What previous scientists detected in the carapaces of clam shrimps was determined (to some degree) by what they expected to find, a single mineral system of either calcium carbonate or calcium phosphate.

METHODS

Specimens were collected in the wild by DCR (Table 1). Our material represents clam shrimps from all but one extant family. In addition, we used *Triops* Schrank, 1803 (Notostraca) as our outgroup. All material was either collected in the wild as adults or as eggs and cultured to adult stage using the same substrate on which the eggs naturally occurred. Adult specimens were killed in 80% ethyl alcohol and transferred after 24 hr to 70% ethyl alcohol. Carapaces were removed under a dissection microscope.

Large branchiopod carapaces were analyzed at the University of Cincinnati using a Horiba T64000 Raman spectrometer (Horiba, Edison, NJ, USA) in single mode with 244 nm laser excitation from a Coherent FreD C Ar+ laser. Sample spots on epibiont-free carapace surfaces were located using an attached Olympus BX41 microscope (Olympus, Tokyo, Japan) and analyzed with a 40× UV objective (NA = 0.50). The laser was focused to a spot size of ~2 μm and had a power at the sample

Table 1. List of the seventeen taxa analyzed, their locality of collection, and the presence or absence of mineral content. (++) indicates a strong peak; (+) indicates a weaker peak.

Taxon	Locality	$\text{Ca}_3(\text{PO}_4)_2$	CaCO_3
<i>Triops</i> sp.	USA, Colorado	+	
<i>Triops</i> sp.	Australia, NSW, Bloodwood, Sue’s Pan		
<i>Lynceus planifasciatus</i> Rogers, Saengphan, Thaimuangphol, & Sanoamuang, 2016	Thailand, Udon Thani Province	+	
<i>Cyzicus</i> sp.	USA, Montana, Powderville	++	
<i>Cyzicus californicus</i> (Packard, 1874)	USA, California, Alameda Co., Parks RFTA	++	+
<i>Ozestheria pilosus</i> (Rogers, Thaimuangphol, Saengphan, & Sanoamuang, 2013)	Thailand, Maha Sarakham province, Bang Nan No, Hwy. 23	+	++
<i>Ozestheria mariae</i> (Olesen & Timms, 2005)	Australia, WA, King’s Rock	++	+
<i>Ozestheria packardii</i> (Brady, 1886)	Australia, NSW, Bloodwood, Sue’s Pan	++	++
<i>Leptestheria compleximanus</i> (Packard, 1877)	USA, Colorado	++	++
<i>Eulimnadia braueriana</i> Ishikawa, 1895	Taiwan, Yangminshan National Park, Siangtian Pond	++	
<i>Eulimnadia diversa</i> Mattox, 1937	USA, California, Butte Co., Durham, Rancho Esquon	++	+
<i>Eulimnadia compressa</i> (Baird, 1860)	Thailand, Udon Thani province	+	++
<i>Limnadia lentiularis</i> (Linnaeus, 1761)	USA, Georgia, Newton Co.	++	+
<i>Australimnadia grobbeni</i> (Daday, 1925)	Australia, Queensland, 16K E of Meandarra		
<i>Paralimnadia urukhai</i> (Webb & Bell, 1979)	Australia, NSW, Bald Rock	+	
<i>Limnadopsis tatei</i> Spencer & Hall, 1896 (<i>sensu</i> Schwentner <i>et al.</i> , 2012)	Australia, WA, Pabellup Swamp	+	
<i>Cyclestheria</i> sp.	Thailand, Maha Sarakham province, Bang Nan No, Hwy. 23		

surface of <1 mW UV, rather than visible excitation, was used to avoid fluorescence that would overwhelm the mineral Raman peaks. Because UV excitation is typically more damaging than visible excitation, to avoid alteration of the carapaces, spectra were collected in a manner similar to those described by Czaja *et al.* (2006) and Vrazo *et al.*, (2018) Areas were mapped using a 9×7 point grid with a spacing of $5 \mu\text{m}$, and each point was analyzed for 1 s (two 0.5 s acquisitions were averaged per point). All 63 resulting spectra from each grid were inspected to ensure homogeneity and averaged to increase the signal-to-noise ratio. Sample areas were imaged before and after each analysis, and only minor surface alteration of the organic component of the carapaces was detected. Data were collected and processed using the software program LabSpec version 5 (Horiba Instruments, Irvine, CA, USA).

RESULTS

Results are presented in Figure 1. Weak calcium phosphate peaks were detected in both *Lynceus* Müller, 1776 (Laevicaudata) and the outgroup *Triops* (Notostraca). All spinicaudatans analyzed exhibited biomineralization with calcium carbonate and calcium phosphate. The peak to the left of the calcium phosphate peak exhibited by *Ozestheria mariae* (Olesen & Timms, 2005) and *Leptestheria compleximanus* (Packard, 1877) is unknown and requires further study. Species of Cyzicidae and Leptestheriidae seem to be the most highly biomineralized clades, with all species except *Cyzicus* sp. (USA) showing peaks for both calcium carbonate and calcium phosphate. The Limnadiidae are more variable, with a higher proportion of species with low peaks (see Table 1). In this context, species that lack peaks (*Australimnadia grobbeni* (Daday, 1925)) seem to be clear cases of loss because the closely related more basal spinicaudatans (following Schwentner *et al.*, 2020) all have mineral peaks. Species of *Cyclestheria* G.O. Sars, 1887 (Cyclestherida) contained no mineral peaks.

DISCUSSION

The Raman spectra obtained (Fig. 1) reveals little about the phylogenetic patterns within Spinicaudata. Spinicaudatans in general have peaks for both calcium carbonate (ν_1 vibration of CO_3^{2-} at $\sim 1085 \text{ cm}^{-1}$; e.g., Urmos *et al.*, 1991) and calcium phosphate (ν_1 vibration of PO_4^{3-} at $\sim 960 \text{ cm}^{-1}$; e.g., O'Shea *et al.*, 1974), suggesting that they may have a dual mineral system and this may be basal for the clade. Weak calcium phosphate peaks were detected in both our laevicaudatans and the outgroup *Triops*, suggesting that attribute may have originated at the base of the Phyllopoda clade. There has never been a suggestion of the basal branchiopods (Anostraca) being biomineralized as they are soft-bodied without a carapace; as such, they were not analyzed in this study. Considering the harder structures on the male second antennae used in mating amplexus (Rogers, 2002) and the dorsal defensive structures in certain species (Rogers *et al.*, 2004), however, at least certain anostracans might warrant investigation. The Cladocermomorpha (Cyclestherida + Cladocera) seem to have representatives with mineral content (Gicklhorn, 1925), so dual mineralization may have been a basal feature of the Onychocaudata. Cladocerans will need to be analyzed in more detail using Raman methods to see if they contain trace mineral peaks.

The Raman analysis, in principle, could reveal the mineral phase present in the carapaces (i.e., aragonite *versus* calcite for calcium carbonate). The spectra, however, are relatively weak, and the spectral differences small, making such a determination difficult with the specimens at hand. We can nevertheless conclude that the specimens exhibit crystallinity (rather than amorphous mineral phases) because the spectra exhibit peaks rather than broad, low humps. The exact locus of mineralization and its variation within the layered chitin microstructure is unclear. The Raman spectra likely penetrated a few microns into the carapace, and thus represent a mostly surficial signal. Most of the specimens we used were wild caught, and thus not raised in environmentally controlled habitats. How

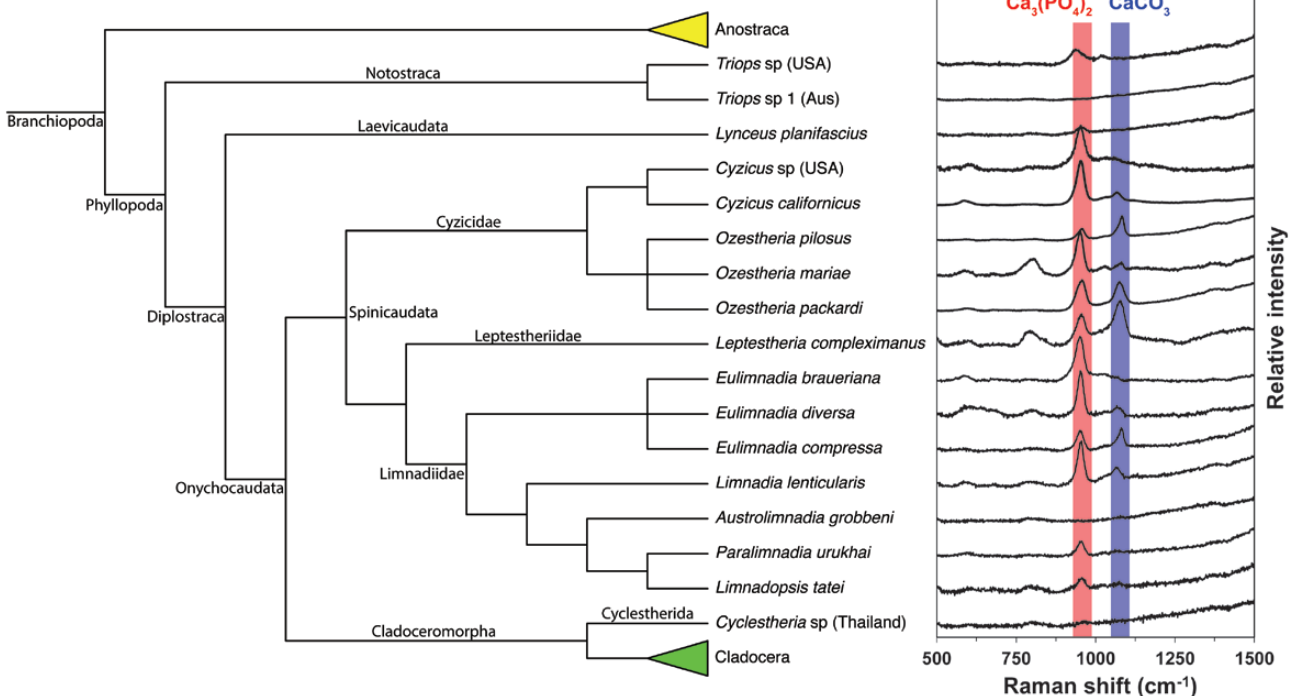


Figure 1. Raman spectra for seventeen species of large branchiopods (fifteen clam shrimps), organized phylogenetically (phylogeny derived from Schwentner *et al.*, 2020). Presence of calcium phosphate ($\text{Ca}_3(\text{PO}_4)_2$) or calcium carbonate (CaCO_3) is indicated by peaks within the vertical bars. This figure is available in color at *Journal of Crustacean Biology* online.

much of the observed mineralization patterns are due to environmental factors is not clear. Future studies should examine how the carapace mineral content varies when mineralizing species are raised in mineral-limited environments, or when non-mineralizing species are reared in mineral-rich environments. Would mineralizing species raised in mineral-limited environments die or would they develop without mineralized carapaces? Can species like *A. grobbeni* be induced to mineralize their carapaces in a mineral-rich environment?

There are several important implications for the fossil record. First of all, a composition of either calcium phosphate or calcium carbonate cannot demonstrate replacement (*sensu* Stigall *et al.*, 2017) without additional corroborative evidence. Second, the dual mineral composition of many species may eventually provide new characteristics to examine when considering fossil and extant clam shrimp phylogeny, especially as the pattern of mineralization in modern species is better understood.

Crustaceans generally rely on calcium carbonate when strengthening their exoskeleton with a mineral phase (Moore & McCormick, 1969). The basal living barnacle *Ibla* Leach, 1825 uses calcium phosphate in its shell plates (Reid *et al.*, 2012), which may be the basal state for barnacles (Gale & Schweigert, 2016). The presence of a dual mineral system had been previously detected in crustaceans. Some malacostracans use calcium carbonate and calcium phosphate in their exoskeleton (BoBelmann *et al.*, 2007) mandibles (Bentov *et al.*, 2016), and some barnacles use both calcite and aragonite in their plates (Bourget, 1987). A dual mineral system, however, has never been documented on a clade scale as presented here. This phenomenon should stimulate future material science research on the properties of the dual mineralization system in clam shrimps and how the dual mineralization relates to their novel mode of growth via molt retention.

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