# Decay and Mineralization of Mantis Shrimps (Stomatopoda: Crustacea)—A Key to Their Fossil Record

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PALAIOS, 1997, V. 12, p. 420–438

*Experiments were carried out on decay and early diagenetic mineralization in the stomatopod* Neogonodactylus *as a basis for the interpretation of fossil specimens of mantis shrimps.* Neogonodactylus *has a robust cuticle that is heavily mineralized in places in contrast to the decapods* Crangon *and* Palaemon, *which have been the subject of similar taphonomic experiments. Decay over 25 weeks resulted in a continuum of morphological stages: (1) swollen, due to osmotic uptake; (2) ruptured, as the exoskeleton split; and (3) partially decomposed, including weakening of the cuticle, decay of the soft-tissues, and disarticulation and fragmentation of the exoskeleton. Two categories of mineralization occurred; the precipitation of crystal bundles of calcium carbonate, and the replacement of soft-tissue and cuticle in calcium phosphate. Calcium carbonate formed as: (1) crystal bundles of various shapes; (2) crusts on the outside of the cuticle; and (3) an amorphous crystalline mass within the cuticle. The amount of soft-tissue mineralized in calcium phosphate increased throughout the experiment. In the later stages the hepatopancreas was often completely mineralized. Muscle tissue was replaced to a lesser extent and mostly in small fragments. Nerve ganglia were occasionally mineralized. The degree of mineralization was much greater than in decapod shrimps, presumably reflecting the higher calcium content and relatively phosphorus-rich cuticle of the stomatopod. The stages of morphological decay observed in these experiments can be identified in fossil stomatopods. SEM observations of fossil material have revealed phosphatized soft tissues similar to those found in the decaying carcasses. The experiments indicate that stomatopods have a relatively high fossilization potential. Their scarce and fragmentary fossil record must be a function of factors other than decay and degradation.*

## INTRODUCTION

Taphonomic studies are crucial to reveal the factors that bias the fossil record of crustaceans. Although most interpretations of the taphonomy of crustaceans are based *a posteriori* on fossil occurrences (e.g., Glaessner, 1929; Mertin, 1941; Mundlos, 1975; Bishop, 1981), the amount of information obtained from experimental studies is increasing rapidly.

Both broad subdisciplines of taphonomy, i.e., biostratinomy and fossil diagenesis (see Müller, 1979), have been the focus of descriptive and experimental studies on decapod crustaceans. The empirical work of Schäfer (1951, 1972) included investigations of the decay and disintegration of brachyuran crabs in shallow sub- and intertidal environments of the North Sea. His work was invaluable in identifying some of the key variables in crustacean taphonomy (Brett and Baird, 1986; Plotnick, 1986). Allison (1986) demonstrated that freshly killed shrimps are very resistant to damage during transport, whereas they disarticulate rapidly following the onset of decomposition. Experimentally controlled laboratory and field experiments (Plotnick, 1986) on a modern caridean shrimp identified scavengers as the probable primary cause of carcass destruction. Further breakdown was caused by bacterial decomposition and disturbance by burrowing infauna. In a study on the fossilization potential of the mud crab *Panopeus,* Plotnick et al. (1988) showed that taphonomic processes are not invariant "filters" through which paleontological information is allowed to pass selectively (Behrensmeyer and Kidwell, 1985), but dynamic phenomena that change over ontogenetic, ecological and evolutionary time scales.

In decay experiments with a polychaete worm and the decapods *Nephrops* and *Palaemon,* Allison (1988) demonstrated that rapid burial and anoxia, traditionally considered to be the main prerequisites for exceptional preservation, may reduce the rate of decay but certainly do not stop it. Briggs and Kear (1993b, 1994) confirmed that early diagenetic mineralization was a critical factor in preserving soft-tissues. Under controlled experimental conditions, they observed the precipitation of crystal bundles of calcium carbonate, and the replacement of soft-tissue in calcium phosphate in the decaying shrimps *Crangon* and *Palaemon.* The nature of the experimentally mineralized soft tissues closely resembled those reported from fossils, indicating that similar processes were involved (Briggs et al., 1993). Baas et al. (1995) demonstrated that chitin is selectively preserved under the same experimental conditions.

Here we describe experiments on the stomatopod *Neogonodactylus oerstedii,* which complement previous work on decay and early diagenetic mineralization in decapod shrimps. This is only the second suite of experiments to document the extensive phosphatization of soft-tissues in the laboratory. The stomatopod cuticle is more robust than that in the decapods investigated, and it is heavily mineralized in places. Decay and mineralization under anaerobic conditions were monitored over a period of 25



0883-1351/97/0012-0420/$3.00

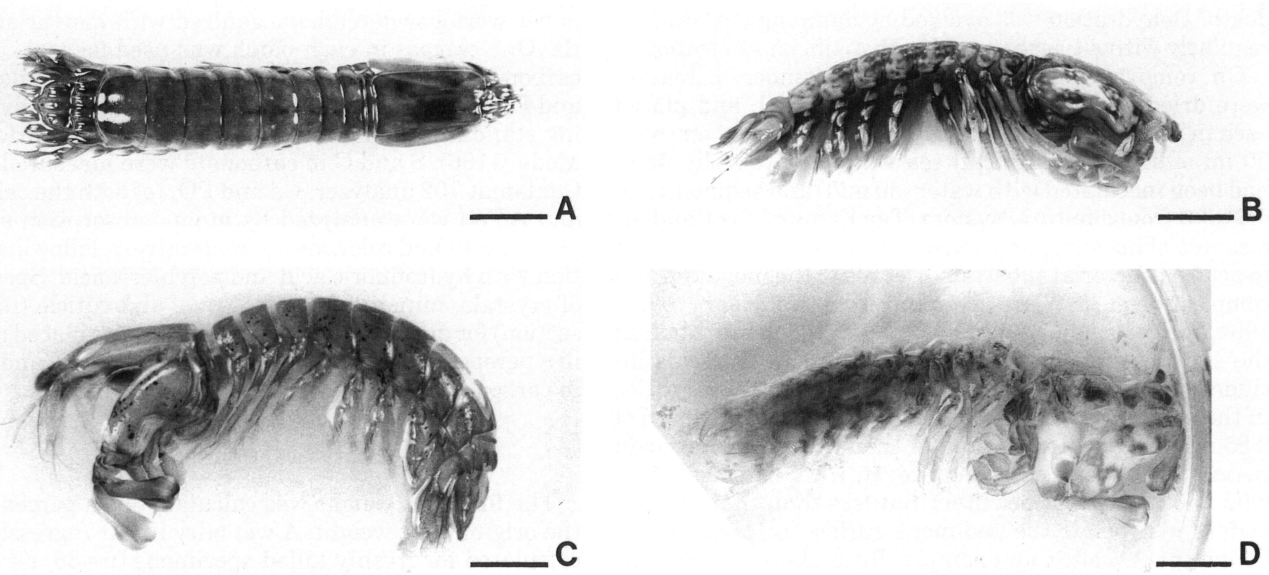


**FIGURE 1**—*Neogonodactylus oerstedii.* (A) Living, dorsal view. Scale bar is 7 mm. (B) Freshly killed, lateral view. Smashing limbs folded beneath the carapace. Scale bar is 8 mm. (C) After 3 days decay. Propodus of smashing limb unfolded, arthrodial membranes swollen especially between the posterior thoracic segments. Scale bar is 6 mm. (D) After 4 weeks decay. Cephalothorax separated from the trunk, smashing limbs detached after slight disturbance. Scale bar is 7 mm.

weeks. The results have general implications for the preservation of soft-tissues and cuticles, particularly in crustaceans. The morphological stages of decay identified in these experiments are evident in fossil stomatopods.

## MATERIAL AND METHODS

Previous experiments investigated the effect of varying conditions on the decay of shrimps (Briggs and Kear, 1994). Here the focus is on how the morphology of the stomatopod influences its preservation potential. Hence all the experiments were carried out under the same conditions. The striking morphological and structural complexity of stomatopods allows the decay and mineralization of contrasting organs and tissues to be monitored in detail in a relatively small crustacean. The limited but well documented stomatopod fossil record facilitates comparative study.

### Material

Stomatopods, also known as mantis shrimps, can be found on most of the world's tropical and subtropical coral reefs, sand, mud, and rubble-strewn coasts. These 10-to-350-mm-long crustaceans are active, alert, and highly visual predators exhibiting intense agonistic behavior while defending their burrows and cavities. Although seldom seen because of their secretive habits, stomatopods are often so numerous as to constitute a major predatory force in sub- and intertidal marine communities (Caldwell and Dingle, 1975, 1976). The most striking morphologic characteristic of stomatopods is the second thoracopod, which is developed as a large raptorial claw. The experiments were carried out on the stomatopod *Neogonodactylus oerstedii* (Hansen, 1895) (Malacostraca, Stomatopoda, Gonodactylidae) (Fig. 1A). *N. oerstedii* is the most common littoral stomatopod in the tropical and subtropical regions of the Western Atlantic, inhabiting a variety of habitats. It ranges in size from 8 to 76 mm. Males are dark, the body bluish with scattered yellow pigment in no particular pattern; females are light, the body cream colored with many scattered black chromatophores giving a speckled appearance overall. Their second thoracopod is a powerful smashing limb with heavily sclerotized dactylus and propodus. The carapace is characteristically divided into three fields by the paired parallel gastric grooves. The trunk is smooth and subcylindrical with inflated carinae on the last abdominal tergite and telson (for more details see Manning, 1969).

Living animals (n = 30; size range 0.39 g to 1.91 g) were obtained from the Fort Pierce area of Florida through the agency of the University of Sussex Centre for Neuroscience, Brighton, UK. The animals were held in aquaria in the Department of Geology, University of Bristol, until required. The aquaria were filled with 35–37‰ artificial sea water, which was aerated and filtered and kept at 23°C. To avoid severe agonistic fighting, hiding places were offered to the animals by placing rocks and short pieces of tubing (length 7 cm, diameter 1.8 cm) in a layer of fine gravel. Morbid or dead animals were not used for the experiments, nor were recently molted individuals. The animals were not fed for two days prior to the experiments.

### Method

The stomatopods were killed by anoxia in order to ensure that specimens were complete and undamaged. They were placed in an empty beaker in the air-lock of an anaerobic cabinet. The air was pumped out of the chamber, which was then twice flushed with oxygen-free nitrogen and twice with an anaerobic gas mixture ($CO_2$, $N_2$, and $H_2$). Due to their tolerance to low oxygen levels, the animals were left in the chamber for 4 to 5 hours to ensure

death. Dehydration was avoided by damping the animals regularly with a tissue wetted with artificial sea water.

On removal from the anaerobic chamber, carcasses were dried by blotting with tissue, weighed, and placed each in a separate experimental vessel (ointment jar) with 50 ml of standard artificial sea water (ASW). The ASW had been inoculated with water (50 ml/l) and sediment (ca. 0.5 ml/l) from a natural system (Tay Estuary, Scotland) as a source of bacteria, and yeast extract (0.1 g/l) was added to act as a bacterial substrate. Details of the inoculum and composition of ASW are given in Briggs and Kear (1993a, 1994). pH was adjusted to 8.00 and oxygen saturation at the start was about 50%. The standard ASW recipe includes no phosphate, but analyzes showed that impurities in the salts used resulted in a phosphate concentration of 3.85 mg per liter. This is greater than the concentration in normal sea water (Lucas and Prévôt, 1991, listed values of 0.02 to 0.27 mg $PO_4$ per liter), but less than that in porewaters just below the sediment surface in Long Island Sound (FOAM site), for example (Ruttenberg and Berner, 1993, reported 10 mg per liter).

Thirty stomatopods were grouped into batches of five each, each batch destined to be sampled at a designated time. For each batch, six separate vessels—five with a carcass, the sixth identical, inoculated, but lacking a carcass—were sealed in a plasticized aluminium bag (method of Cragg et al., 1992) with Merck Anaerocult A (Merck Ltd., Poole, Dorset, UK.). This method creates anaerobic conditions within an hour (and corresponds to condition 1c of Briggs and Kear, 1993a, 1994). The vessels were incubated at 20° ± 0.5°C.

### Sampling

The six batches were sampled after 3 days, and 1, 2, 4, 8, and 25 weeks, respectively. The color of the ASW was noted, and the presence or absence of bacterial films at the air interface and on the bottom of the jar was recorded by visual inspection. The pH and oxygen content of the ASW were measured (procedures and instruments as in Briggs and Kear, 1993a). The morphologic sequence of the decay state was recorded using a binocular microscope. Special attention was paid to the morphological and structural condition of distinctive body parts like the raptorial limbs, the carapace, and the telson. The wet and dry weight of 4 of the 5 carcasses were measured as in Briggs and Kear (1994). One carcass of each batch was stored in the freezer for future analyses of organic composition (see Appendix).

All of the sampled carcasses were examined using a binocular microscope. Two carcasses in each batch were selected for examination with the scanning electron microscope (SEM), with mineralization as a prime target. Samples for SEM examination were coated in gold and examined at 7–10 kV. Mineralized parts and representative pieces of the cuticle from these two carcasses were analysed by electron microprobe (EM). Backscatter images of some of the EM samples were photographed to document the mineralization patterns in and on the cuticle.

### Chemical Analysis

Specimens for chemical analysis (Appendix) were oven dried on glass-fiber filter paper and then specimen plus paper were powdered/homogenized with mortar and pestle. One carcass in each batch was used for total organic carbon (TOC), S, and CHN ratio analyses, and one for Ca and $PO_4$ analyses. TOC and CHN ratios were analyzed using standard methods (Elemental Analyzer "Carlo Erba" Model 1106). S and C in carbonate were measured with a Coulamat 702 analyzer. Ca and $PO_4$ (of both the carcasses and ASW) were analyzed by atomic absorption spectrophotometry and colorimetry, respectively, following digestion with hydrofluoric acid and perchloric acid. Specimens of crystals, mineralized soft-tissue, and cuticle (in cross-section) for analysis in the microprobe were placed in holes in a perspex plate, immersed in resin, polished, and coated in carbon.

### Statistical Comparison

The final wet weight was calculated as a percentage of the original wet weight. A wet : dry linear regression was calculated for freshly killed specimens ($n=36$, $r^2=0.937$). This was used to predict initial "baseline" dry weights. Final dry weights were expressed as a percentage of these "baseline" values. Data were processed using the statistical options of Microsoft Excel 4.0 and the statistical package SYSTAT 5.21. A one-way analysis of variance (Fully Factorial, Bonferroni mean comparison) was performed to examine the weight changes between the different time intervals. A two-way analysis of variance (Fully Factorial), was used to compare the decay rate of the shrimp *Crangon* in the experiments of Briggs and Kear (1994), with that of the stomatopods. In this analysis only the data for corresponding time intervals were used. The data from the chemical analyses were not subjected to statistical analysis due to the small number of samples ($n=1$ for each sample batch). All chemical analyses were repeated on a second sample from the same specimen in order to minimize error. The data for weights and pH are presented in the Appendix, which also identifies the specimens that were used for particular analyses.

## MORPHOLOGICAL STAGES OF DECAY

Disintegration of the mantis shrimp took place in a sequence of morphological stages. These stages, which are based on detailed examination of all five specimens in each sample batch, are broadly similar to those in decaying decapod shrimps (Briggs and Kear, 1994). Hence the emphasis in what follows is on the features that distinguish stomatopods.

*Freshly killed.*—Killing resulted in no significant changes in the appearance of the stomatopod (Fig. 1A, B). When observed in ASW, the color pattern remained the same, the body was stretched, the antennules were directed anteriorly as were the antennae, the scaphocerites remained slightly curved backwards towards the body, the raptorial limbs were folded underneath the carapace, the walking legs were stretched, the pleopods hung loosely underneath the abdomen, and in most carcasses, the uropods were spread laterally.

*3 days.*—The colors faded. The carapace lifted slightly anteriorly due to osmotic uptake. The arthrodial membranes of the body showed swelling, particularly those separating the last 4 thoracic tergites. Osmotic pressure