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Did shell-crushing crabs trigger an escalatory arms race in the aftermath of a Late Neogene regional mass extinction event? An experimental test

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ABSTRACT

A regional mass extinction event in the late Neogene western Atlantic is widely thought to have generated evolutionary opportunities for survivors, including enemy-related adaptation (escalation). The *Strombus alatus* species complex is one potential example of this phenomenon. Strombid gastropods are abundant in the Plio-Pleistocene fossil record and Recent in subtropical Florida, and the percentage of these shells bearing a row of short spines on the last whorl increased from nearly zero to almost 100% over this time. As shell ornamentation is one of the most frequently cited defenses against both peeling and crushing predators, we exposed live spined and spineless *S. alatus* to the stone crab *Menippe*, one of its natural enemies and the predator responsible for shells scars commonly found on modern and fossil *S. alatus* shells, to test whether the increase in expression of shell spines in this species complex is consistent with an adaptive or induced response to intensifying predation pressure from durophagous crabs. We also utilize random variation in prey shell length, diameter, and lip thickness to quantify the relative importance of additional shell parameters thought to deter attacks from durophagous crabs. The central finding of this study is that neither thicker shell lips nor the modern configuration of spines determine whether *S. alatus* will be more likely to survive *Menippe* attacks or have less severe shell damage. In our experiments, the only shell trait associated with reduced damage and increased probability of survival was whorl diameter. We conclude that menippid crabs, at least those crabs within the range of large, adult sizes used in this experiment, probably did not play a primary role in the changing expression of *Strombus* spines on the last whorl in the post-Pliocene of Florida or elsewhere in tropical America. This conclusion is consistent with the position that faunal-scale increases in expression of defensive shell traits in the post-Pliocene of Florida were driven more by differential extinction of lightly armored species than escalatory responses to increasing crab predation pressure. However this conclusion is tentative and additional data are needed to explore this hypothesis fully.

1. Introduction

A period of environmental upheaval that triggered a regional extinction event in the late Neogene western Atlantic is widely thought to have generated evolutionary opportunities for survivors in the form of speciation (Allmon et al., 1993; Jackson et al., 1993; Allmon, 2001; Johnson et al., 2007) and enemy-related adaptation (i.e., escalation) (Vermeij and Petuch, 1986). Escalation, the idea that biological hazards, such as competition and predation, and adaptations to those hazards have increased over time (Vermeij, 1987, 1994), was inferred by Vermeij and Petuch (1986) from a "moderate" post-Pliocene increase in the percentage of sand-dwelling gastropod genera that possess anti-predatory shell traits specific to lip-peeling crabs, such as an occluded or reinforced aperture. The notion that escalation could begin so rapidly (within 1 Ma) after loss of up to 70% of Pliocene taxa (Stanley and Campbell, 1981; Stanley, 1986; Allmon et al., 1993), however, is controversial. Disruptions or reversals of escalatory trends, even if temporary, are the normal outcome of extinction events (Vermeij, 2013) where dominant, high-powered predators or competitors are lost and not immediately replaced by invasion, and environmental stresses, such as a decline in primary productivity, impose selection pressures on survivors (e.g., reduced body size, earlier sexual maturation, etc.) that run counter to trends in adaptation to biotic factors (e.g., increased body size, investment in adult defenses, etc.) (Vermeij, 1987). If post-extinction escalation did occur, it would imply both the (1) rapid recovery of primary productivity, perhaps through the shift in ecological dominance from one type of primary producer to another, and (2) the rapid return of intense top-down pressure by competitors and consumers (Vermeij, 2004: 242). Although it can take substantial time for high-powered competitors and predators to re-evolve, invasion of high-powered species form adjacent areas less affected by extinction would speed up this phase of recovery.

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At present, the increase in proportion of armored taxa in the aftermath of this extinction event is suggestive of intensified selection from enemies, but this, as noted by Vermeij and Petuch (1986), this conclusion is not yet supported by any specific ecological data. Additionally, no data were presented on changes in the relative abundance of narrow- versus broad-apertured gastropods, which may be a better indication of the average escalation state of the community as a whole before and after the Pliocene (e.g. Jemvall and Fortelius, 2002). Other plausible instances of escalation in the post-Pliocene of Florida, such as microevolutionary increases in shell thickness and size of some bivalves, have also been portrayed convincingly as isolated, co-evolutionary responses to highly specialized gastropod predators rather than as a broad, assemblage-level phenomenon involving generalist durophagous enemies (Rooperaine and Beussink, 1999; Dietl, 2003). An alternative hypothesis is, thus, that trends documented by Vermeij and Petuch (1986) reflect differential extinction of broad apertured taxa due to incidental factors unrelated to escalation, although it is unclear what incidental factors those might be.

If shell-crushing or peeling predators did trigger escalation in gastropods following the late Neogene extinction event, its most conspicuous manifestation would be the simultaneous, independent acquisition of shell spines and knobs – putative anti-predatory adaptations (Palmer, 1979) – across several genera of soft-sediment dwelling strombid gastropods (*Lobatus costatus* and *Lobatus raninus* species complexes, *Eustrombus gigas* species complex; *Strombus alatus* species complex) from the Pliocene to the Recent in subtropical Florida (Guest et al., 2008; Landau et al., 2008, 2011). Extant *Strombus* species are subjected to a wide array of predation pressures from durophagous enemies. Vertebrate predators, such as the cownose ray *Rhioptera bonasus*, the loggerhead sea turtle *Caretta caretta*, and various durophagous teleosts have been known to crush whole *Strombus* using oral or pharyngeal jaws (Yamaoka, 1978; Palmer, 1979; Taylor et al., 1980). The mantis shrimp *Gonodactylus* has been reported to peel the shell of young *S. alatus* and attempt to hammer a hole through the ultimate whorl via its smasher-type dactylus (Bertness, 1982; Balukm and Radwanski, 1996). Crabs such as *Menippe* and *Calappa* are capable of peeling and crushing adult *S. alatus*.

The *S. alatus* complex is of particular interest as it is represented in Florida as a single, morphologically changing lineage, and Pliocene to Recent trends in its morphology are well documented (Hargreave, 1995). *Strombus* is also one of the most abundant survivors of this extinction event in both Pleistocene fossil deposits (Geary and Allmon, 1990) and modern coastal habitats (Clench and Abbott, 1941). This population characteristic is important, because common taxa are more likely to exhibit general adaptive trends than rare taxa, whose specializations may not be representative of assemblage-level patterns (Jernvall and Fortelius, 2002).

Since the Pliocene, the percentage of *Strombus* spp. shells in Florida bearing a row of short, conical spines on the last whorl has increased from close to zero to nearly 100%, while the maximum number of spines on the last whorl has increased from less than three to around eleven (Goodrich, 1944; Petuch, 1994; Hargreave, 1995; Herbert et al., 2004) (Fig. 1). Similar trends are seen in other fossil *Strombus* species from the Caribbean (Landau et al., 2008, 2010, 2011; Freiheit and Geary, 2009). Following Vermeij and Petuch (1986), Herbert et al. (2004) speculated that morphological changes in the *S. alatus* complex were possibly an escalatory response triggered by intensifying attacks from durophagous crabs, which are abundant in modern habitats and Plio-Pleistocene shell beds where *S. alatus* and its fossil predecessors occur (Britton and Morton, 1989; Portell and Agnew, 2004). The distinctive scars left by crab chelae are the most common predation trace on fossil and modern *Strombus* shells (Herbert et al., 2004), which suggests that crab predators were potentially important selective agents of *Strombus* morphology (Ditel and Herbert, 2010).

Here, we employ an experimental approach to test the hypothesis that the shell spines acquired by *Strombus* spp. in the aftermath of the late Neogene extinction event deter predatory attacks by the most common decapod predator of gastropods in coastal habitats in the Gulf of Mexico, the stone crab *Menippe* (Bert, 1985; Brown and Haight, 1992; Beck, 1995, 1997). Random variation in prey shell length (columella height), diameter, and lip thickness between mature *S. alatus* used in this experiment allowed us to quantify the relative importance of additional shell parameters previously cited to deter attacks from durophagous crabs in other gastropod species (e.g., Hughes and Elner, 1979; Vermeij, 1982; West et al., 1991; Rochette et al., 2007). Testing whether shell spines do, in fact, increase survival in *Strombus* prey exposed to crabs is a critical test of the hypothesis that spine evolution in *Strombus* occurred, at least partly, in response to durophagous crabs. We conducted a predator–prey experiment with live *Menippe* fed extant *S. alatus*, where we compared the outcomes of *Menippe* attacks on *S. alatus* having the modern morphology of 11 spines with the outcomes of attacks on *S. alatus* that had been mechanically altered

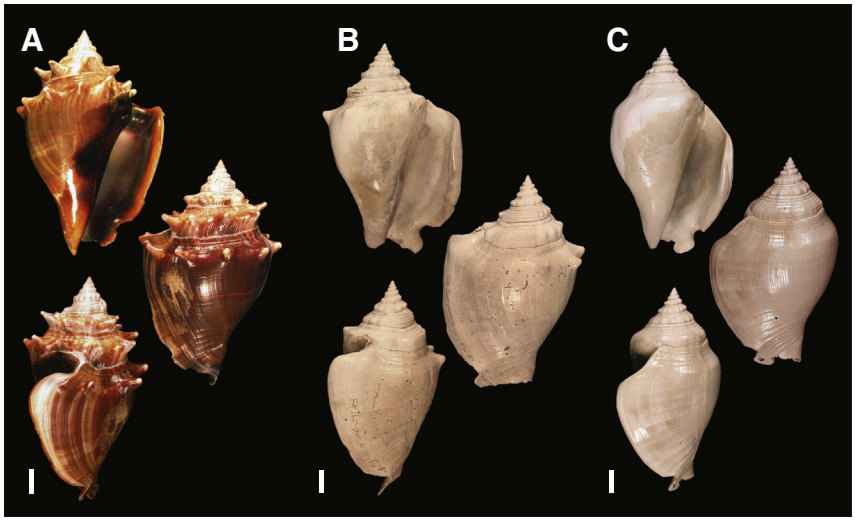

Fig. 1. *Strombus* sp. shells from Florida showing changes in the typical number and placement of shell spines through time. A. Recent *S. alatus* from Bonita Beach, Lee County, Florida. B. *S. alatus*, Ft. Thompson Formation (0.95–0.22 Ma), Leisey Shell Pit, Ruskin, Hillsborough County, Florida. C. *Strombus evergladesensis* Petuch, 1991, Bermont Formation (1.6–1.1 Ma), Longan Lakes Shell Pit, Naples, Collier County, Florida. Scale bar = 1 cm.