

CHANGES IN PREDATORY BEHAVIOR & EFFICIENCY: GASTROPOD DRILLING PATTERNS IN MIOCENE-PLIOCENE *TURRITELLA* (GASTROPODA)

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The escalation of predator-prey interactions over the Phanerozoic is described as an "arms race" among the Gastropoda. Examples of escalation have been extensively documented on the scale of hundreds of millions of years, however, these patterns are not well documented on shorter time scales. Effective escalation of prey defenses should cause a drop in predatory efficiency. We study the efficiency of Naticid and Muricid predation upon Turritelline gastropods from the Miocene to the Pliocene. These predators leave a well preserved trace of predation in the form of a borehole in the shell of the prey. This study focuses on 18 species of Miocene and Pliocene *Turritella* from the southeastern United States. Over five thousand individual shells were examined and measured, collected from 13 localities from Maryland to southern Florida.

Predatory efficiency is determined by a number of factors: shell thickness at drillhole site, vertical location of drillhole, percent of shells that have multiple drillholes, and percent of shells that contain incomplete drillholes. Shell thickness at drillhole and location of drillhole are measured because predators would benefit by expending less energy drilling into the thinnest part of the shell that is nearest the visceral mass of the prey. Multiple complete boreholes represent at least one failure to obtain food. Incomplete boreholes represent a drilling attempt which has failed to produce food at the cost of metabolic energy.

While the intensity of Naticid and Muricid predation of *Turritella* increases (χ^2 , $\alpha < .01$), predators become less efficient from the Miocene to the Pliocene. Decreased predatory efficiency is indicated by an increase in the number of shells with multiple and incomplete drilling sites (χ^2 , $\alpha < .01$). Although predators appear to have little radial preference, they indicate strong vertical preference for centrally located drilling sites (t-test, $\alpha < .01$). Predators appear to be drilling into thicker parts of Turritelline shells and thus expending more energy in drilling - however, this pattern is not statistically significant (χ^2 , $\alpha > .20$).

We show that the efficiency of Naticid and Muricid predators decreased from the Miocene to Pliocene. Decreased efficiency of predators might result from newly evolved structural changes in prey shells, new prey escape responses or problems in predator recognition of live versus dead prey shells resulting from high densities of both living and dead individuals.

It remains to be seen whether predatory efficiency declines over longer time scales. In light of previous studies which have concentrated on evolution in the shell shape and ornamentation of prey in response to predators, a more promising and direct measure of the efficiency of predation may lie in the study of the frequency of multiple and incompletely drilled shells. By this method we might better judge the effectiveness of defense mechanisms and the evolutionary significance of predator-prey escalation.