



Plio–Pleistocene drilling predation in Florida bivalves: Predator identity, competition, and biotic change



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ABSTRACT

Identifying gastropod predators from the morphology of their drill hole traces is an important step in testing the disruptive effects of prey evolution on the prey size selectivity behaviors of predators. For bulk sampled bivalves of the genus *Chione* from the late Neogene of Florida, temporal patterns of prey size selectivity differ depending on whether drill holes from naticid and muricid gastropods are lumped together or separated. When drill hole producers are identified to family level using revised experimental criteria developed specifically for this study system, we find that naticid and muricid prey size selectivity responds in different directions and at different times, but both groups exhibit change in prey size selectivity beginning around 2.5 Ma. We reject previous conclusions that changes in drilling gastropod prey handling behaviors were driven by changes in prey morphology associated with a species turnover event at 1.8 Ma. Prey density, threats from enemies, and habitat structure were also changing throughout the study interval, but none of these factors alone provides a complete explanation for observed changes in predator behaviors for either family. We conclude that multiple factors drive predator behavioral change, and that different predator types have different sensitivities to these factors.

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1. Introduction

Mass extinction events are widely thought to slow, reverse, or end long-term trends in adaptation, thereby playing a dominant role in shaping evolutionary history. Such disruptions could be triggered, in theory, by losses of clades with ecologically important innovations or by changes in the fitness landscape that favor competitively inferior opportunists that invest more heavily in reproduction than enemy-related adaptations (e.g., Gould, 1985, 1990; Jablonski, 1986, 2005, 2008). Others have argued, however, that the disruptive effects of extinction are typically counterbalanced by rapid recovery of both food producers and selection pressures necessary to drive the process of enemy-related adaptation (Vermeij, 1989, 1999:249). If true, the effects of extinction on long-term adaptive trends may, in fact, be brief and minor.

One of the ways investigators have approached this problem is to quantify the duration and magnitude of disruptions of biotic interactions between gastropod drilling predators and their bivalve prey in the aftermath of mass extinction events. If extinctions disrupt adaptive trends by selectively removing “difficult” prey, i.e., bivalves having energetically costly defensive adaptations, such as shell ribs, lamellae, and spines (Vermeij, 1987), then predators should forage during the recovery phase in a way consistent with relaxed selective constraints

on prey handling and prey-size selection behaviors (Kelley and Hansen, 1996). Prey-size selectivity can be quantified in this study system by measuring the prey shell length and drill hole diameter for each attack in a sample, where drill hole size serves as a proxy for predator size (Kitchell et al., 1981). The relationship between predator and prey sizes conveys information about manipulation limits of the predator as well as the ratio between energetic gain from ingested prey biomass and the costs of prey handling; this cost is primarily a function of the time it takes to complete a drill hole (Kitchell et al., 1981; Kitchell, 1986; Kowalewski, 2002). Conversely, during background times prior to an extinction event or following “complete” recovery, increased investment in defenses by prey might drive predators to select prey near their manipulation limit in order to maximize net energy return and overall foraging efficiency (Kitchell et al., 1981; Boggs et al., 1984; Kelley, 1988, 1991). This general theoretical framework, however, reflects a strongly prey-centric view of biotic interactions, which may not be accurate. Other factors, such as the presence or absence of the predator's own enemies, should also influence foraging decisions (Brown and Kotler, 2004; Dietl et al., 2004).

Here, we re-examine the history of gastropod drilling predation on the venerid genus *Chione* von Mühlfeld, 1811 in the context of a regional mass extinction event in Florida roughly 2 Ma, with new emphasis on tracking the individual responses of the two major families of gastropod drilling predators, the Naticidae and the Muricidae. Massive species turnover, which led to the loss of roughly 70% of Pliocene molluscan taxa, has been documented throughout the region (Stanley and Campbell, 1981; Stanley, 1986; Allmon et al., 1993; Jackson et al.,

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1993; Petuch, 1995), but *Chione* and its primary drilling predators survived the extinction event (e.g., Guerrero and Reymont 1988; Petuch, 1994; Roopnarine and Beussink, 1999). This system, therefore, avoids the nearly impossible task of trying to infer disruption and recovery of prey selection behaviors when the types of predators and prey before and after an extinction are different.

One of the changes suspected by previous authors to have triggered disruption of predator behaviors in the immediate aftermath of this extinction event was a change in shell morphology of *Chione* prey associated with replacement of the Pliocene-to-Early Pleistocene *Chione erosa* Dall, 1903 with the middle Pleistocene-to-Recent *Chione elevata* (Say, 1822) (Roopnarine and Beussink, 1999). *Chione erosa* has a slightly longer lunule, longer shell, a more dorsal position of the hinge, and more elaborate sculpture relative to *C. elevata* (Roopnarine, 1995, 1996) (Fig. 1), but none of these changes would have presented drilling predators with a more or less escalated prey (Roopnarine and Beussink, 1999). Instead, Roopnarine and Beussink (1999) argued that morphological novelty alone would have been sufficient to disrupt or confuse prey handling behaviors of drillers. Their analysis of prey selection behaviors during this biotic crisis appeared to confirm that the stereotypy of prey size selectivity declined coinciding with species replacement within *Chione*, but that predators recovered rapidly by the Late Pleistocene (Roopnarine and Beussink, 1999).

A potential confounding factor in the Roopnarine and Beussink (1999) results is the mixing of data from drill holes produced by different types of predators. Although identifying the producers of drill holes can be difficult (Kowalewski, 2002), it is an essential step when one is interested in tracking the prey selection behaviors of drilling gastropods through time. The necessity for this step is dictated by the fact that the relationship between drill hole size and predator size, prey size selectivity, and a predator's response to prey adaptations can be different for different types of predators (Ansell and Morton, 1985; Harper and Morton, 1997; Carriker and Gruber, 1999; Urrutia and Navarro, 2001; Daley et al., 2007). Mixing predation traces from multiple predator types potentially obfuscates these relationships and responses, and different levels of mixing at different times can produce artifacts

resembling ecological disruption or recovery, even if the prey selection behaviors of individual predator types remained unchanged.

Most studies attempt to avoid this problem by employing classic criteria for identifying predators from their drill hole morphology. The Naticidae are generally understood to produce large, countersunk holes with beveled sides, whereas species of the family Muricidae are diagnosed by the presence of smaller, straight-sided holes (e.g., Ziegelmeier, 1954, 1957; Fretter and Graham, 1962; Reymont, 1966; Carriker, 1969). There are, however, numerous exceptions to these criteria in which muricids produce naticid-like drill holes and vice versa (Carriker and Yochelson, 1968; Guerrero and Reymont, 1988; Gordillo, 1998; Gordillo and Amuchástegui, 1998; Harper and Peck, 2003; Reymont and Elewa, 2003; Ishida, 2004; Vasconcelos et al., 2004; Morton, 2005; Herbert and Paul, 2008; Harper et al., 2011). In Florida, extant species of the muricid genera *Chicoreus* and *Phyllonotus* have been shown experimentally to drill large, countersunk holes that resemble those produced by naticids (Herbert and Dietl, 2002; Dietl et al., 2004; Dietl and Herbert, 2005). Given the importance of muricids as drilling predators of *Chione* in the Recent (Paine, 1963), it is likely that the holes identified by Roopnarine and Beussink (1999) as naticid were produced by a mix of both naticid and muricid predators. We hypothesize that changes in drilling predation documented by Roopnarine and Beussink (1999) reflect, at least in part, varying degrees of mixing of naticid and muricid drill holes in different Neogene assemblages and not simply behavioral responses by a single predator type.

Our efforts to address the problem of predator identity for this study system led us to develop a complementary set of diagnostic criteria based on experimental observations where predator identity was known with certainty through direct observation. Dietl et al. (2004) showed that reliable diagnoses to the family level are possible for Florida predators using drill hole placement; the muricids *Chicoreus dilectus* (A. Adams, 1855) and *Phyllonotus pomum* (Gmelin, 1791) drill large, beveled holes in *Chione* almost exclusively over the ventral half of the prey shell and generally away from the direct center of the valve, while *Neverita delessertiana*, the naticid gastropod dominant throughout most of Florida, drills similar large, beveled holes almost exclusively on or near the umbo. Samples analyzed by Roopnarine and Beussink (1999:Fig. 8) contain a variable mix of drill holes over the umbo and ventral half of the shell, which points strongly to a mix of predator families and not, as they claimed, variation in drill hole placement preference among naticids. Using the revised predator identification criteria that incorporate drill hole placement, the potential for identification errors at the family level can be reduced to near zero for holes at the umbo and ventral half of the shell (Dietl et al., 2004). Identification errors are possible for drill holes positioned closer to the center of the valve, but *Neverita* rarely produces such holes, which occurred less than 1% of the time in the Dietl et al. (2004) experiments. Thus, the effect of such errors should be minimal. We use these recently developed criteria to re-evaluate the response of drilling predators to species turnover in the Plio–Pleistocene of Florida.

2. Materials and methods

We tabulated drilling predation and abundance data for bulk collected valves sampled from the four, major Plio–Pleistocene faunal units of Florida, all of which represent inner shelf to outer bay facies (Petuch, 1982; DuBar et al., 1991; Willard et al., 1993; Missimer, 2001). These include the Late Pliocene Pinecrest Beds of the Tamiami Formation (~3.5 to 2.5 Ma), the Early Pleistocene Caloosahatchee Formation (~2.5 to 1.8 Ma), the Middle Pleistocene Bermont Formation (~1.7 to 1.1 Ma), and the Late Pleistocene Fort Thompson Formation (~0.95 to 0.22 Ma) (Fig. 2). We consider the Caloosahatchee Fm. to be Early Pleistocene in age following a recent update in stratigraphic nomenclature (Ogg, 2008 with update from the International Commission on Stratigraphy [2009]), which moved the Pliocene–Pleistocene boundary from 1.79 Ma to 2.5 Ma. Ages and stratigraphic relationships among the

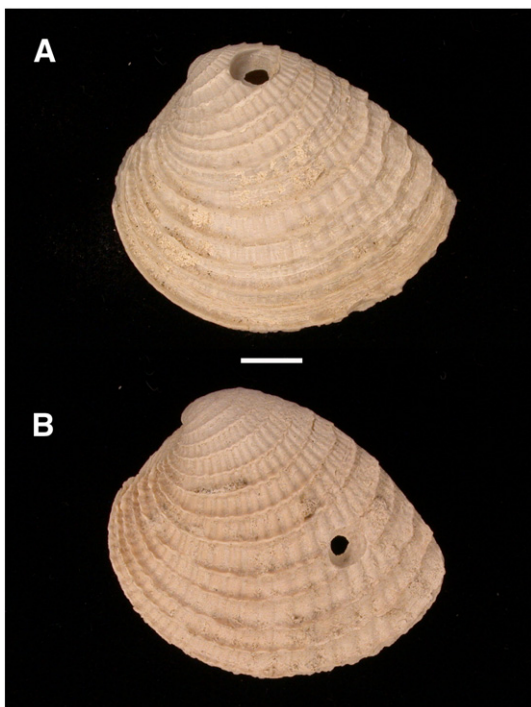


Fig. 1. *Chione* from the Late Neogene of Florida. (A)—*Chione erosa*, Caloosahatchee Formation, (B)—*Chione elevata*, Bermont Formation. Scale = 0.5 cm.

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