The fossil record of drilling predation on barnacles

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ABSTRACT

The fossil record of drilling predation has been studied in detail for a few major invertebrate groups (bivalves, gastropods, brachiopods, and echinoids), while other prey (e.g., scaphopods, serpulids, decapods, and barnacles) have been largely neglected. Herein, we report on drilling predation using an extensive collection of Cretaceous–Quaternary barnacles (>50,000 specimens). In total, 312 drill holes of predatory origin were found in Eocene–Holocene wall and opercular plates of balanomorph and scalpellomorph barnacles. The drilled specimens originated from localities in the USA, Jamaica, Panama, The Netherlands, Belgium, Antarctica, South Africa, Chile, and Venezuela, suggesting that drilling predation on barnacles was a worldwide phenomenon during the Cenozoic. Muricid gastropods are the inferred producers of the majority of the drill holes; two drill holes were likely caused by octopods. Drilling frequencies lack major temporal trends and appear low (<10%), consistent with observations in modern ecosystems that muricids are facultative drillers and commonly kill barnacles without drilling. Drill holes are placed non-randomly in balanomorph wall plates: they occur preferentially between plates in the interplate region, on and around the rostrum, and in the middle part of shell (height-wise). Drill holes in opercular plates occur preferentially in scuta rather than terga despite a notable taphonomic bias: scuta are preserved more frequently than the less robust terga are (2.22:1 based on a bulk sample). Drill holes in wall plates are commonly incomplete (23.4%), but, as documented for extant barnacle prey, successful attacks can be often accomplished via non-penetrative drilling. Also, drill holes are significantly larger in larger barnacles. The results provide limited support for the hypothesis that a reduction in the number of wall plates, tubes within wall plates, and strong external sculpture may have evolved as a result of muricid drilling predation of balanomorphs during the Cenozoic.

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1. Introduction

The fossil record of predator–prey interactions has been investigated most extensively using drill holes produced in prey skeletons by drilling predators (e.g., Kelley and Hansen, 2003; Huntley and Kowalewski, 2007). These trace fossils, generally referred to as *Oichnus* ispp. or *Sedilichnus* ispp. (Zonneveld and Gingras, 2014), are easily recognizable, fossilize well, have modern counterparts, and are found in shells of a variety of invertebrates. However, an overwhelming majority of previous studies centered on drill holes in post-Jurassic bivalves and gastropods (e.g., Kowalewski et al., 1998; Kelley and Hansen, 2003; Klompmaker, 2009; Chattopadhyay and Dutta, 2013; Mallick et al., 2014; Paul and Herbert, 2014; Klompmaker and Kelley, 2015, and many more), as these molluscs tend to be common, are relatively well-preserved compared to other invertebrates, and are easy to collect. Prey clades that have also received attention with regard to

drilling predation, although less frequently, include echinoderms (e.g., Kowalewski and Nebelsick, 2003; Złotnik and Ceranka, 2005), brachiopods (e.g., Leighton, 2003; Kowalewski et al., 2005; Baumiller et al., 2006; Tyler et al., 2013), and ostracods (e.g., Reyment et al., 1987; Reyment and Elewa, 2003). Prey that have been studied in more detail in recent years are scaphopods (Yochelson et al., 1983; Klompmaker, 2011; Li et al., 2011), annelids (Klompmaker, 2012; Martinell et al., 2012), chitons (Rojas et al., 2014), and decapod crustaceans (Pasini and Garassino, 2012; Klompmaker et al., 2013). Most of these studies are limited in scope being based on specimens from a single locality and stratigraphic level (but see Yochelson et al., 1983; Klompmaker et al., 2013).

Drilling predation in molluscs is often attributed to naticid and muricid gastropods (e.g., Kelley and Hansen, 2003), although other predatory drillers are known (e.g., Kowalewski, 2002). Whereas naticids were not reported to drill modern barnacles (Taylor et al., 1980; Barnes, 1999), drilling predation by muricids and octopods on modern barnacles has been documented in numerous studies (e.g., Connell, 1961; Radwin and Wells, 1968; Menge, 1974; Pratt, 1974; Barnett, 1979; Palmer, 1982, 1988, 1990; Perry, 1985; Guerra and Nixon, 1987; Hart and Palmer, 1987; Nixon and Maconnachie,

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1988; Barnes, 1999; Gordillo, 2001; Sanford and Swezey, 2008). In contrast, few studies have been devoted to drilling predation on barnacles in the fossil record. To our knowledge, drill holes have only been reported from isolated occurrences of "subfossil" barnacles from Antarctica (Jonkers, 2000: p. 251); the Pleistocene of Russia (Nielsen and Funder, 2003: *Oichnus paraboloides* Bromley, 1981), Jamaica (Collins et al., 2009: *O. simplex*), and Chile (Gordillo, 2013); and from the Pliocene of the USA (Florida) (Klompmaker et al., 2014: *O. ovalis* Bromley, 1993) and Spain (Donovan and Novak, 2015: *O. simplex* Bromley, 1981). Lastly, Gale and Sørensen (2015: fig. 4D, 19O; 2014: fig. 17F) documented the only known gastropod drill holes in Cretaceous barnacles: two drill holes were found in Campanian barnacles from Sweden. Our survey of figures in the systematic literature on fossil barnacles yields additional examples of specimens that contain drill holes of possible predatory origin (De Alessandri, 1906: pl. 4.24, Pleistocene of Italy; Zullo and Miller, 1986: fig. 3f, Pleistocene of the USA (North Carolina); Davadie, 1963: pl. 34.7, Pliocene of Morocco; Carriol and Schneider, 2013: fig. 2, Pliocene of central Chile; Yamaguchi, 1982: pls. 45.2b, 47.1a, Miocene of Japan; Buckeridge, 1983: pl. 4i, Miocene of New Zealand; Zullo, 1992: fig. 15.15, Miocene of the USA (California); Withers, 1953: pls. 31.4, 42.3, Oligocene of Hungary). These examples suggest that drilling predation in barnacles may have been much more common in the fossil record than reported so far and thus deserve more detailed investigation. The evolutionary history of barnacles as prey is particularly interesting because predation pressure by drilling gastropods has been postulated as a cause of reduction of the number of wall plates in Cenozoic Balanomorpha (Palmer, 1982). Here we report the results of an extensive study on this understudied prey of drilling predators based on barnacle collections from the Cretaceous–Quaternary originating from North and South America, Europe, Africa, and Antarctica. We also explore the role of drilling predation on morphological evolution of the balanomorph barnacles.

2. Methods

The Cretaceous–Quaternary collections of barnacles in the invertebrate paleontology collection of the Florida Museum of Natural History (FLMNH-IP) at the University of Florida (UF), consisting mostly of barnacles from the southeastern USA and circum-Caribbean, were surveyed for the presence of drill holes of inferred predatory origin. The cataloged collections contained 47,867 cirriped specimens, dominated by balanomorphs (>90%). Additionally, a barnacle specimen with a drill hole from the Pliocene of Langenboom (The Netherlands) deposited in the Oertijdmuseum and a small lot of barnacles from the Miocene of Miste (Winterswijk, The Netherlands) stored in the Naturalis

Biodiversity Center were studied. Nearly all drilled balanomorph barnacles (see Fig. 1 for morphological features of barnacles) had skeletons that included six wall plates, except for UF 245098 (four wall plates). The following data were recorded for each specimen that contained at least one drill hole of predatory origin: (1) the number of drill holes; (2) the type of drilled plate [i.e., wall (= parietal) plate or opercular plate (tergum or scutum)]; (3) completeness of the drill hole (complete or incomplete); (4) the specific location of the drill hole: a) which of the 12 plate and interplate regions (= overlap zones at plate margins with alae and radii or suture zone) was drilled, b) whether the drill hole was located at the base, middle or top part of a plate or interplate region; (5) outer drill hole diameter; (6) the maximum diameter of an intact barnacle shell measured from the rostral to carinal plate; and (7) the height of the drilled plate or interplate region (for scuta this was the maximum length). Digital calipers (precision = 0.03 mm) were used for measurements. The relationship between drill hole size and specimen size was evaluated using reduced major axis regression, a bivariate analysis optimized for assessing two dependent variables with comparable measurement errors.

To assess spatial distribution of drill holes across different regions of the barnacle skeleton (i.e., site selectivity or stereotypy), the drilling frequencies were tallied for each of the 12 wall plate and interplate regions. DF is defined here as the total number of specimens with at least one drill hole (complete or incomplete) divided by the total number of specimens (see also discussion). Because those 12 regions vary notably in surface area, we quantified the surface area of each interplate and plate regions, for three randomly selected, well-preserved balanomorph barnacles with six wall plates (UF 250777, 250939, and 251028). These specimens were photographed from all sides and the area of each plate and interplate region was measured using ImageJ 1.46r. The mean for the areas of the three specimens was used to estimate average proportional surface area of the six plate and six interplate regions. The average surface areas were then used to develop an expected frequency of drill holes under the null hypothesis that attack sites were distributed randomly across barnacle plate and interplate regions. A Monte Carlo simulation was used for each of the 12 plate and interplate regions to estimate (1) expected drilling frequencies, (2) 95% confidence intervals, and (3) p-values under the null hypothesis that drill holes were randomly distributed. This simulation was carried out by assigning 312 drill holes (i.e., the number of drill holes observed in the actual data) to 12 regions with probabilities given by their proportional surface areas. The simulation was repeated 10,000 times and the resulting frequency distribution was used to compute the estimates listed above. Concurrently, the standard deviation of drill hole frequencies across the 12 regions was computed for each iteration and the resulting null distribution of standard deviations was compared
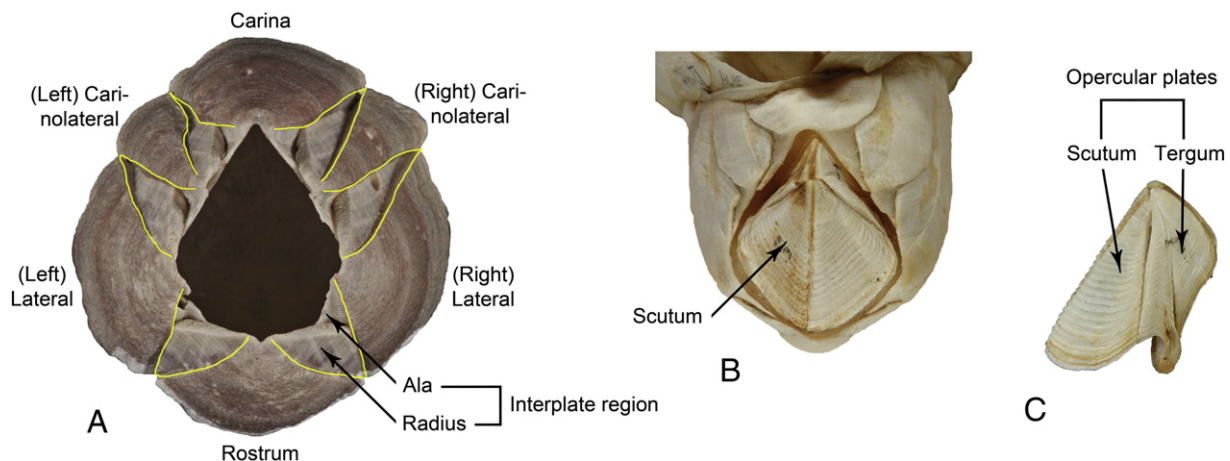

Fig. 1. Morphological features of balanomorph barnacles. A. Names of the six wall plates; six interplate regions outlined in yellow. "Left" and "right" are arbitrarily based on the orientation of the barnacle. B. Top view of the placement of opercular plates in a barnacle shell, attached to another barnacle. C. (Right) lateral view of articulated opercular plates.