The First Evidence of Predatory or Parasitic Drilling in Stylophoran Echinoderms

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The first evidence of predatory or parasitic drilling in stylophoran echinoderms

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Drillholes are common in many different echinoderm classes, but have yet to be reported in homalozoans. A borehole in the Late Ordovician echinoderm *Enoploura* is the first evidence of drilling in Stylophora. The level of preservation and environmental setting suggest this drilling occurred while the organism was alive, thus supporting a predatory or parasitic interpretation.

Introduction

Boreholes, of either predatory or parasitic origin, have been described in several different groups of echinoderms, including crinoids (Moodie 1918; Branson 1964; Brett 1978; Baumiller 1990; Baumiller and Gahn 2002), blastoids (Baumiller and Macurda 1995; Baumiller 1996), rhombiferan cystoids (Kluessendorf 1983), and echinoids (Nebelsick and Kowalewski 1999; Neumann and Wisshak 2006). Many of these drillholes, which fall into the ichnogenus *Oichnus*, are circular in plan view with either a cylindrical or beveled shape and penetrate no deeper than the plate thickness. These types of boreholes have been attributed to drilling by gastropods, octopods, and worms in modern settings (Bromley 1981). These traces, if determined to been drilled in a live organism, are one of the few pieces of direct evidence of biotic interactions in the fossil record and can give insights into the behavior and ecology of fossil organisms.

One group of echinoderms in which drilling predation has not been reported are the stylophorans. Mitrate stylophorans are unusual within the echinoderms in that they are non-pentaradiate and often show no symmetry. Stylophorans are composed of a three-part, flexible appendage (aulacophore) and a highly flattened theca (Lefebvre 2003). Almost all reconstructions interpret stylophorans as unattached, benthic organisms, but the living orientation as well as the function of the aulacophore has been highly debated (Jefferies 1967; Parsley 1988; Kolata et al. 1991). This paper reports the first known example of drilling in stylophora.

Institutional abbreviation.—CMC, Cincinnati Museum Center, Cincinnati, USA.

Geologic setting

A slab containing two specimens of *Enoploura popei* was collected from a roadcut along US 62/68 (formerly State Rte. 3071) between KY 9/AA Highway and KY 8 near Maysville, Mason County, Kentucky, USA, located on the eastern limb of the Cincinnati Arch. The slab was part of a geographically extensive hardground horizon described by Sumrall et al. (1999) near the base of the Bellevue Member of the Grant Lake Formation (middle Maysvillian Stage, Cincinnatian Series, ~445 Ma). This layer occurs at the top of a set of packstones and grainstone beds that range between 10 and 25 cm in thickness. The upper surface of the hardground is irregular and has abundant encrusting bryozoans, brachiopods, and edrioasteroids.

Description

The specimen discussed herein is a single borehole present on the larger of two mitrate stylophoran specimens preserved on a 30 cm by 17 cm plate (Fig. 1). The slab also contains abundant brachiopods (*Hebertella occidentalis* and *Platystrophia ponderosa*) and thick ramose trepostome bryozoans. The slab contains eight oblong borings, which are on average 1.58 mm (SD 1.2 mm) wide, 12.03 mm long (SD 10.6 mm), and 0.83 mm deep (SD 0.65 mm), may overlap, and occur in brachiopods, bryozoans and the hardground itself (Fig. 2). These borings are most likely excavations of domiciles which are common in Cincinnatian hardgrounds. However, no other perpendicular boreholes were observed in brachiopods, bryozoans or the hardground surface.

The theca of the smaller of the two stylophoran specimens is 6 mm wide and is preserved with the flat side of the theca down with the anterior end elevated at a 45° angle. The theca of the larger individual with the borehole is 13.5 mm wide and 23 mm long and is preserved prone, also with the flat surface down. Both individuals are preserved in a thin mud drape overlying the irregular hardground. The circular borehole is 0.88 mm in diameter and is located approximately in the center of the b supracentral plate on the curved surface of the theca, overlying the central body cavity. The borehole is shallow (<0.2 mm, measured by placing a pin into the borehole) and penetrates only the thickness of the plate. The borehole has a slightly irregular shape which may be due to taphonomic alteration. The mitrate is relatively complete with the aulacophore preserved to the styloid plate. The aulacophore is parallel to the theca with a thin gap between it and the hardground surface indicating preservation above the hardground as opposed to becoming incorporated into the surface as is the case with many brachiopods (Wilson and Palmer 2001).

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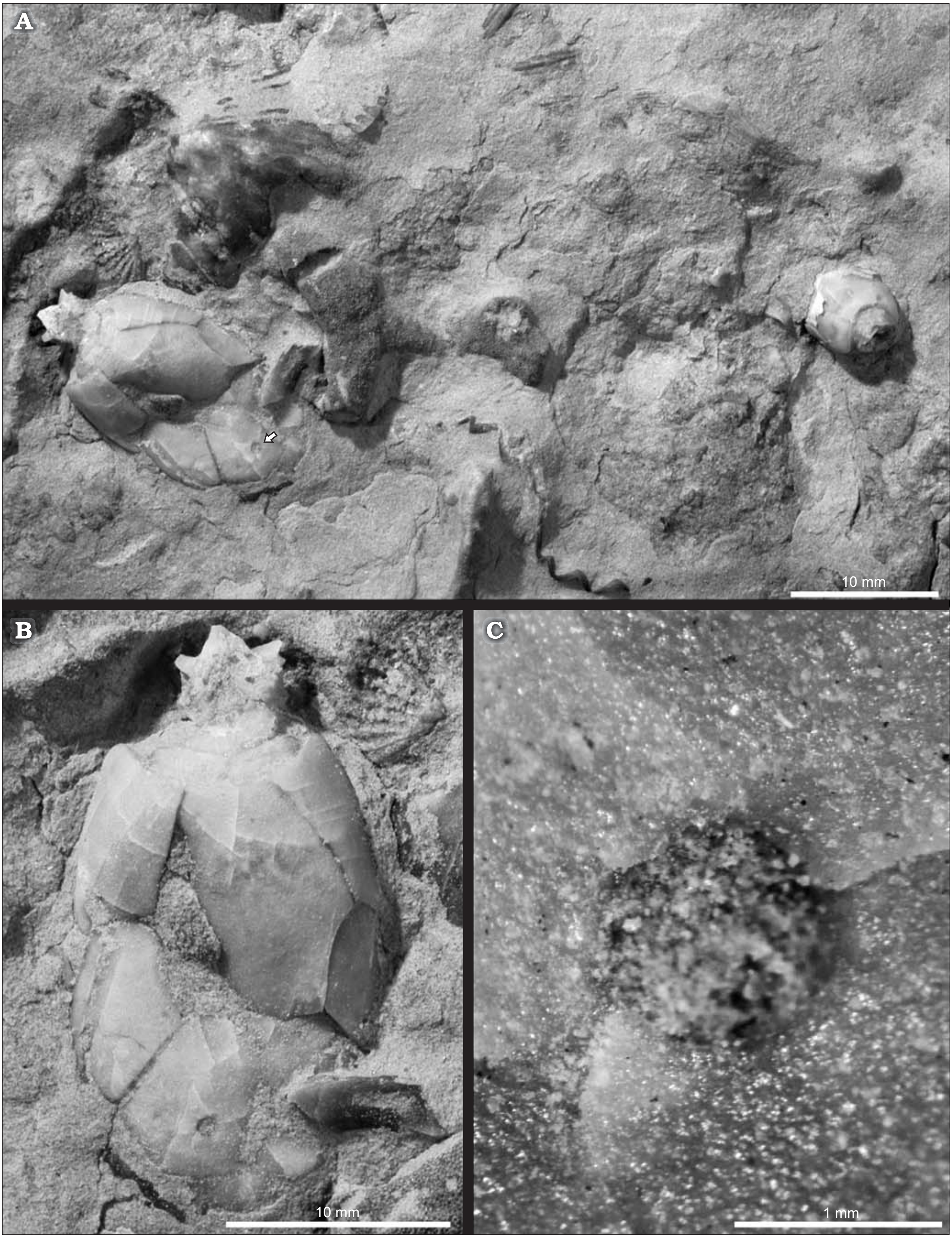

Fig. 1. **A**. A slab from Maysville, KY (CMC IP50706) with a drilled specimen of the stylophoran mitrate *Enoploura popei* Caster, 1952. The hole indicated by an arrow. **B**. Close up of the drilled specimen. **C**. Detail of the borehole.

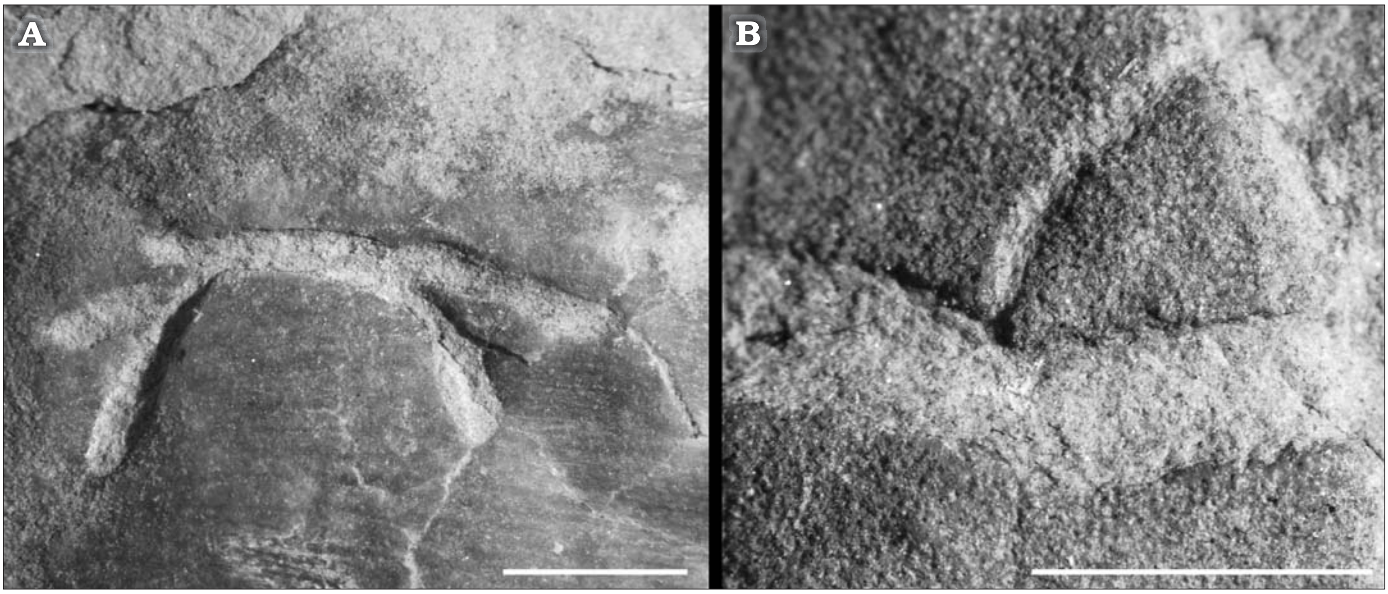

Fig. 2. Horizontal boring on the slab from Maysville, KY (CMC IP50706). **A**. Overlapping burrows in the shell of the brachiopod *Rafinesquina.* **B**. Burrows in a bryozoan. Scale bars 10 mm.

Parsley (1991) described two species of *Enoploura* from the type Cincinnatian. The two species differ in the shape of the styloid flanges (*Enoploura popei* has large rounded flanges, while the less common *E. balanoides* has plowshare shaped styloid flanges) and the presence of subtle ornamentation on *E. balanoides* (Parsley 1991). Since these two species co-occur throughout the Maysvillian and the aulacophore, and surface ornamentation are often not well preserved, species differentiation is difficult. The specimen in this study appears to lack ornamentation and the partially preserved styloid plate appears to be rounded placing it within *E. popei*. *Enoploura* is interpreted as living with flat side of the theca oriented downwards with the mouth located on the distal end of the proximal aulacophore and the anal opening occurring on the distal aperture of the theca (Parsley 1991). The aulocophore is interpreted as both a feeding and locomotor appendage, while the distal spines and styloid plates acting to stabilize the animal during feeding (Parsley 1991). Alternatively, *Enoploura* has been considered to belong to a subphylum of chordates and interpreted to live inverted compared with the echinoderm orientation with the mouth on the opposite end of the theca and the aulocophore used only in locomotion (Jefferies 1967).

Discussion

Boreholes from the type Cincinnatian have been previously reported in brachiopods (Kaplan and Baumiller 2000) and bryozoans (Erickson and Bouchard 2003). The interpretations of these boreholes have been varied (Fenton and Fenton 1931; Carriker and Yochelson 1968; Kaplan and Baumiller 2000; Wilson and Palmer 2001), but it has been assumed that they are biotic in origin. These borings, which fall under the ichnogenera *Trypanites, Sanctum*, *Oichnus*, and the embedment pit *Tremichnus*, have been interpreted as domichnial traces, most likely formed by amphipod-like crustaceans (Erickson and Bouchard 2003) or 'worms' (Palmer and Wilson 1988; Brett 1985; Wyse Jackson 2005), or as Praedichnia (Ekdale 1985) traces formed by boring gastropods (Kaplan and Baumiller 2000).

A predatory or parasitic interpretation of the *Enoploura* boring is supported by several lines of evidence. Homalozoans are weakly articulated and it has been hypothesized that they would only stay articulated from a few hours to a day after death (Brett et al. 1997), an inference supported by experiments with modern weakly sutured echinoderms (Meyer and Meyer 1986). Given the preservation of both the theca and the aulacophore, this individual was not only buried soon after death, but the borehole was likely drilled while the animal was alive. This interpretation is also supported by preservation on a hardground, which is a setting characterized by minimal sedimentation prior to final burial (Brett et al. 1997).

Secondly, the borehole presented in this study meets some of the criteria used to distinguish predation such as circular shape, orientation perpendicular to the theca, smooth sides, full penetration of the plate, and only one borehole on the theca (Carriker and Yochelson 1968; Ebbestad and Tapanila 2005). Other criteria such as prey and site selectivity (Ebbestad and Tapanila 2005) require large sample sizes and cannot be applied to a single borehole. However, the rarity of *Enoploura* should be noted, such that even with a high boring percentage, more than one bored individual from this occurrence is very unlikely.

Thirdly, the borehole in the *Enoploura* differs significantly from those in the associated hardground in several aspects. The borings into the hardground are wider, deeper, and over a centimeter longer on average, indicating a different driller than the producer of the borehole in the *Enoploura*.

The identity of the borer cannot always be determined; however, the relationship between crinoids and gastropods may give some insight into the potential borer. Although there is no conclusive evidence of gastropod boring in the type Cincinnatian, the likelihood of gastropods having the ability to bore is supported by the observation of the gastropods *Cyclonema* and *Naticonema* either attached to the tegmen or associated with the arms of the crinoid *Glyptocrinus* (Morris and Felton 1993). Even though no boreholes have been reported in *Glyptocrinus*, the repeated instances of prolonged attachment of the gastropods to the tegmen of *Glyptocrinus* indicates that these gastropods share a coprophagous ecologic niche with those that have been shown to drill into crinoids (Baumiller 1990; Baumiller and Gahn 2002). This association has been observed a few meters below the extensive hardground and *Cyclonema* is known to occur throughout the Bellevue Member of the Grant Lake Formation (Thompson 1970).

The rarity of borings in *Enoploura* compared with the repeated association of *Cyclonema* with *Glyptocrinus* may be due to the general rarity of stylophorans or the viability of *Enoploura* as prey/host organisms. *Enoploura* would be accessible to attack living on the seafloor, however, crinoids with large dense filtration fans and gluttonous feeding behavior (Holland et al. 1991) would likely provide a much more ample source of food for a parasite or predator.

If drilling is more likely to occur on the exposed surface of the prey organism, stereotypy in the site of the borehole in *Enoploura* could indicate life position. Though stylophorans are rare in this instance, *Enoploura* (McLaughlin et al. in press) and other stylophorans (Kolata and Jollie 1982) are locally abundant. Therefore, further instances of boring in stylophorans should be sought as an indicator of life position, which is a point of contention in the debate over the phylogenetic affinities of this group.

This borehole is amongst the oldest examples of predatory/parasitic boring in the phanerozoic (Brett and Walker 2002) and fits in with other examples of low frequency boring during the early Paleozoic (Kowalewski et al. 1998). Most early Paleozoic boreholes occur in brachiopods (Brett and Walker 2002). However, this example shows that other organisms could be drilled as well.

Conclusions

The presence of a borehole in an articulated specimen of the mitrate *Enoploura popei* represents the first evidence of drilling within the homalozoans. The lack of previous reports of boreholes may be due to the general rarity of these echinoderms as well as a low frequency of drilling. Alternatively, they may not be a preferred prey item for boring predators. Given that the borehole was most likely drilled while the mitrate was still alive based on the preservation, this borehole is more consistent with predation or parasitism than with the creation of a domicile. Given a sufficient sample, the location of boreholes in stylophorans could be an important line of evidence in the determination of living position of these organisms.

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