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Additional evidence for the drilling behavior of Paleozoic gastropods

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Although the record of Paleozoic drillholes is long and extensive, evidence pertaining to the identity of the drillers is sparse. The most conclusive evidence, a driller "caught in the act", has been documented only once (Baumiller 1990). In that example, a drillhole in the calyx of a crinoid was found directly beneath an attached platyceratid gastropod. Additional evidence for drilling by platyceratids has been circumstantial, i.e., based on the association of platyceratids with certain blastoids and crinoids, and the presence of drillholes in other crinoid and blastoid taxa. To a skeptic, the lack of congruence between drilled and platyceratid-infested crinoids and blastoids is not sufficient evidence that platyceratids were the drillers. More conclusive evidence requires examples of drillholes in taxa that are known to have been platyceratid-infested, preferably from localities where both infested specimens and drilled specimens co-occur.

Two drilled specimens of *Arthroacantha carpenteri* (Hinde, 1885) were collected from the Barret Paving Material Quarry in Unit nine of the Middle Devonian (Givetian) Silica Shale, Sylvania County, Ohio, USA (Fig. 1). This locality has yielded thousands of specimens of *A. carpenteri*, many of which are platyceratid-infested (Kesling and Chilman 1975). Therein lays the importance of the two specimens: members of a single species, *A. carpenteri*, are infested and drilled at a single locality.

Evidence that the drillholes were made by infesting platyceratids and not by predators includes: 1) growth scars surrounding the drillhole, consistent with the size and shape of platyceratids, 2) drillhole position in the anal interray, where platyceratids typically attach, 3) poorly developed spine facets on the scarred region of the calyx, suggesting that the gastropods impeded spine development where they attached, and 4) swelling around the drillholes, indicating a growth reaction by the host to the drillhole.

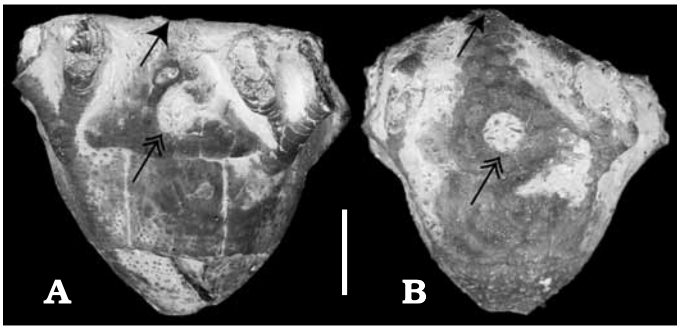

Fig. 1. Specimens of *Arthroacantha carpenteri* (Hinde, 1885) with drillholes. Each photograph displays the anal interray, position of the anal vent (single arrowheads), and the location of platyceratid drillholes (double arrowheads); scale bar 1 cm. Note the presence of a reaction rim surrounding the drillhole and underdeveloped spine facets below it. Specimens are deposited at the University of Michigan Museum of Paleontology (UMMP). **A**. UMMP 73711. **B**. UMMP 73712.

Attached platyceratids are typically positioned over the anal vent of fossil crinoids and have been most commonly interpreted as coprophages, feeding on crinoid excrement with no ill-effect to their hosts (Bowsher 1955). However, mounting evidence suggests that, at least in some instances, platyceratids were kleptoparasitic, stealing nutrients from the crinoid gut (Baumiller and Gahn 2002, Gahn and Baumiller in press). The drilling of *Arthroacantha* is unique in this context; all previously reported drilled crinoids bear a long anal tube which has been interpreted as an anti-platyceratid infestation device (Keyes 1888). In camerates lacking anal tubes, such as *Arthroacantha*, a platyceratid could access nutrients directly through the anal vent. However, *Arthroacantha* represents one of the only cases of multi-snail infested crinoids, with a single snail positioned directly over the anal vent (Kesling and Chilman 1975); in that case, the other snails were thought to utilize a different feeding strategy (Baumiller 2002). The specimens described herein indicate that this need not have been the case, as drillholes may have allowed a second platyceratid access to the crinoid hind gut and the nutrients within.

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