NON-PREDATORY DRILLING OF MISSISSIPPIAN CRINOIDS BY PLATYCERATID GASTROPODS

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ABSTRACT. The conical hole in the tegmen of a Mississippian crinoid (*Macrocrinus mundulus*) directly underneath the shell of a platyceratid gastropod, *Platyceras* (*Orthonychia*) sp., and similar holes in other Mississippian crinoids (*Batocrinus irregularis* and *B. icosidactylus*) demonstrate the drilling abilities of platyceratids. This is the first case of drilling by an archaeogastropod. Drilling on the crinoid host by the gastropod was non-predatory; the relationship was probably parasitic. This study, the first to identify unequivocally a Palaeozoic borer, supports the notion that gastropod drilling has evolved several times.

EVIDENCE implying predation on Palaeozoic invertebrates is well documented (Fenton and Fenton 1931; Brunton 1966; Rohr 1976; Ausich and Gurrola 1979). Examples include conical holes, mostly in brachiopods, which have been attributed to Palaeozoic gastropods because of their similarity to drillholes produced by Recent predatory gastropods (Cameron 1967; Sheehan and Lespérance 1978; Smith *et al.* 1985). This interpretation is not universally accepted, since the Palaeozoic taxon responsible for them has not been conclusively identified (Carriker and Yochelson 1968; Sohl 1969). The discovery of a borehole in a Mississippian crinoid, directly beneath an attached platyceratid gastropod, is the first definitive demonstration of drilling activity by a Palaeozoic gastropod.

PLATYCERATID-CRINOID INTERACTION

The archaeogastropod family Platyceratidae (Knight *et al.* 1960) is well known for its association with crinoids (Meyer and Ausich 1983). Generally, the gastropod is firmly attached to the crinoid calyx usually above the base of the arms. Its position, commonly covering the crinoid anus, and the close conformity of its margin to the morphology of the calyx, has suggested commensalism and that platyceratids were coprophages on crinoid wastes (Keyes 1890; Bowsher 1955). Recently it has been argued that platyceratids were parasites feeding on crinoid gametes (Lane 1984). The parasitic interpretation is supported by the smaller size of gastropod-infested crinoids as compared to uninfested ones (Rollins and Brezinski 1988).

Commonly, the gastropod sits directly over the crinoid anus, which is flush with the tegmen, or upper portion of the calyx. However, several platyceratids have been found situated on the crinoid tegmen but well away from the anus (Lane 1978). In such instances the infested crinoids have a long stout anal tube, with the anus at its apex, while the platyceratid rests at the base of the tube. In this position the gastropod could not extract anything from the crinoid without drilling into the host. Therefore, to test the hypothesis that platyceratids were capable of boring their tube-bearing hosts, I serially ground a crinoid with *Platyceras* (*Orthonychia*) sp. at the base of its long tube.

PLATYCERATID DRILLHOLES

In the collections of the Field Museum of Natural History (FMNH) I found a well-preserved specimen of *Macrocrinus mundulus* (Batocrinidae) with a species of *Platyceras* (*Orthonychia*) at the base of the anal tube. Specimen P. 19426, which was collected at Canton, Indiana, USA, from rocks of Tournaisian age, was ground perpendicular to the oral–aboral axis (long axis of the anal tube)
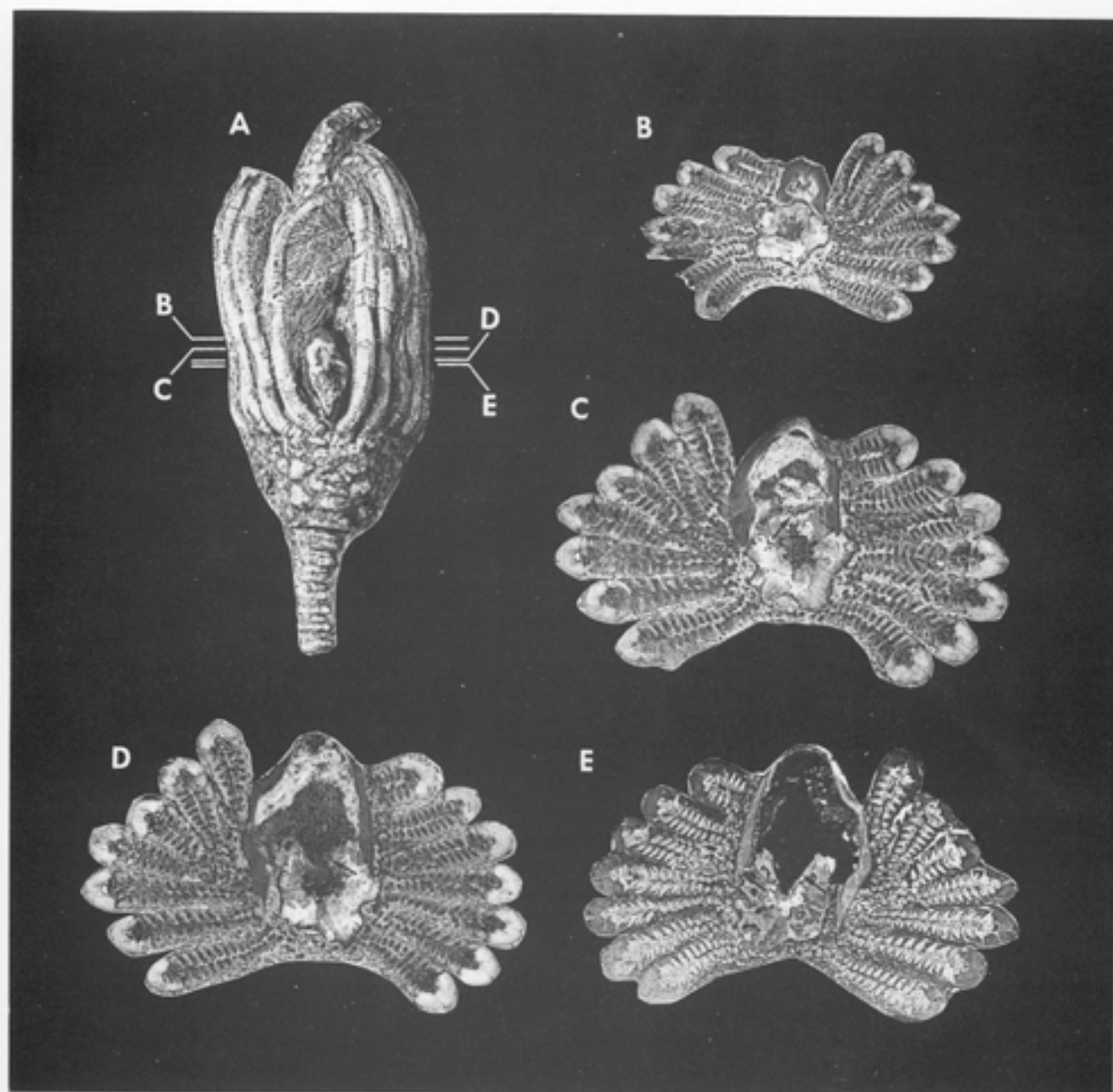
TEXT-FIG. 1. Specimen of *Macrocrinus mundulus* (FMNH P.19426) with a long anal tube and *Platyceras* on its tegmen. (A) Lateral view of specimen with lines B, C, D, and E indicating positions at which photographs B, C, D, E of ground sections were taken. Ground surfaces are perpendicular to the plane of the page and the long axis of the specimen, × 1·4. (B) Section through the arms, anal tube and the anterior of the *Platyceras*. Note that the anal tube plate directly beneath the platyceratid appears intact, × 3·0. (C) Section 1·0 mm below B. Arrow points to a small concavity in the anal tube plate beneath the platyceratid, × 3·0. (D) Section 1·0 mm below C. Arrow points to drill hole. Note contrast between hole filled with dark matrix and light colour of anal tube plates, × 3·0. (E) Section through centre of drill hole. Note that hole penetrates to centre of anal tube and the tight fit between the test of gastropod and the anal tube, × 2·9.

at 0·5 to 1·0 mm intervals, starting at the apex of the tube (text-fig. 1). The serial sections revealed a circular, conical hole (3 mm outer diameter) beneath the central, anterior portion of the gastropod shell. The hole is easily recognized from the colour contrast between the white plates of the anal tube and the red matrix filling the body cavity of the gastropod and the hole underneath it.

In addition, 27 specimens of Visean *Batocrinus icosidactylus* and *B. irregularis* from the collections of the Field Museum and Indiana University, Bloomington, USA, also possessing a long anal tube, were found with previously undescribed holes in their tegmina. The location of these holes is highly stereotyped: they are either just below or at the base of the anal tube (text-figs. 2 and 3). The holes also exhibit little variation in morphology; they are round in plan view, cylindrical to conical in cross-section, with a mean outer diameter of 2·2 mm (range from 1·4 to 3·2 mm) (text-fig. 2H). The morphology and position of these holes match those of the hole in *Macrocrinus* beneath *Platyceras* (text-figs. 1E, 2H).

Platyceratids occur with the aforementioned batocrinids in localities of the Salem Limestone (Cummings *et al.* 1905), a fact consistent with the interpretation that these gastropods were responsible for the drillholes. The lack of an association between *Platyceras* and *Batocrinus* in these localities may be a taphonomic artifact. When platyceratids are associated with crinoid tegmina, articulated crinoid arms are also preserved. This implies either that the arms prevented the post-mortem separation of the two organisms or that the process leading to the disarticulation of the arms from the crown also led to the detachment of the gastropod from the crinoid. *Batocrinus* with preserved arms have not been described. The absence of platyceratids on *Batocrinus* is thus not inconsistent with this mode of preservation.

These results establish the boring abilities of the Mississippian *Platyceras* (*Orthonychia*), the first unequivocal example of a drilling Palaeozoic gastropod.

DISCUSSION

Non-predatory nature of drillholes

The boring by *Platyceras* does not necessarily imply predation on the crinoid. Several lines of evidence suggest that the relationship was non-predatory. The tight fit between the margin of *Platyceras* and the tegmen of *Macrocrinus* (text-figs. 1D, 1E), U-shaped attachment scars surrounding the boreholes (text-fig. 2G), instances of multiple boreholes, and healed (or incomplete) boreholes on *Batocrinus* all indicate that the association was long term and that drilling was not fatal to the crinoid. Furthermore, Recent parasitic capulid gastropods, which have a shell morphology very like the platyceratids, also drill their host (Orr 1962; Kosuge and Hayashi 1967).

Whether this relationship was beneficial, neutral, or detrimental to the crinoid cannot be determined conclusively. Although drilling itself was probably detrimental, the feeding strategy of platyceratids is most relevant in distinguishing between the three alternatives. If the gastropods fed exclusively on crinoid wastes, then their position at the apex of the anal tube, directly over the crinoid anus, would have sufficed. It is possible, however, that these relatively large gastropods would have been unstable in this position due to the small size of the distal end of the tube. Drilling at the base of the tube would have permitted feeding in a more stable orientation. More probably the gastropod extracted from the crinoid more than just waste matter. Camerate crinoid food grooves converge subtegminally and carry within them food particles collected by the dense filtration fans. By inserting its snout into the tegmen the gastropod could have extracted food from these grooves. This would have involved penetrating the crinoid gut wall, since in camerates the subtegminal food grooves form closed tubular conduits leading directly to the fore-gut (Haugh 1975); a similar situation has been described for the parasitic prosobranch, *Echineulima*, whose proboscis was found to pierce the intestinal wall of its host echinoid (Lützen and Nielsen 1975). In crinoids without an anal tube this could have been accomplished without drilling, simply by using the existing anal opening through which to insert the snout beneath the tegmen. Such a strategy would not have worked with crinoids possessing a long tube, due to the greater distance of the anus from the food grooves lying deep below the tegmen. Drilling would be essential. This may be an
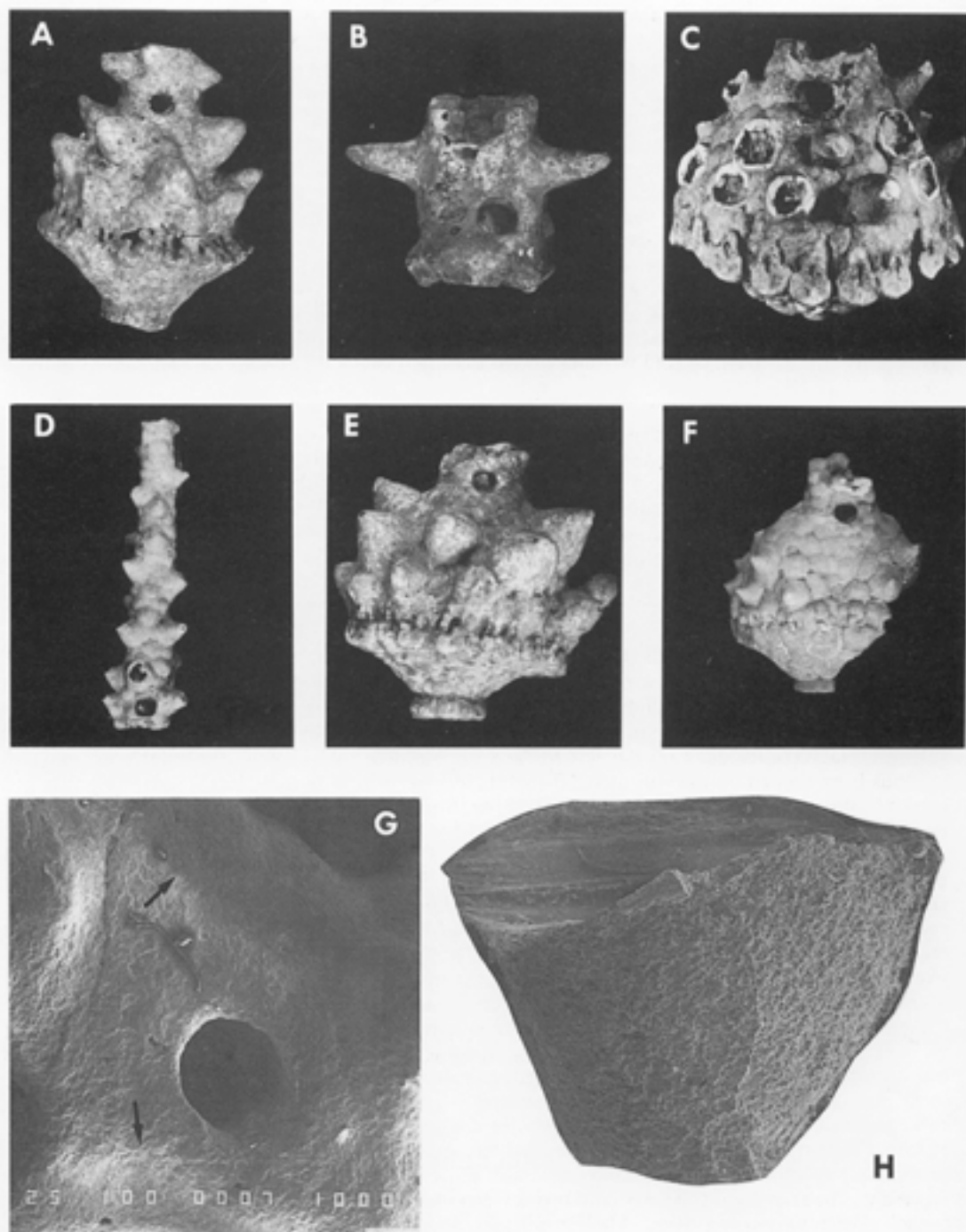
TEXT-FIG. 2. Drillholes in bactocrinids from the Salem Limestone. (A) *Batocrinus icosidactylus* (FMNH P.19393), ×1·9. (B) Anal tube of *B. icosidactylus* (FMNH P.19392), ×2·5. (C) *B. icosidactylus* (FMNH P.19394), ×2·2. (D) Anal tube of *B. icosidactylus* (FMNH 19394), ×1·4. (E) *B. icosidactylus* (FMNH P.21506), ×2·0. (F) *B. irregularis* (FMNH P.19402), ×2·1. (G) SEM of *B. icosidactylus* (FMNH P.19402). Arrows point to U-shaped scar around hole, ×8·8. (H) A latex cast of drillhole in *B. icosidactylus* (FMNH PE.1957). Orientation of cast is with the top corresponding to the outer surface of the anal tube and the bottom to the inner surface, ×2·3.

TEXT-FIG. 3. A reconstruction of the calyx of *Batocrinus* with part of the anal tube. Actual drillholes projected onto reconstruction. Note stereotypic position of holes,

'arms-race' (Vermeij 1987) in which crinoids evolved an anal tube in response to gastropod parasitism, which in turn led to the evolution of platyceratid drilling. Though highly conjectural, this hypothesis may be tested by determining whether anal tubes evolved preferentially in gastropod-infested lineages, and whether platyceratid drillholes are found in crinoids without anal tubes.

The drilling habit and 'evolutionary radiations'

Other evolutionary implications of the drilling habit of *Platyceras* hinge upon our knowledge of the systematics of this group. Although archaeogastropods are probably not a true clade (Hickman 1988), if the taxonomic scheme proposed by Knight *et al.* (1960) is correct with regard to platyceratids, *Platyceras* represents an example of independent evolution of drilling in gastropods that did not lead to a major diversification (Smith *et al.* 1985; Fürsich and Jablonski 1984). Platyceratid generic diversity did not undergo major changes during or after the Mississippian (Bowsher 1955), and their extinction at the end of the Permian (Bowsher 1955, but see Bandel 1988) coincides with the extinction of other invertebrates, including most of their crinoid hosts.

A pre-Mississippian origin of the platyceratid drilling habit is possible, for platyceratids as well as bored echinoderms are found in rocks of Ordovician to Permian age (Bowsher 1955; Brett 1978; Paul 1971). In most instances, however, these borings are in the form of pits which do not penetrate the skeletal plates of the host echinoderm, and their origin has been attributed to various epizoans. Whether platyceratids were responsible for any of these pits remain to be examined.

It has been argued that evolutionary 'failures' of taxa with drilling abilities resulted either from deterministic causes related to the adaptive value of this innovation (e.g. inability to drill rapidly) or from factors unrelated to the innovation itself but affecting rates of speciation and extinction (Smith *et al.* 1985; Fürsich and Jablonski 1984). The identification of the innovation-bearing taxon provides an excellent opportunity for testing these ideas. Thus the suggestion that the lack of a hard skeleton (Smith *et al.* 1985) contributed to the evolutionary failure of Palaeozoic drillers must be rejected for the shelled *Platyceras*. Furthermore, the non-predatory nature of these drillholes forces us to make a distinction between predatory and parasitic drilling, as well as between their evolutionary implications.

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