Enigmatic organisms preserved in early Ordovician macroborings, western Utah, USA

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Abstract. Macroborings in the Lower Ordovician Fillmore Formation, western Utah, USA, occasionally contain fossil remains of enigmatic organisms. In the most complete specimens a common morphology can be observed. The calcified body wall of the animal is vase-shaped, mimicking the shape of the boring itself. An ovoid body leads up to a neck that contains either a single or double cylinder near the aperture of the boring. The incomplete preservation of the specimens is not sufficient to identify the biological affinity of the organism at this time, but a review of potential groups is warranted. While such groups as barnacles, bivalves, mitrates, and a host of worm-like forms are potential boring inhabitants, none fit what is known of the morphology of the specimens from Utah. Regardless, recognition and future identification of these animals will lead to a greater understanding of complex hardground trophic systems during the Ordovician Bioerosion Revolution.

Keywords. Bioerosion, macroboring, hardground, Ordovician Bioerosion Revolution, Fillmore Formation

Introduction

No body fossils representing organisms that are obviously capable of macroboring behavior have been found in rocks prior to the Pennsylvanian, and macroborings themselves are not abundant in rocks earlier than that age. Macroborings identified as *Gastrochaenolites* Leymerie, 1842 occur in the Lower Ordovician Fillmore Formation at Skull Rock Pass (SRP), western Utah, USA (Ekdale et al. 2002; Benner et al. 2004). Several specimens of these macroborings contain the presumed body fossils of enigmatic organisms. This is only the second known occurrence of an animal fossilized inside a pre-Pennsylvanian macroboring (Wilson and Palmer 1998).

Because of the physically and chemically erosive environments in which hardground dwellers live, it is unlikely that a borer without a thickly shelled body would

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M. Wisshak, L. Tapanila (eds.), *Current Developments in Bioerosion*. Erlangen Earth Conference Series, doi: 10.1007/978-3-540-77598-0_3,

survive. While it is unknown whether the organism was responsible for excavating the boring or was a secondary inhabitant, it is clear that these specimens represent an important source of new information regarding hard substrate infaunalization during the Ordovician Bioerosion Revolution (Wilson and Palmer 2006).

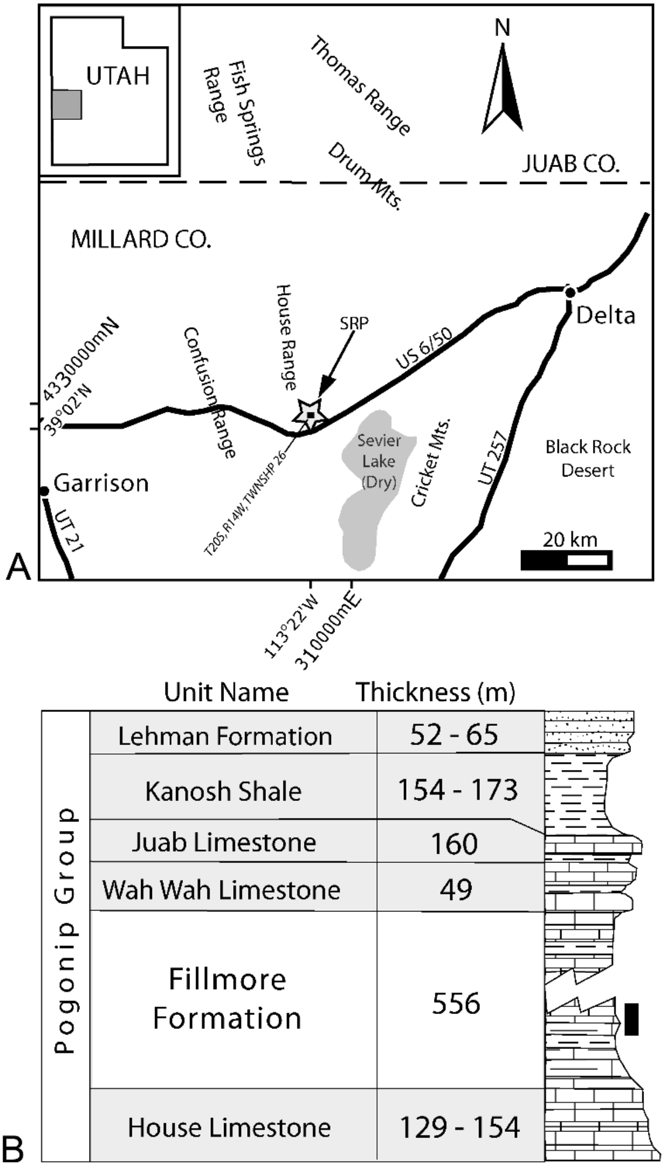


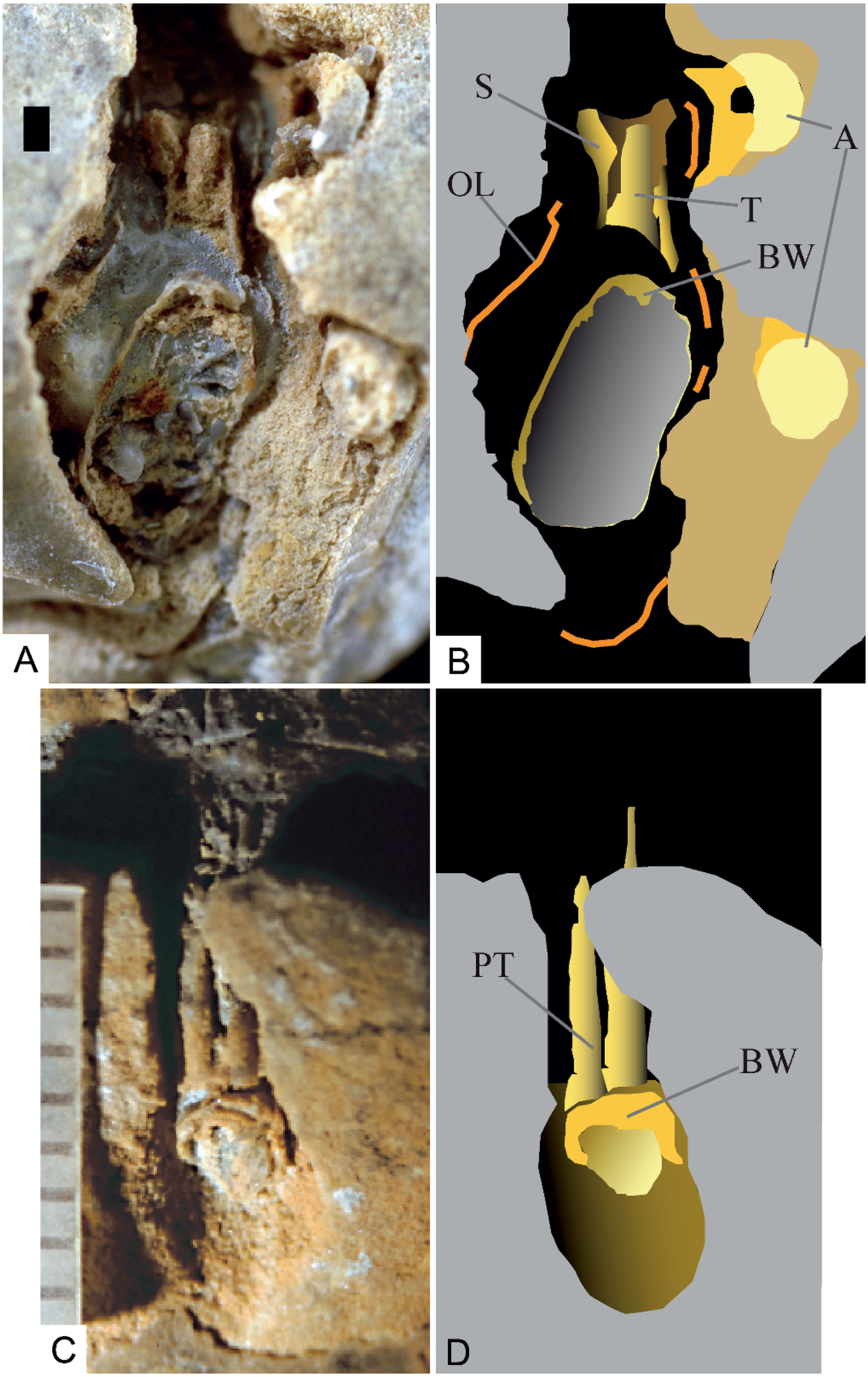
Fig. 1 Location and stratigraphy of the study area in the Fillmore Formation. **A** Pyramid Section locality at Skull Rock Pass, Utah. **B** Generalized stratigraphy of the Lower Ordovician Fillmore Formation showing the location of the Pyramid Section (black bar). Modified from Hintze (1973)

Geological setting

Macroborings containing the enigmatic organisms discussed in this paper occur in hardground surfaces in the Lower Ordovician (Ibexian) Fillmore Formation at SRP in Millard County, Utah (Fig. 1A). At the study locality, nearly 100 m of limestone and shale are exposed in outcrop, arranged in meter-scale shallowing-upward cycles (Hintze 1973; Dattilo 1993; Evans et al. 2003) (Fig. 1B). Surfaces interpreted as hardgrounds are present on many different rock types, including nodular lime mudstone, sponge-algal mud mounds, and flat pebble conglomerates (Dattilo 1993; Benner et al. 2004).

Description of body fossils within borings

In situ body fossils were found inside borings in four limestone cobbles from SRP hardground surfaces (J. S. Benner 2002, Masters Thesis Collection, Department of Geology and Geophysics, University of Utah). These surfaces were examined in the field for the presence of borings (Benner 2002; Benner et al. 2004), but it was not until portions of hardgrounds were investigated in the lab that organisms were found inside some of the borings. Because of the small sample size, the full morphology and identity of these organisms is not yet known, making it difficult to ascertain whether they were the organisms responsible for the borings or merely were secondary inhabitants utilizing the excavation for living space (i.e., nestlers). In borings that preserve the most complete body fossils, a common feature is the presence of singular (Fig. 2A-B) or paired (Figs. 2C-D, 3A-B) calcareous tubes, occasionally within a sheath of calcite (Fig. 2A-B). Diameter of the tubes is between 0.5 and 0.75 mm. When the inside of the boring is exposed due to erosion of the cobble surface, a larger portion of the body fossil can be observed at a deeper, wider point within the boring (Figs. 2A-B, 3C-D). The main body of the fossil is vase-shaped, with an outer 'body wall' preserved as a thin layer of calcite. Typically, the interior of the body wall contains bioclasts in a micrite matrix (Figs. 2A, C, 3C). Longitudinal and transverse sections through the body are available. In one longitudinal section (Fig. 3C-D), the tube or neck portion of the body leads from a funnel-shaped aperture of the boring to the main body cavity. The posterior (deepest) portion of the body is tapered, and the whole body fits tightly within the boring. In transverse section (Fig. 3E-F) it appears that the body is bilaterally symmetrical with axes that give an elliptical aspect, a shape that is common to the *Gastrochaenolites* borings described from SRP (Benner et al. 2004). An idealized reconstruction of the boring and the body fossil show that the boring chamber and body are elliptical, while at the hardground surface, the cross-sectional aspect of the aperture of the boring and tubes of the body fossil are circular (Fig. 4).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Discussion

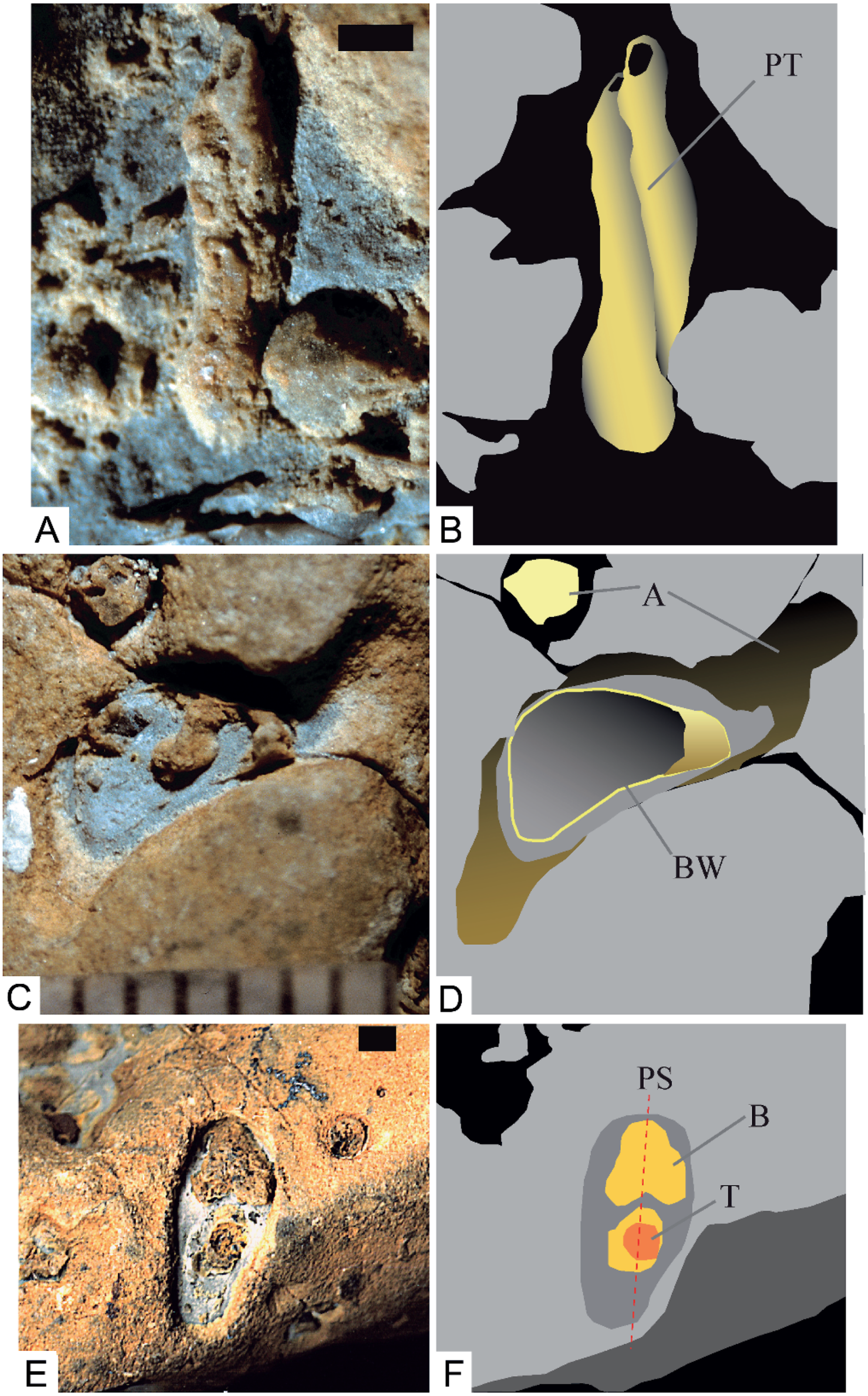
Marine invertebrates bore into rock in response to a variety of ecological and physical pressures (Bromley 1970, 1978; Warme 1975, 1977), such as predation avoidance, protection from high-energy waves / currents, and specialized feeding habits. Infaunal borers occupy important niches in benthic marine ecosystems, often in the lower tier of suspension feeding communities, and the boring strategy has proved to be a very successful one (Bromley 1970, 1978; Warme 1975, 1977; Jones and Pemberton 1988; Ekdale and Bromley 2001). Protection provided by a lithic substrate has resulted in success in an extremely competitive trophic structure. The borings in Fillmore Formation hardgrounds represent the earliest known attempts at a *Gastrochaenolites*-type strategy, and they provide evidence for more complex hardground trophic structures than were previously thought to exist in the Early Ordovician.

It has been asserted that evolution of new body plans during the Ordovician biotic radiation was driven by the ability to exploit new habitats, including those at and below the sediment-water interface (Bambach 1985). The rise in the abundance and diversity of epifaunal suspension feeders in Lower Ordovician hardgrounds (e.g., Wilson et al. 1989, 1992) that were exploiting similar food resources could have led to the evolution of the *Gastrochaenolites*-type behavior. If this were the case, the advent of the *Gastrochaenolites*-type behavior may have been a precursor to the creation of a new body plan more suited to hard substrate habitat (Palmer 1982; Bambach 1985).

Evidence is scant that the Fillmore body fossils are the remains of the animals that were responsible for creating the *Gastrochaenolites* borings. The tight fit of the body within the boring may indicate either the bioerosional modification of the original boring to fit the body of a borer, or the restricted growth of the body of a nestler (e.g., Savazzi 1994). However, because the potential exists to identify the organism inside the boring, consideration of certain groups is necessary, including those that are not known from direct body fossil evidence in the Fillmore Formation.

The borings described here exhibit some similarities to those produced by cirripeds, particularly acrothoracican barnacles (Ahr and Stanton 1973). The acrothoracicans may have their earliest ancestor in the Cambrian, but this group is only known in fossil form since the Devonian (Rodriguez and Gutschick 1970, 1977). What is known about the morphology of the boring made by these

Fig. 2 Photos of enigmatic organisms in two bored cobbles from the Fillmore Formation at Skull Rock Pass with corresponding labeled diagrammatic sketches. For descriptions see text. Specimens held in research collections in the Department of Geology and Geophysics, University of Utah. **A-B** Longitudinal section through boring showing body inside with attached tube. Body outline is a thin layer of calcite and the interior is filled with bioclastic material. Note two semi-cylindrical features to the right of the individual oriented normal to the plane of the photo. These represent transverse sections through the necks of two other individuals. Scale bar = 1 mm. **C-D** Oblique view of partially eroded specimen. Body with attached paired tube is visible. Scale in mm. For this and all subsequent figures: BM = boring margin, OL = outer lining, BW = body wall, B = body, T = single tube, PT = paired tubes, S = sheath (around tubes), A = aperture, PS = plane of symmetry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animals makes it unlikely that it is a producer of *Gastrochaenolites* (e.g., Seilacher 1969; Rodriguez and Gutschick 1977). Acrothoracican borings do not have the characteristic neck of *Gastrochaenolites*, which is a key feature of the Fillmore Formation borings and their inhabitants. Borings emplaced into hard substrates by *Lithotrya* Ellis and Solander, 1786 are cylindrical to subcylindrical in shape and taper near the bottom (e.g., Dineen 1990). These borings, if preserved in the fossil record, should be ascribed to the ichnogenus *Trypanites* Mägdefrau, 1932 and are not representative of the borings from the Fillmore Formation. In addition, no evidence exists for cirripedian skeletal material in the borings or elsewhere in the entire Fillmore Formation.

Bivalves are the most common producers of *Gastrochaenolites*. Except for the Upper Ordovician occurrence of mytilaceans in Ohio (Whitfield 1893; Pojeta and

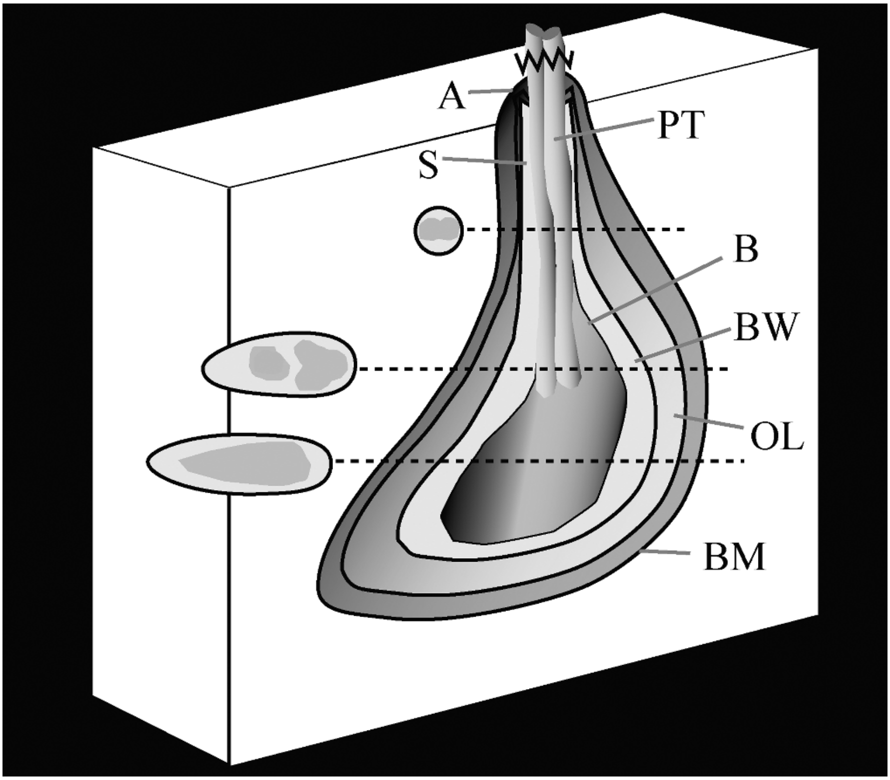

Fig. 4 Idealized rendering of the body inside the boring showing three cross-sections through the body along the length of the boring. (See Fig. 2 for abbreviations)

Fig. 3 Photos of enigmatic organisms, cont. **A**-**B** Set of paired tubes leading out of the surface of a bored cobble. Scale bar = 1 mm. **C**-**D** Longitudinal section through partially eroded boring showing body outlined by thin calcite lining leading up (to the right) to a funnel-shaped boring aperture. Scale in mm. **E**-**F** Transverse section through body inside boring. Scale bar = 1 mm. (See Fig. 2 for abbreviations)

Palmer 1976; Wilson and Palmer 1988), no other bivalves capable of boring into indurated substrates have been identified in Paleozoic rocks. Pojeta (1971) and Bambach (1985) suggested the existence of siphonate bivalves which eventually gave rise to epifaunal, nonsiphonate forms as early as the Upper Cambrian. It is possible that the infaunal, boring life habit of bivalves developed early in the siphonate forms, and if so, it may have allowed some types of bivalves to produce the borings in the Fillmore Formation. The thin calcite lining that outlines the body of each organism is reminiscent of the calcite lining secreted by some bivalve borers (e.g., by some mytilids and gastrochaenids), but that alone is not sufficient for body fossil identification.

Mitrate (stylophoran echinoderm) bioclasts have been found in the Fillmore Formation (Sprinkle and Geunsberg 1995). The stylophoran body plan and inferred life habits offer no indication of the ability to penetrate hard substrates, but some workers interpret them as soft substrate infauna (e.g., Sutcliffe et al. 2000). The enigmatic body fossils in the Fillmore Formation lack any indication of a plated skeletal structure, but their overall shape approximates that of an inverted mitrate.

Recent *Gastrochaenolites* are known to have been made by a variety of organisms, including some worm-like forms, so barnacles, bivalves and mitrates are not the only animals to be considered in this discussion. Sipunculans (e.g., Rice 1969) and some polychaetes (e.g., Bromley 1978: fig. 8) can create vase-shaped biogenic structures that would be referred to the ichnogenus *Gastrochaenolites*, and they may have been a prevalent part of the hardground communities in the Lower Ordovician. However, due to their low fossilization potential, it is unlikely that their identification would ever be more than speculative.

Conclusions

While it is impossible at this time to assign the enigmatic body fossils in the Fillmore Formation to a particular animal taxon, it is nonetheless important to recognize their existence as inhabitants of the macroborings. More specimens need to be discovered and examined before more detailed interpretations can be made. It may be that these body fossils represent more than one of an as-yet undescribed soft-bodied hardground dweller that has been preserved under unusual circumstances. Regardless of biologic affinity, these animals are evidence of a more complex hardground community than previously known, and their discovery lends credence to the recognition of significant evolutionary advances that occurred early during the Ordovician Bioerosion Revolution (Ekdale and Bromley 2001).

Acknowledgments

Improvements to the manuscript were made by reviewers M. Wilson and K. Kleemann, and editors L. Tapanila and M. Wisshak. B. Dattilo first introduced the authors to the Skull Rock Pass section.

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