SHELL HOLES
OR
PREDATION EFFECTS ON SHELL STRUCTURE OF THE MIOCENE SCAPHOPOD *CADULUS*

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Have you ever wondered, about the seashells that one finds on the beach, how the holes are made in the shell and why they are there?

Here in southwestern Florida our beaches are literally littered with such shells – a mecca for shell collectors.

Usually it is the bigger colourful mollusk shells that attract collectors for jewelry and other decorative items. However, there are holes in micromollusk shells too, not normally seen too easily without a microscope, and this is an article of their origin.

The marine species, Cadulus (Dall 1892), show very little variation in structure and are one of the smallest of all mollusks with the simplest of shell structure and anatomy. The shells of the species are usually less than 1 cm in length. The shape of the shell along with the coloration and the number of curious slots appearing along the edge of the smaller posterior end of the shell are considered the basis for distinguishing the various species.

The only study of scaphopod shell borings in the literature is a study by Yochelson, Dockery, and Wolf (1983) of Dentalium species found in the Holocene mud of the Mississippi delta. A Dentalium is about four times larger than a Cadulus, the shell of the study.

INTRODUCTION

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METHODS

A total of 997 specimens of Cadulus (Dall 1892) were collected from sites recorded in the literature both by Dall (1892) and Mansfield (1930) in Liberty and Leon Counties, Florida. The collection interval is from the uppermost section of the Miocene Jackson Bluff Formation (formerly the Choctowhatchee Formation (Mansfield 1930)). The site is located on the Leon County side of the Ochlocknee River just below Lake Tarquin Dam.

Of the 997 specimens collected, only 41 exhibited complete boreholes. Because the scaphopod shell breaks smoothly around its circumference, another two specimens had “half holes” which permitted easy examination of the cross-section of the borehole. The view from the exterior of the hole gives an impression that the walls slope inward more or less smoothly, however, cross-sections show that the wall of the hole is uniformly inclined. Characteristically, the sides of the hole are concave, so that the hole appears bowl-shaped (Figure 1). The concave side of the tube is dorsal and almost all the holes are located on the dorsal half of the circumference; however, the location is commonly lateral rather than directly dorsal. The boreholes are as many on the right side of the shell as on the left. The author considers that each boring is a separate attack by a predatory gastropod.

BOREHOLE MORPHOLOGY

The borehole forms an area of weakness in mollusks because of the predominantly crosslamellar structure of the shell (Hay and Wise, 1970). The fractures tend to be radial, while the fractured edge is commonly smooth and sharp. The Cadulus shell thickness shows little individual variation along the length of the tube, except at the apertural margin. The further from the aperture that the hole was bored, the greater the thickness of shell that had to be penetrated. There are no reports in the literature on rates of boring for naticid gastropods, but muricids can bore 0.3 mm per day through an oyster shell (Carriker, and Van Zandt, 1972). Shell structure and mineralogy affect rates of penetration. The holes in the shells are distinctly oval and are more strongly oval on the interior than on the exterior shell surface (Figure 2). It is thought by the author that the uniform crosslamellar shell structure affects the direction of penetration.

The simplest explanation for the oval shape of the predation hole is geometric. As the surface of the shell is bored is essentially uniformly curved in all directions, the radula of the predator are acting on a sphere. In the longitudinal direction of a boring there is virtually no change in curvature; thus, the drilling is into a cylinder. However, as the odontophore and radula in the mouth of the predator snail are not circular organs, they sweep laterally to approximate a circular shape. This would be more difficult and probably less efficient in penetrating a cylindrical form. Also, the crystal structure of the Cadulus shell also affects the shape of the hole.

The physical relationship of prey to predator is not obvious, for there have been no reports in the literature of a scaphopod in the process of being bored. Because the long axis of the drill hole is aimed with the shell length of the scaphopod tube, probably the gastropod was also aligned in this general direction. The lateral margins of the foot could grasp the scaphopod tube. It is speculated that the prey commonly attacked the scaphopod when it was in its living position; that is, with the apex slightly above the mud and the aperture and most of the tube immersed in the substrate. Unfortunately, no features exist to suggest how deeply the aperture might have been buried have been reported. Nevertheless, from what is known of the life habits of living scaphopods, most of the shell must have been below the sediment-water interface; but researchers cannot document a single boring that may have been far enough toward the apex to have been above the sediment. In oyster predation by muricids (Carriker, 1955, 1970), the prey oyster is above the substrate, and the valve is free of sediment. Some muricids capable of drilling occasionally do crawl on soft bottoms but seem never to drill while on such a bottom (Carriker, 1961, 1969). Four naticid species are known: Neverita dupticata (Say), Natica marochiensis (Gmelin), Natica menkeana Philippi, and Natica canrena (Linnaeus). None of the holes examined show morphologic differences. All four predators produced a borehole having essentially the same morphology. However, based on the size of the hole, the larger borings of Neverita duplicata and Natica canrena cannot be related to preying on Cadulus.

It is instructive to describe the shape of the hole as well as its size. The ratio of hole width to length indicates deviation from circularity, since the external margin of a hole is bilaterally symmetrical and the inner margin very nearly so. The inner margin is more oval than the exterior, while the lateral margins of the holes are uniform in outline. Both the external margin and the inner margin of the hole are quite sharp and without any beveling of the edge. Also noted is that there is no irregular shelf of unbored shell material left as a partial floor to the hole, and the inner edges are bilaterally symmetrical. Both the inner and outer margins of the borehole appear oval, but the external opening is closer to circularity.

No area of etching surrounds the hole. Even though the microscopic sculpture of the shell is sharp, it seems unlikely that any erosion by geologic processes over time has affected the margin of the borehole in the collected specimens. The SEM (Scanning Electron Microscope) micrographs (Figures, 3, 4, and 5) show the concave inward bowl-shaped walls of the hole. The thin inner shell appears fibrous and is strikingly different from the thick outer cross-lamellar layer. Near the juncture of the two layers, the curvature of the hole wall changes dramatically, and this change may be related to the differences in shell structure. No evidence of any radular rasp marks on the walls of the hole was observed, while examination at lower magnification showed the walls of the hole to be smooth and sharp. Similar predator characteristics are noted from SEM micrographs of a bored hole of another smaller gastropod, Caecum regulare Carpenter 1858, from the Recent sediments of Water Island, US Virgin Islands (Mitchell-Tapping, 1978 and 1979) (Figures 6 and 7).

PREDATION SITE

Although borings may occur anywhere along the shell circumference, the dorsal side is preferred. The more significant preference seems to be laterodorsal. In this position, part, if not most, of the shell of the predator gastropod would be near or above the sediment-water interface. More boreholes are found on the right side of the aperture. It is thought that the shell of the naticid would not likely to come in contact with the Cadulus shell, the choice of bore site on the right side of the aperture would insure that the axis of the snail was inclined away from the shell. However, if the predator positioned itself on the left side, its shell might be in contact with that of the scaphopod.

The naticid could have crawled from apex to aperture, or it could have crawled upward along the tube. Movement in the latter direction would provide less chance for the shell of the predator to come in contact with the more strongly curved apical area of the scaphopod. It would also provide a less curved surface, in a longitudinal direction, for the snail to drill. Large holes show asymmetry between the narrow ends of the oval. In most holes, the side toward the apex is more steeply inclined than the side toward the aperture. Fretter and Graham (1962) researched the mechanics of naticid boring and thought that the anteriorward slope of the hole should be steeper. Other researchers reported that the shape and movement should promote some slight asymmetry of the hole, regardless of the geometry of the prey shell (Carriker and Van Zandt, 1972). Therefore, the asymmetry of the hole would indicate that the predator first crawled along the tube toward the apex.

Most of the borings are dorsal, but a few borings are found in the ventral area. These holes have a smaller average size than those in the dorsal area, which possibly indicates that a small predator, which could not manipulate the shell, found it more difficult to bore upward from the ventral side. However, if specimens of Cadulus were exposed during a storm, they would be much more subject to predation.

Another speculative point is the relationship of prey size to borehole size. The mechanics of naticid predation have not been studied as much of those of the muricids. Carriker and Van Zandt (1972) concluded the larger the snail, the larger the prey and, presumably, larger naticids bore larger holes than smaller ones. Fretter and Graham (1962) thought that the diameter of the bored scaphopod is related to the size of the hole and so to the size of the foot of the prey. This relationship is irrespective of the total length of the prey. Fretter and Graham (1962) also inferred that the naticid crawled along the scaphopod tube until it reached a point where the foot was conveniently situated, that is, extending part way around the circumference. Yochelson, Dockery, and Wolf (1983) suggest that this positioning is closely related to the anatomy of the scaphopod since the organism is capable of considerable retraction is demonstrated by its anchoring of the extended body and subsequent pulling of the shell forward as it burrows into the substrate (Dinamani, 1964; Trueman, 1968).

The ability of the scaphopod to retract its soft parts a long distance within the tube also may explain why the predator gastropod does not simply reach into the aperture to eat the soft parts.

Muricid gastropods have a long proboscis, whereas naticids have a short one; if the predator had been a muricid, it might have been able to reach the soft parts through the aperture. Alternatively, perhaps the feeding habits of the naticids are so stereotyped toward boring that they are unable to recognize a free meal, but more likely the shortness of the proboscis prevents them from attacking at the apertures (Yochelson, Dockery, and Wolf, 1983). The short proboscis may also explain in part why the hole is finished neatly, rather than left with a projecting shelf as is characteristic of muricid predations (Yochelson, Dockery, and Wolf, 1983).

IDENTITY OF THE PREDATOR

The morphology and position of the boreholes indicates that naticids were the predators. The edges of the borehole, almost without exception, are sharp. Carriker (1961) noted differences in the behavior of muricid and naticid gastropods that bore and also differences in the relative size of the accessory boring organ. In both groups the boring organ is critical, for when it is removed, the animal cannot bore (Carriker and Van Zandt, 1972). The muricid hole is gently beveled, that is, inclined, on its upper slopes (Carriker, 1961), whereas the naticid boring is not. Muricid gastropods commonly leave a shelf at the base of the hole once the radula has finally penetrated the shell (Carriker, 1970), whereas naticids make a much neater hole. In effect, the naticid appears to complete the removal of the inner shell layer before dining on its prey. Also, naticid holes commonly are nearly circular while Carriker and Van Zandt (1972) found a very slight degree of ovalness in muricid holes, the long axis of the hole being parallel with the long axis of the foot of the predator. However, unless one looks with extreme care, both naticid and muricid holes would appear similar.

Geometry of the prey is often cited as having an influence on selection of the drilling site, since Cadulus shells show little variation in the position of the hole, it is concluded that the longitudinal position of the boring is related to the presence of soft parts and not related to the geometry of the shell (Yochelson, Dockery, and Wolf, 1983). As there is such a close relationship of the borings to the position of the organs inside the tube, it is speculated that somehow the predator can sense, probably by slight vibration of the shell caused by retraction of the mantle movement, and thus able to locate a suitable site for drilling. This concept is also supported by research by Yochelson, Dockery and Wolf (1983); however, Berg (1975) suggested that “internal anatomy seems less important in determining borehole position.”

CONCLUSIONS

This study considers that predation holes of Cadulus are not distributed at random, and that the Miocene predation rate was seldom higher than a few percent. It is also considered that the smooth surface of the shell make predation holding and grasping of the gastropod very difficult.

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LIST OF FIGURES

Figure 1. Light microscope digital micrograph of a borehole showing the apparent circularity of the hole at lower magnification. The length of the specimen is 0.7 cm.

Figure 2. Light microscope digital micrograph of a borehole showing the actual oblong shape of the hole at higher magnification.

Figure 3. SEM micrograph of a Cadulus specimen at low magnification.

Figure 4. SEM micrograph of a Cadulus at higher magnification showing no etching by acid of the borehole.

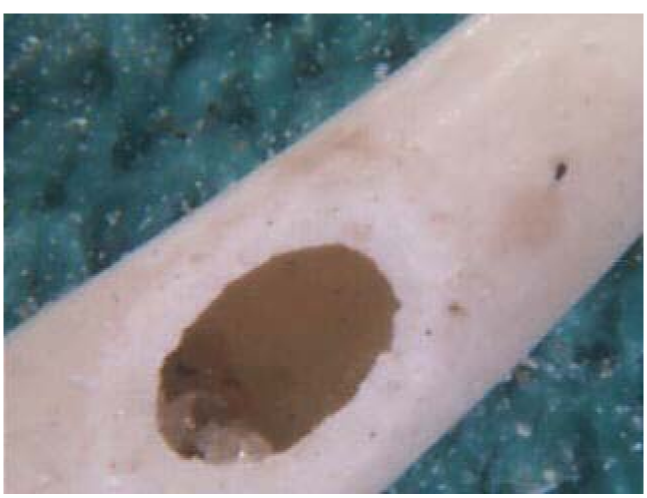
Figure 5. SEM micrograph of the interior wall of the Cadulus.

Figure 6. SEM micrograph of a Caecum at low magnification. The length of the specimen is 0.5 cm.

Figure 7. SEM micrograph of a Caecum at higher magnification showing no etching by acid of the borehole.

FIGURES

Figure 1



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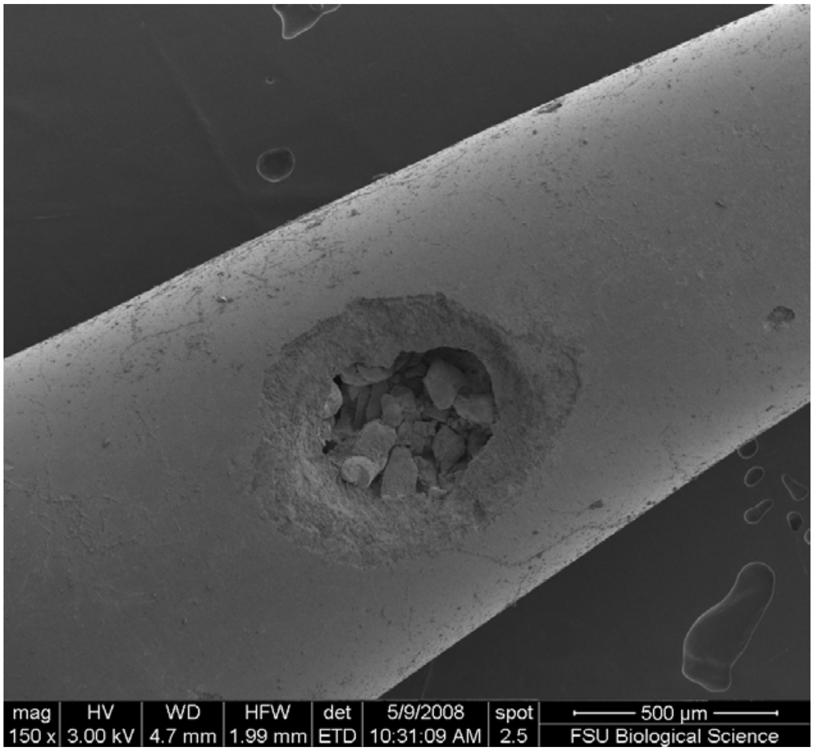

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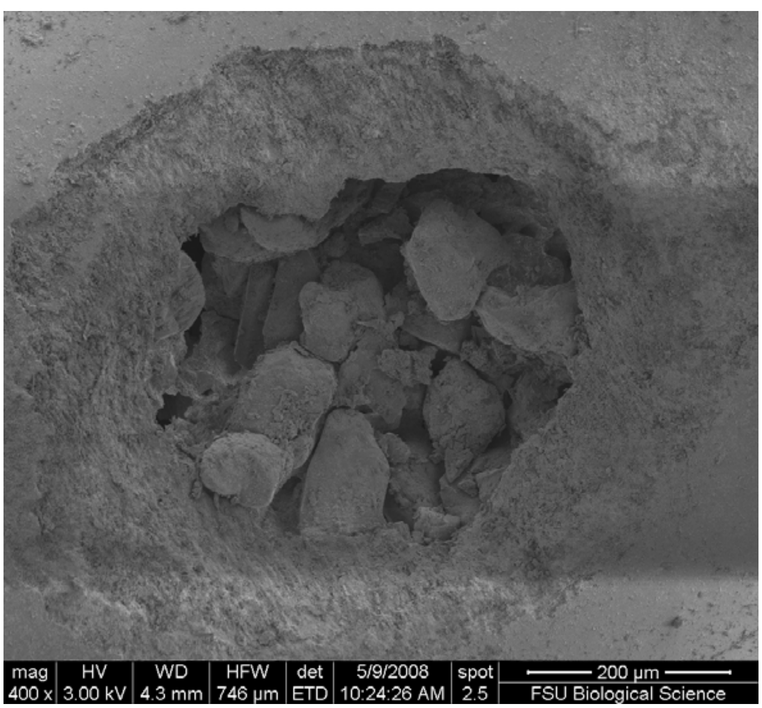

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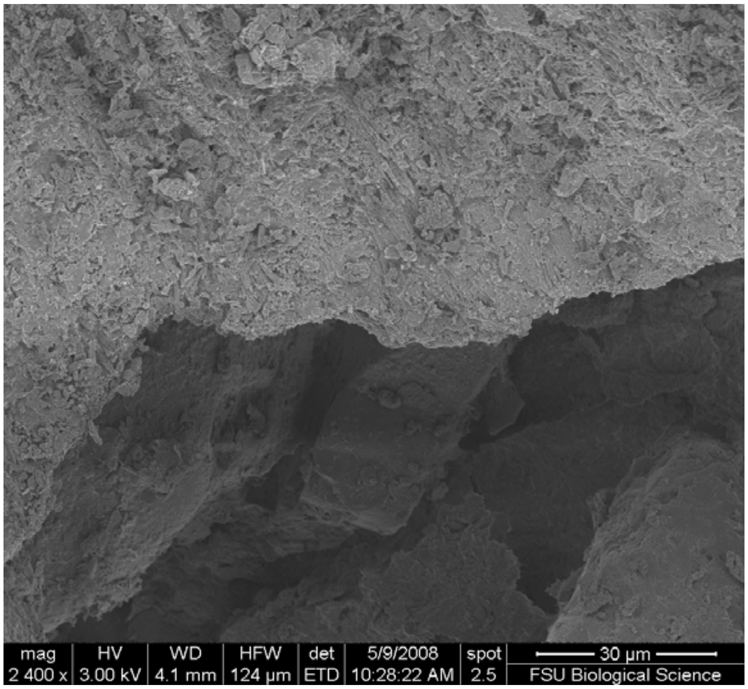

Figure 5

Figure 6

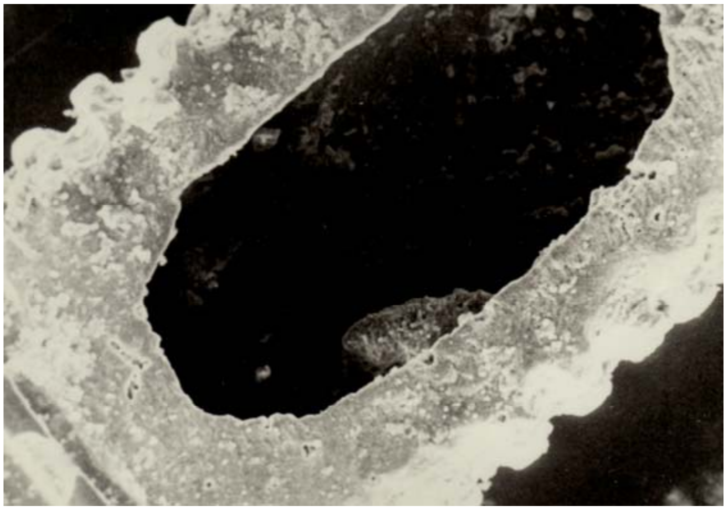

Figure 7