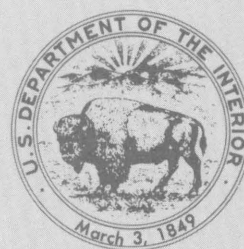


Predation on Sub-Holocene Scaphopod Mollusks from Southern Louisiana

GEOLOGICAL SURVEY PROFESSIONAL PAPER 1282



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By ELLIS L. YOCHELSON, DAVID DOCKERY, and HEIDI WOLF

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Boring of scaphopod shells by naticid gastropods, which can be documented back to the Late Cretaceous, is most common on coarsely ribbed species



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PREDATION ON SUB-HOLOCENE SCAPHOPOD MOLLUSKS FROM SOUTHERN LOUISIANA

By ELLIS L. YOCHELSON, DAVID DOCKERY,¹ and HEIDI WOLF²

ABSTRACT

A scaphopod mollusk, *Dentalium (Dentalium) laqueatum* Verrill, is common in the sub-Holocene fauna from the "mud lumps" at the mouth of the Mississippi River. More than 50 percent of the individuals have been bored; nearly 20 percent of these organisms had non-fatal shell breakage during life. The infaunal life habit of the scaphopods and the characteristics of the boreholes suggest that naticid gastropods were the predators. The holes are not bored at random, but were evidently positioned where they would intercept internal organs of the scaphopod. Holes are slightly more common on the right side, as an observer would look into the aperture, and more common in a dorsal position. Some relationship also exists between the size of the hole and the diameter of the shell. Apparently, the naticid predator crawled along the dorsal side of the tube from the aperture toward the apex until it found an appropriate site to drill.

Predation on scaphopods by naticid gastropods can be documented back to the Late Cretaceous. The rate of predation observed in fossil and Holocene specimens commonly is low, in the 1-5 percent range; however, coarsely ribbed scaphopod species show a high rate of predation. Theoretical considerations suggest that coarse ribs would facilitate burrowing into coarse sediments, such as shell pavements, though no observations on the relationships of scaphopod shell morphology and sediment type exists. Naticid gastropods seldom penetrate fine-grained sticky sediments, so the degree of predation seen in collections of fossil scaphopods may give some indication of the original character of the sediment.

INTRODUCTION

The ephemeral islets, or "mud lumps," at the mouth of South Pass of the Mississippi River have long commanded interest. They are now accepted as diapir structures, in which strata of sub-Holocene age (about 15,000 years old) from beds probably more than 100 m below the sea floor of the Gulf of Mexico (Morgan, Coleman, and Gagliano, 1968) are raised to the surface. Clay and silt forming these "mud lumps" contain a diverse molluscan fauna, including scaphopods. Scaphopods feed by using their captaculae to gather microorganisms such as foraminifers from the surrounding sediment (Dinamani, 1964b). The abundant foraminifers in the sediments of the "mud lumps" pro-

vide a logical explanation for the abundance of scaphopods at the locality. Palmer (1975) observed piles of broken foraminifer tests adjacent to Jurassic scaphopods, suggesting that these microorganisms have been an important part of the scaphopod diet. An unusually large proportion of scaphopods at South Pass have been bored, and it is this feature that is investigated.

The surprisingly high degree of predation at this locality independently attracted two of us to this study. Yochelson made a surface collection from the "mud lumps"; this collection was measured and studied in Washington, D.C., by Wolf. Dockery examined scaphopods in the collections of the Department of Earth Sciences, Tulane University, New Orleans, La., which had accumulated as a result of repeated trips to the "mud lumps." These Tulane specimens were obtained by screening and washing of sediment as well as by surface collecting. Because the Tulane collection was larger than the Washington collection, a more sophisticated statistical approach was used there to handle data on predation. Some differences in the results of the two investigations may be related to the much larger sample size at Tulane and to the greater number of smaller individuals obtained by sieving of the sediments. Observations of scaphopod morphology, apart from data from boreholes, are based on the Washington collection.

The specimens studied by Dockery are housed at Tulane University. The figured and unfigured specimens studied by Wolf and Yochelson are housed in the Division of Mollusks, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

ACKNOWLEDGMENTS

A trip to the Mississippi "mud lumps" was arranged by Emily Vokes, Department of Earth Sciences, Tulane University, with the good offices of Shell Oil Corporation. While at the locality on April 23, 1977, 15 members of the party donated the scaphopods that they col-

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lected to Yochelson. Wolf's participation in this project was during a Colgate University program in January 1978, under the supervision of Robert M. Linsley. Computer time for Dockery was obtained through the Department of Earth Sciences, Tulane University.

Norman F. Sohl, U.S. Geological Survey, Washington, D.C., shared his knowledge of Mesozoic predation with us. M. R. Carriker, University of Delaware, Lewes, Del.; John Kraeuter, Virginia Institute of Marine Sciences, Gloucester Point, Va.; Louie Marinovich, U.S. Geological Survey, Menlo Park, Calif.; and C. P. Palmer, British Museum (Natural History), London, gave helpful advice and guided us to pertinent literature. Joseph Rosewater, Division of Mollusks, National Museum of Natural History, Smithsonian Institution, Washington, D.C., permitted the examination of types and the large collection of Holocene scaphopods under his charge.

IDENTIFICATION OF THE MOLLUSKS FROM THE "MUD LUMPS" AND PREDATION ON *DENTALIUM*

Gastropods and pelecypods in the fauna were identified by consulting Abbott (1974) and Warmke and Abbott (1961). The overall degree of predation of the mollusks was low, as shown in the Tulane collections. Predation by boring was more widespread among bivalve genera than among gastropods. The bivalves *Gouldia cerina* (C. B. Adams), *Mulinia lateralis* (Say), small valves of *Anadara boughmani* Herlein, *Pleuromeris armilla* (Dall), and *Corbula* sp. show a moderately high percentage of bored valves. The gastropod *Turritella* is noteworthy for the amount of boring. For example, 57 percent of 281 specimens of *Turritella exoleta* (Linnaeus) and 39 percent of specimens of *T. acropora* Dall were bored; a few additional species of gastropods showed evidence of predation at a much lower level. Although none of these borings have been studied in detail, they are similar to the borings on *Dentalium*.

In contrast to the number of bored gastropods and pelecypods, only 18 of 183 specimens of *Cadulus* (*Platyschismoides*?) cf. *C. (Platyschismoides?) elongatus* Henderson (39 in Washington, under USNM 780590, and 144 in Tulane collections) were bored. All these borings were positioned along the middle third of the tube; details of the boreholes are similar to those in *Dentalium*. Evidently, *Cadulus* was not a preferred prey.

Scaphopods were identified with reference to Henderson (1920). His figured specimens as well as specimens identified by him in the biologic collection of the National Museum of Natural History, Washington, D.C., were examined by us. We are confident of the assignment of specimens to *D. (Dentalium) obscurum*

Dall (under USNM 780952) (pl. 1, fig. 3), but we are less certain of the identity of the most abundant species (USNM 780951) (pl. 1, figs. 1, 2, 4). This latter species shows the fine reticulate ornament of *D. (Dentalium) laqueatum* Verrill, but that species characteristically has nine ribs. *D. (Dentalium) texasianum* Phillipi is less well known but is reported as six ribbed and lacking fine reticulation. We have decided to use Verrill's name; although eventually it may be appropriate to name a new species for this material, such action should be delayed until the variation in both *D. (Dentalium) laqueatum* and *D. (Dentalium) texasianum* is better known. In addition to these two common species of *Dentalium*, two specimens, lacking boreholes, of a third undetermined species of scaphopod were present (USNM 780953).

In the Washington collection, 235 specimens of *D. (Dentalium) laqueatum* Verrill are available, of which 121 show evidence of predation. These are divided into groups on the basis of the number of longitudinal ribs. A few specimens show one to three supplementary ribs bifurcating an interarea; they are also tabulated below, denoted by a "+" sign:

No. of ribs	Specimens not bored	Specimens bored	Total	Percentage bored
5+1	0	2	2	100
6	15	13	28	46
6+1	2	1	3	33
6+2	1	0	1	0
7	85	89	174	51
7+3	1	0	1	0
8	10	15	25	60
8+3	0	1	1	100

The overall degree of predation was 52 percent. Not all the unbored shells are complete, and a few may have contained a hole in the missing part of the shell. However, we judge that, at most, only 1 or 2 percent additional specimens might have been bored. Two specimens each bear two borings; four individuals bear only incomplete borings, but they are counted as having been bored.

Borings in *D. (Dentalium) laqueatum* are more common in the Tulane collection, 291 of 478 specimens having been bored.

Three variants of rib number were distinguished:

No. of ribs	Specimens not bored	Specimens bored	Total	Percentage bored
6	33	42	75	56
7	145	223	368	61
8	8	26	33	79

The overall degree of predation is 61 percent. The three variants of *D. (Dentalium) laqueatum* show that the percentage of individuals bored increases with the increase in number of ribs. This trend also appears in the smaller Washington collection.

The Washington, D.C., collection also contains 29 specimens of *D. (Dentalium) obscurum* Dall, of which 13 (45 percent) were bored. This species shows several variants in rib number, but individuals are too few to indicate any relationship between number of ribs and degree of predation. In the Tulane collection, 16 of 48 specimens (34 percent) of this species were bored, but the predation rate varies widely among the rib-number variants. The numbers summarized below probably are too small to be significant in demonstrating increase of predation with increase in number of ribs:

No. of ribs	Specimens not bored	Specimens bored	Total	Percentage bored
9	13	9	21	45
10	16	6	22	27
11	2	0	2	0
12	1	1	2	50

LONGITUDINAL AND CIRCUMFERENTIAL DISTRIBUTION OF BORINGS IN *D. (DENTALIUM) LAQUEATUM*

The position of the borings along the length of the shells of *D. (Dentalium) laqueatum* was determined by two different methods. Shells in the Washington, D.C., collection were measured by Wolf by moving a Swiss Map Measurer (Dietzgen Inc.)³ along the convex (longest) surface from apex to aperture. The relative position of the borehole was projected onto this ventral surface, regardless of where it was on the circumference.

Specimens were judged to be complete when the apertural margin was thin and translucent to light. A few of the specimens may have lacked part of the apex, but, at most, only 1–2 mm was missing. All specimens were measured at least three times to insure accuracy.

Forty specimens of the seven-sided variant of *D. (Dentalium) laqueatum* were measured; they ranged in length from 1.9 to 5.0 cm (mean 3.4 cm \pm 0.92). The position of the borings was calculated as percentage of the distance from apex to hole against the total length. The lowest value was 30 percent and the highest 70; these extremes are atypical but are not a consequence of poor measurement or broken material. The average distance to the borings was approximately 45 percent of the length; 38 of the 40 holes were between 38 and 59 percent of the total shell length.

To check for possible relation between size of the organism and longitudinal position of the holes, measurements of the six shortest shells were pooled. Average length was 2.3 cm, and percentage of distance to boring was 44 percent. For the six largest shells, the average length was 4.9 cm and the percentage distance 45 per-

cent. To check for possible differences around the circumference, the distance to holes on or near the plane of bilateral symmetry in the dorsal and the ventral quadrants were averaged separately; both were essentially the same.

One five-sided variant, 7 six-sided variants, and 10 eight-sided variants were also measured. These ranged from 1.3 to 5.2 cm in length, with an average of 2.9 cm. The lowest percentage distance to boring was 33 and the highest 73; the average percentage was 49. The average percentage for six-sided specimens was 44, whereas that for eight-sided individuals was 52. The number of specimens probably is too small for these percentages to be significant.

Figure 1A–D illustrates the bore radial position of 123 boreholes on 121 specimens of *D. (Dentalium) laqueatum* in the Washington collection, divided into four variants of rib number. With the exception of a single hole centered on the dorsal rib of a six-sided specimen, all borings were between ribs. A large hole may impinge upon an adjacent rib, but, with the one exception, a rib was not a site for boring. On those specimens in which an extra rib was intercalated, the boring was situated on a wider interspace. As noted, four of these specimens each show an incomplete boring. In addition, one specimen had one complete hole and an incomplete one in an adjacent interarea. One specimen contained two holes, both in the same interarea.

In the Tulane collection, emphasis was given to the seven-ribbed variant of *D. (Dentalium) laqueatum*, for which 323 mostly complete specimens were available (fig. 1E–G). Procedure for measurements made on this variant differs from those used by Wolf. Definitions of measurements are:

- (1) Arch height (A), greatest displacement of the concave dorsal margin of the tube from the apex to anterior cord.
- (2) Bore diameter (BD), greatest diameter of the borehole at the exterior surface.
- (3) Bore longitudinal position (BLP), percentage of the shell length to which the borehole was displaced from the anterior aperture. This percentage was calculated from the measurement of total length along the chord from the apex to the aperture and the chord length from the aperture to the boring.
- (4) Bore radial position (BRP), radial location in which interspace the borehole occurred. The interspaces are numbered from 1 to 7 in a clockwise manner as viewed looking into the aperture, the apex upward in the life position.
- (5) Diameter (D), diameter of the anterior aperture.
- (6) Length (L), length of the cord from the apex to the dorsal edge of aperture.

³Any use of trade names in this publication is for descriptive purposes only and does not constitute endorsement by the U.S. Geological Survey.

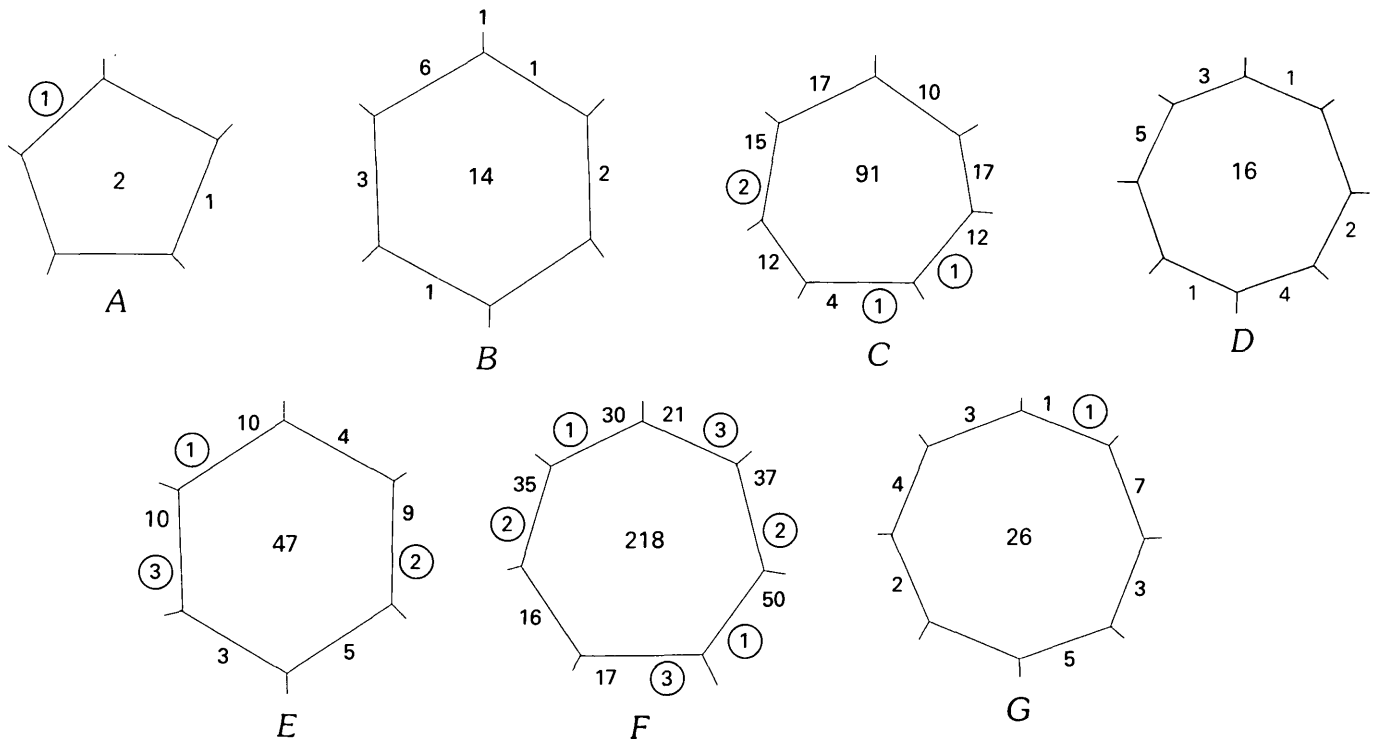


FIGURE 1.—Circumferential distribution of borings in rib variants in two samples of *D. (Dentalium) laqueatum*: A–D, Washington collection, and E–G, Tulane collection. Incomplete borings are circled; total number of complete and incomplete borings is given in the center of each outline sketch. In designating position, side 1 is to the upper right in every rib variant. The sketch is a view of the aperture as seen by an observer looking into it, the apex upward in life position.

Measurements of 204 bored specimens were tested in a correlation matrix for any relationship between position and size of the boring and morphology and size of the shell. The means and standard deviations of measurements for specimens bored and not bored were also calculated. All values are in millimeters except for the longitudinal position of the borehole, which is a percentage, and the bore radial position, which is a value from one to seven. The correlation matrix is as follows:

D	L	A	BLP	BRP	BD	
1.000	0.944	0.700	0.010	0.081	0.223	D
	1.000	.731	.013	.040	.210	L
		1.000	.020	.022	.206	A
			1.000	-.006	-.132	BLP
				1.000	.114	BRP
					1.000	BD

Means and standard deviations (SD) measurements of the 204 bored specimens are:

D	L	A	BLP	BRP	BD	
4.037	34.542	3.096	53.603	3.932	1.402	Mean
1.122	10.557	1.063	8.085	1.984	1.377	SD

Means and standard deviations for measurements of the 119 specimens not bored are:

D	L	A	
3.500	29.130	2.567	Mean
1.121	10.493	1.063	SD

Relationships among the shell dimensions are obvious without the use of a correlation matrix, but their relationship, if any, to the selected position of boring by the predator is less evident. There is no correlation of the longitudinal or radial borehole position with the size of the *Dentalium* shell. A correlation slightly higher than the 5-percent level of significance (the 5-percent level at two degrees of freedom is 0.138) occurs between the bore diameter and the shell dimensions, not unexpectedly, as the larger predators might select the larger prey. The correlation of the borehole diameter with the radial position of the borehole is slightly less than the 5-percent level. The mean and standard deviations of the longitudinal position of the borehole indicate a strong preference by the predator to bore along the midsection of the shell, as noted in the Washington collection.

The larger *Dentalium* shells were also those more commonly bored, as indicated by the differences between the means of specimens bored and not bored.

The various size groups of seven-sided individuals are tabulated below:

Length in mm	Specimens not bored	Specimens bored	Total	Percentage bored
60+	1	2	3	67
55-59.9	0	4	4	100
50-54.9	5	11	16	69
45-59.9	4	18	22	82
40-49.9	10	31	41	76
35-39.9	16	33	49	67
30-34.9	20	31	51	61
25-29.9	17	35	52	67
20-24.9	20	25	45	56
15-19.9	19	14	33	42
10-14.9	7	0	7	0

As observed in the smaller Washington collection, the circumferential distribution of boreholes around *D. (Dentalium) laqueatum* shells is not random; more boreholes are found at some interspaces between ribs than at others, as shown in figure 1E-G. On the six-ribbed shells, the boreholes are concentrated in interspaces 2, 5, and 6. On the seven-ribbed form, borings are most common in interspaces 2, 3, 6, and 7. On the eight-ribbed form, they are concentrated in interspaces 2, 4, and 7. No count was made of the five-ribbed variant in the Tulane collections. In all these variants, the opposing interspaces just to the right of the dorsal rib and on, or just to the left of, the ventral margin (as viewed toward the aperture) show the lowest frequency of boreholes.

A few specimens show more than one incomplete boring. One seven-ribbed specimen has three shallow incomplete borings in interspaces 1, 2, and 4 and a complete boring in interspace 6, all of which are similar in size. As interspaces 1 and 4 are least commonly bored, a predator may have abandoned these sites in favor of one in which it could better grasp the shell with its foot. Another seven-sided specimen had two complete borings. One specimen has an incomplete boring that is partly on a rib. As in the Washington collection, all other borings were centered in the interspaces; the increased shell thickness along the rib may have discouraged the predator from siting there, but more likely the upward projection interfered with positioning of the predator's foot and thereby discouraged drilling through a rib.

Relatively few incomplete boreholes are found compared with the number of complete ones. If each boring is considered a separate attack by a predatory gastropod, the percentage of incomplete boreholes in the Tulane collection is 15 percent for the six-ribbed individuals, 5 percent for the seven-ribbed forms, and 4 percent for the least common eight-ribbed variant. The seven-ribbed individuals are by far the most common. The percentage of incomplete boreholes is low for all

variants; when considered along with the number of attacks, the six-ribbed variant is the least vulnerable. There seems to be no obvious reason why drilling is apparently less effective on this variant.

Of the 13 bored specimens of *D. (Dentalium) obscurum* examined in Washington, 12 show one boring. None of the holes is centered on a rib, but, because of the more numerous ribs, holes impinge more on adjacent ribs; predation was not seen in the areas where an intercalated rib was present. Almost all the holes are on the dorsal half of the circumference, but they are more commonly lateral than directly dorsal. About as many are on the right side of the shell as on the left. One specimen with two complete borings has one on the upper lateral right and one on the upper lateral left side.

Five drilled specimens of *D. (Dentalium) obscurum* were complete enough to treat by the map-measurer method. The shells range in length from 2.1 to 3.0 cm, averaging 2.3 cm. The percent distance to the borehole ranges from 39 to 52, averaging 44.

Except for the count of predation given earlier, no study of the Tulane specimens of *D. (Dentalium) obscurum* was undertaken.

MORPHOLOGY OF THE BOREHOLE

Because the scaphopod shell breaks smoothly around its circumference, some specimens have "half holes" and permit easy examination of the cross section of the boring (pl. 2, fig. 1; pl. 3, fig. 1). Viewing the hole from the exterior gives an impression that the walls slope inward more or less smoothly, but the cross sections show that only in the exceptional hole is part of the wall uniformly inclined. Characteristically, the sides of the hole are concave, so that the hole is bowl shaped.

The borehole forms an area of weakness, and a third of the Washington specimens examined are broken; these specimens show the circumference of the shell and allow ready observation of both shell thickness and borehole morphology. Because of the predominantly crosslamellar structure of the shell (pl. 2, figs. 2, 4) (Hass, 1972), the fracture tends to be radial (Joseph Carter, oral commun., 1977), and the fractured surface is commonly smooth and sharp (pl. 2, fig. 6).

Although we did not measure shell thickness of any individuals, our impression is that thickness shows little individual variation along the length of the tube, except at the apertural margin. The farther from the aperture that the hole was bored, the greater the thickness of shell that had to be penetrated. In a small hole, the shell thickness penetrated was 0.4 mm; in a large hole, it was 0.9 mm. No data are available on rates of boring for naticid gastropods, but muricids can bore 0.3 mm per day through an oyster shell (Carriker, Williams, and Van Zandt, 1978, p. 126); no doubt, shell structure and mineralogy affect rates of penetration.

The gross morphology of the borehole in 40 specimens of *D. (Dentalium) laqueatum* in the Washington collection was examined. Length and width measurements of the holes were taken on the exterior and interior using a 20 x 20 grid under 18x magnification. One significant point is that the long axis of the hole was invariably aligned along the long axis of the shell.

On the external shell surface, the length of holes ranged from 0.2 to 4.1 mm, with a mean of 2.4 mm (± 0.69); the width ranged from 1.0 to 3.3 mm, with a mean of 2.0 mm (± 0.55). On the internal shell surface, length of holes ranged from 0.9 to 2.8 mm, with a mean of 1.6 mm (± 0.44); width ranged from 0.7 to 2.3 mm, with a mean of 1.1 mm (± 0.3).

We also plotted the hole size relative to width of the scaphopod at the point of boring for specimens in the Washington collection (fig. 2). The plot shows a wide

scatter, but in general the wider the position where the scaphopod was bored, the larger the hole. Carriker and Van Zandt (1972b, p. 221-225) found a general relationship of borehole size to size of predator in the muricid *Urosalpinx*. Berg (1975) suggested this relationship in naticids, but provided no supporting data.

The holes were grouped into four quadrants—one centered ventrally, one dorsally, and two laterally—to test for a preference in the size of the hole and its circumferential position. Holes were also divided into groups according to the maximum borehole length on the outer shell surface: small (2.4-4.2 mm), medium (4.3-6.2 mm), and large (6.3-8.1 mm). Of the 15 holes in the ventral quadrant, 54 percent were small, and, of the 14 holes in the dorsal quadrant, 36 percent were small. The average length of the borings on the dorsal and ventral sides was the same, 3.5 cm.

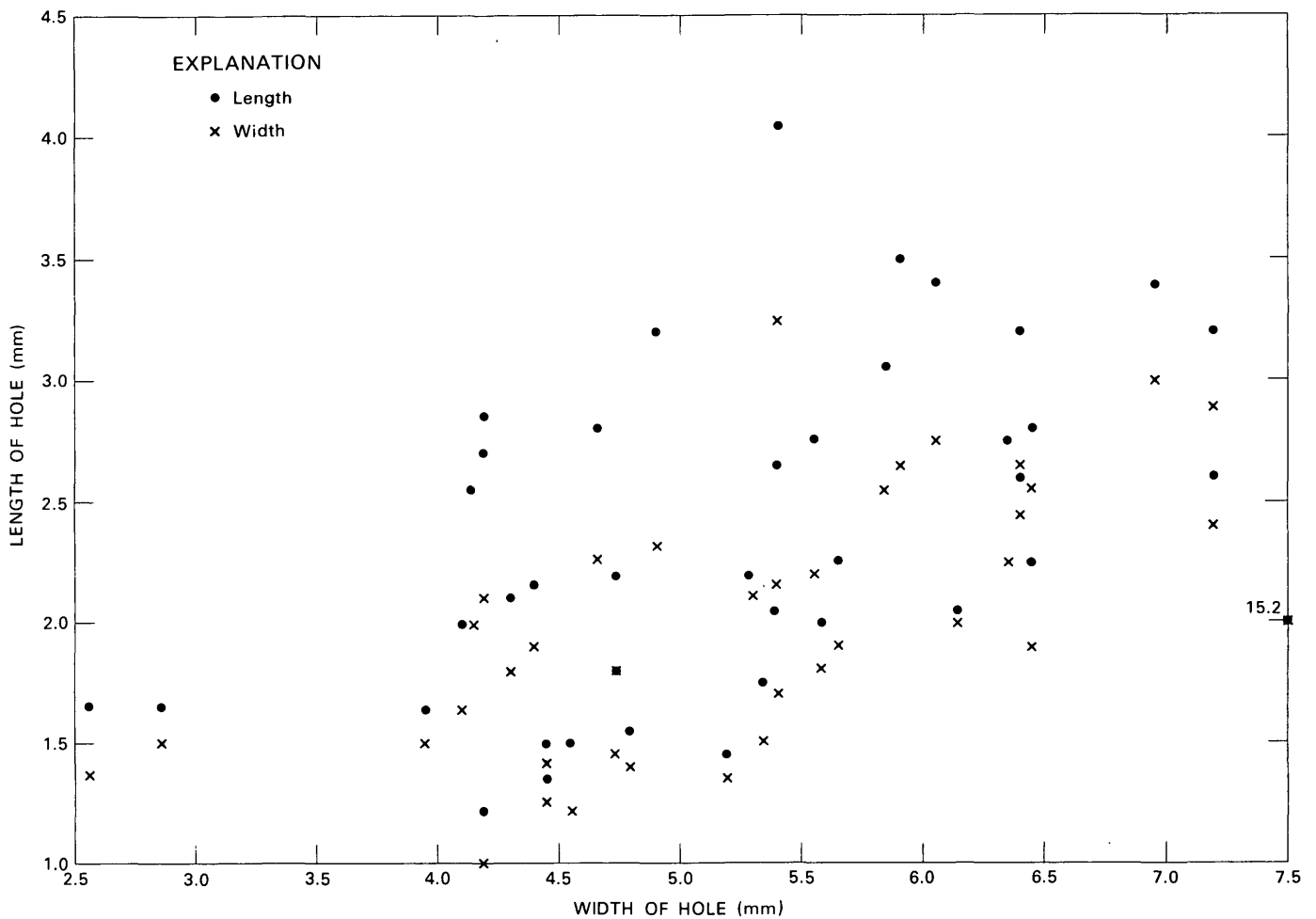


FIGURE 2.—Relationship of length and width of 40 specimens of *D. (Dentalium) laqueatum* Verrill to length and width of borehole in the shell.

It is instructive to describe the shape of the hole as well as its size. Because the external margin of a borehole is bilaterally symmetrical and the inner margin very nearly so, the ratio of width to length indicates deviation from circularity. For the exterior in the 40 holes, this ratio ranged from 100 percent—a circular hole—to 72 percent. The mean was 86 percent, with a standard deviation of 7 percent. For the interior margin, the maximum was 96 percent—nearly a circular hole, but an unusually wide one—and the minimum was 53 percent. The mean of the interior was 69 percent, with a standard deviation of 10 percent. The inner margin is more oval than the exterior; as noted earlier, the long axis of the hole is parallel to the ribs. So far as we can determine, the lateral margins of the holes are uniform in outline, except for the few boreholes that impinge on a rib on one side and not on the other.

The external margin of the hole commonly is sharp and without any beveling of the edge, for the fine ornament on the interarea may be followed to the edge of the depression at almost every one of the holes (pl. 1, fig. 4). The inner margin of the hole is also quite sharp. No irregular shelf of unbored shell material is left as a partial floor to the hole, and, in almost all examples, 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.

Many of the drillings were examined at moderate magnification, and collectively they conveyed an impression of general similarity of form. One "half hole" was examined in more detail by scanning electron microscope (SEM) (fig. 2). The close relationship of the fine ornamentation to the crosslamellar structure of the shell is evident (pl. 2, figs. 1–3). This same point emphasizes how sharp is the contact between the outer circumference of the hole and the outer shell surface. No area of etching surrounds the hole (pl. 2, fig. 3). Because even the microscopic sculpture of the shell is sharp, it seems unlikely that erosion by geologic processes has affected the margin of the borehole.

The SEM photographs show the concave inward bowl-shaped walls of the hole (pl. 2, figs 1, 4). The thin inner shell appears fibrous and is strikingly different from the thick outer crosslamellar layer (pl. 2, figs. 2, 5). Near the juncture of the two layers, the curvature of the drill-hole wall changes dramatically, and this change may be related to the different shell structure (pl. 2, figs. 2, 4). Finally, there is no evidence whatsoever of any radular rasp marks on the walls of the hole (pl. 2, figs. 2, 4, 5). Other specimens examined at lower magnification also showed the drill-hole walls to be smooth and sharp.

In examining the borings on 15 specimens of *D. (Dentalium) obscurum*, we did not observe any percep-

tible difference in size or shape from those on the more abundant species.

OTHER POSSIBLE PREDATION ON *DENTALIUM*

We have observed an apertural peculiarity of *D. (Dentalium) laqueatum* in that some specimens show an irregularity at the apertural edge, which is then repaired by subsequent shell growth (pl. 3, figs. 4, 5). This irregularity was noted in 43, or 18 percent, of the specimens in Washington. Many were moderately complete specimens, but there might have been an irregularity in those lacking the most mature part of the shell; thus, perhaps as many as 20 percent of the specimens may have been broken and repaired. A depression in the longitudinal profile is present at the side of the irregularity, but within the subsequent millimeter or two the shell has increased to its former size, and expansion continues uniformly through later growth (pl. 3, figs. 4, 5).

These breaks characteristically have a jagged outline, and almost none are circular or subcircular around the circumference of the margin. Breakage is random in terms of the dorsal, ventral, or lateral parts of the aperture, for only eight shells show breakage confined to part of the aperture. Almost certainly the breaking only affected the shell and did not involve the mantle edge, because during later growth of the shell, the ribs and fine ornament continue in the same pattern and the same position as on the earlier part.

A few shells show multiple breaks. Of the 43 examined, four have two growth interruptions (pl. 3, fig. 5), one has three, and two have four; after the fourth break, the shell of one specimen grew with slight deviation from the plane of bilateral symmetry, but the ribs were still straight and uniformly spaced (pl. 3, fig. 6). An example of wasted effort is recorded in a shell repaired twice and then bored.

Similar breakage and repair has been seen by John Kraeuter (oral commun., 1978) in other species of *Dentalium*, though seldom such a high percentage. We speculate that these scaphopods may have been attacked by a fish or a crustacean but that those individuals who survived either were not protruded or were able to retract into the shell rapidly enough to avoid injury to the soft tissues.

Some of the specimens might have been exhumed during life by storms and broken before they reburrowed; however, in spite of thinness near the aperture, the shells are strong, and this possibility seems unlikely.

Of 29 specimens of *D. (Dentalium) obscurum*, 5 have been broken and then repaired. The breaks are similar

to those in *D. (Dentalium) laqueatum*. We did not observe any breakage in the *Cadulus* specimens.

ONTOGENETIC CHANGE IN *D. (DENTALIUM) LAQUEATUM*

The available specimens of *D. (Dentalium) laqueatum* show no apparent variation in logarithmic curvature, the prime feature of growth. The five, six, and eight-ribbed variants are uncommon relative to the seven-ribbed form. Even rarer are those specimens in which one or two of the sides is bifurcated by an accessory rib (pl. 1, fig. 2). Commonly these accessory ribs do not begin at the apex but are intercalated about a centimeter below it. The relative height of the ribs decreases during ontogeny (pl. 3, figs. 2, 3); apparently this is a regular feature of growth and not an abrupt gerontic change, but more observations of large individuals are needed to confirm the interpretation. The fine ornamentation appears constant on all individuals examined (pl. 1, fig. 4; pl. 2, fig. 1). Growth lines are obscure in the apical area but are slightly coarser along most of the shell length. Specimens do not show crowding of the growth lines near the aperture, which might indicate gerontic growth. However, the one shell area of significant ontogenetic change is at the apical area (pl. 4).

The sequence of change appears as follows: During early growth stages, the apex bears a tiny circular opening that increases in diameter as shell length increases. At the next stage, the margin is indented by a "V" formed ventrally, making a keyhole shape, the sides of the "V" being inclined at an angle as great as 45° to the line of bilateral symmetry (pl. 4, fig. 1); this "V" is commonly between major ribs but need not be directly ventral and may be inclined to the left or right. Concurrent with increase in length, the base of the "V" then gives rise to an incipient slit parallel to the ribs (pl. 4, fig. 2). Increase in the diameter of the apical hole continues so that the upper part of the "V" is steadily reduced in width and depth until it ultimately disappears. The final stage consists of the apical hole, breached by an elongated slit occupying all or most of an interarea between two ribs (pl. 4, fig. 3).

There appears to be no literature on the mechanism of resorption in modern scaphopods. The scanty accounts of soft-part morphology suggest that the apical area is lined by a mantle like that at the aperture. Thus, this organism apparently is simultaneously building the tube at the aperture, while the animal is within the sediment, and absorbing the apex, which protrudes up into the water.

The apices of the 6 smallest specimens, of 6 near the mean length, and of the 8 largest individuals in the Washington collection were measured. The shortest

specimen that did not show any modification of the circular apical opening had a length along the convex (ventral) side of 1.9 cm; the largest having an unmodified apex was 4.0 cm. Commonly, an indentation in the margin of the apical aperture appears when a shell is about 3.3 cm long, but one specimen only 2.2 cm long shows an incipient "V"-shaped notch. Specimens ranging from 4.1 to 4.9 cm in length show a prominent "V" or a slit. Resorption may be quite irregular; in many specimens, neither the apical area nor the slit is smooth. The longest slit observed was approximately 2.8 cm long on a shell 5.0 cm long; the slit has an average width of 0.6 mm. In this group of 20 specimens, of the 9 specimens that have slits, 2 have the slit ventral, 3 have it on the lower right lateral, and 4 on the lower left lateral.

A similar sequence and some individual variation among apical slits were found by Yancy (1973) in Permian *Prodentalium*. The large amount of individual variation in a modern species should be noted, for obviously one should not place much reliance on features of the slit in attempting to differentiate fossil species.

The incipient "V" found at the apex of some specimens is different in inclination and in shape from a boring that lies on a line of fracture and now forms a half circle (pl. 3, fig. 1). One should be wary of confusing this feature with true apical characters of a scaphopod. In addition to the difference in shape, these "half holes" occur where the shell is far thicker than at the apical area.

Few complete specimens of *D. (Dentalium) obscurum* are available, and these had a smaller average size than the sample of *D. (Dentalium) laqueatum*. However, we did observe a slit 2.7 mm long in a shell 4.9 cm long. With regard to variation in rib number in this species: of the 29 specimens, 12 have 9 ribs; 1 has 2 intercalated ribs among 9; 11 have 10 ribs; 3 have 1 intercalated rib among 10; and 2 have more than 10 ribs.

DISTRIBUTION OF BORINGS IN FOSSIL AND PRESENT-DAY SCAPHOPODS OF EASTERN NORTH AMERICA

To determine whether predation on scaphopods by naticid gastropods is a newly developed (Holocene) habit, we surveyed Cretaceous to Holocene collections, limiting our examination to those collections containing a large number of specimens. We have seen no evidence of predation on North American Paleozoic scaphopods. We have not studied any American Triassic or Jurassic samples; a few Triassic scaphopods from Austria and Italy examined by Yochelson in 1975 at the Naturhistorisches Museum, Vienna, did not show any borings.

Examination of about 75 scaphopods in the Mesozoic biological collection of the National Museum of Natural

History, Washington, D.C., did not show any evidence of predation. In the stratigraphic collections, borings in scaphopods were observed in the Ripley Formation (Cretaceous) fauna. About 5 percent of the specimens of *Cadulus obnustus* (Conrad) at Coon Creek, Tenn., were bored, but the much larger *Dentalium intercalatus* (Wade) from this same locality does not show predation. A variety of pelecypods and gastropods from Coon Creek were also bored. In a collection from the Ripley Formation, 2.6 miles below Eufaula, Ga. (USGS 28433), we did find 14 out of 105 specimens of *Cadulus* bored, and borings in 4 out of 71 of a finely ribbed species of *Dentalium*. Many of these *Dentalium* species are broken, and the percentage of predation may be slightly higher.

The biological collection of Cenozoic scaphopods at the National Museum of Natural History contains about 1,200 specimens. In 300 specimens from the Vicksburg Formation or Group, Oligocene, at several localities, *D. (Dentalium) mississippiensis* (Conrad), a moderately coarse ribbed species, showed 5–15 percent predation. Scattered smaller collections, totaling about 400 specimens, from a variety of localities in the Miocene of North Carolina and Virginia show a low percentage of predation. The only Miocene species significantly preyed upon were *D. (Dentalium) carolinense* (Conrad) and *D. (Dentalium) attenuatum* (Say), both coarse-ribbed species. We estimate that 3 percent of the approximately 400 shells were bored, although as many as 25 percent of the specimens in an individual collection of these two species showed boreholes. In addition, 1,500 scaphopods in the stratigraphic collections from the Claiborne Group, Eocene, of Alabama were surveyed, but only one borehole was seen.

Part of the Holocene biological collection at the National Museum of Natural History was surveyed. Approximately 3,700 individuals were examined in some detail. In general, boreholes were limited to a very small percentage of the specimens. However, a few species did show abundant evidence of predation. Collections of *D. (Dentalium) laqueatum*, regardless of their geographical location or depth, commonly show predation. Similarly, *D. (Dentalium) taphrium* Dall showed high levels of predation (almost 30 percent) at Cape Lookout, N.C. Collections from areas off Florida showed more moderate levels of predation. *D. (Dentalium) ceratum* Henderson, found in generally deeper water, and *D. (Dentalium) striolatum* (Simpson), found in more northern locations and in very deep water, both showed still lower levels of predation, affecting about 10 percent of the specimens. All four species are coarse ribbed.

In 1978, Yochelson examined the collections of fossil scaphopods at the British Museum (Natural History) through the good offices of C. P. Palmer. He saw no

evidence of borings in Paleozoic or Mesozoic specimens. The oldest boring observed in British scaphopods is in *Entaliopsis brevis* (Deshayes) from the *Corbula* bed of the Thanet Sands, Paleocene, at Bishopstone along the Thames Estuary west of Margate, Kent, in southeastern England. Finally, Yochelson in 1978 requested June Chatfield, curator of marine invertebrates, to search the collections of Holocene scaphopods at the National Museum of Wales, Cardiff, for borings in scaphopods. She confirmed that predation by boring was pervasive but was at a very low level, except in coarse-ribbed species.

IDENTITY OF THE PREDATOR

The identity of the predator on 50 percent of the *Dentalium* in the Mississippi "mud lumps" is a matter of interest. Although various organisms bore for a variety of reasons, we are convinced that these holes result from predation. Furthermore, we are satisfied that they were made by either a muricid or a naticid gastropod. 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 (ABO) that secretes a softening agent onto the shell. In both groups the ABO is critical, for when it is removed, the animal cannot bore (Carriker and Van Zandt, 1972a). The naticid ABO is placed mostly within the borehole. In contrast, the ABO of *Urosalpinx* and its relatives extends in a narrow area surrounding the hole (Carriker, 1969), and part of this chemically weakened area is then scraped off by the radula. As a consequence, the muricid hole is gently beveled, that is, inclined, on its upper slopes (Carriker, 1961), whereas the naticid boring is not.

Carriker (written commun., 1979) noted that the naticid ABO possesses a ring of mucous-secreting cells around the periphery of the gland, which might restrict the area of shell etching by ABO fluids. The holes in the scaphopods of the "mud-lump" fauna are steeply sloping, and the inner part of the hole has curved bowl-shaped walls. Muricid gastropods commonly leave a shelf at the base of the hole once the radula has finally penetrated the shell (Carriker, 1970), whereas the 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.

Naticid holes commonly are nearly circular. Carriker and Van Zandt (1972b) did find a very slight degree of ovalness in muricid holes, the long axis of the hole being aligned parallel with the long axis of the foot of the predator. However, unless one looks with extreme care, both naticid and muricid holes would be

categorized as "circular"; they appear drilled in the sense of a circular shaft penetrating the shell. The holes that we have investigated in the *Dentalium* shells are distinctly oval and are more strongly oval on the interior than on the exterior shell surface. Perhaps the uniform crosslamellar shell structure affects the direction of penetration. If so, we would expect to see a difference between the shape of boreholes on shells of pelecypods and gastropods that have thick crosslamellar structure and those that do not. Such a difference has never been reported, and we see no evidence of it in the borings in other mollusks of the "mud-lump" fauna.

The simplest explanation for the oval shape is geometric. On most gastropod and pelecypod prey, the surface that is bored is essentially uniformly curved in all directions; thus, the ABO and radula are acting on a sphere. In contrast, the logarithmic curvature of the scaphopod shell is slight. In the longitudinal direction of a boring there is virtually no change in curvature; thus, the drilling is into a cylinder. Because the odontophore and radula in the mouth of the snail are not circular organs, they sweep laterally to approximate a circular shape. This would be more difficult and probably less efficient in penetrating the cylinder. The longitudinal ribs may also affect the shape of the hole, but their effect is more likely to be secondary. The area between them is flattened, and the ABO can be positioned easily. When a hole does impinge upon a rib, the margin of the hole immediately adjacent to the rib is very little affected.

The physical relationship of prey to predator is not obvious, for no one has observed a scaphopod being bored. Because the long axis of the drill hole is aligned 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. We speculate that the prey commonly attacked the scaphopod when it was in its life position; that is, with the apex slightly above the mud and the aperture and most of the tube below the substrate. The concave side of the tube is dorsal.

We examined the apical area of the scaphopods in hopes of finding some staining or epizoan growth that might give data on life position; Tenery and Rowett (1979) have noted the presence of epizoans on the ventral apical area of a giant Pennsylvanian scaphopod. Unfortunately, we have found no features to suggest how deeply the aperture might have been buried. Nevertheless, from what is known of the life habits of living scaphopods, most of the shell must have been below the sediment-water interface; we 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, p. 51), 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. The position of the boring relative to the within-sediment position of the scaphopod is nearly as strong support of naticid predation as is the morphology of the hole. In this connection, it is interesting to note that the gastropod *Turritella*, many species of which live as part of the shallow infauna, also shows a high frequency of predation at the "mud lumps."

Four naticid species are known from the "mud lumps." The number of specimens and height of largest specimens in the Tulane collection is: *Neverita duplicata* (Say), 7 specimens, largest, 25 mm; *Natica marochiensis* (Gmelin), 55, largest, 15 mm; *N. menkeana* Philippi, 77, largest, 9 mm; and *N. canrena* (Linnaeus), 33, largest, 26 mm. None of the holes examined show morphologic differences. Either one species was responsible for all predation, or, more likely, all four presumed predators produced a borehole having essentially the same morphology. The larger borings seen in the *Dentalium* shells could have been the work of *Neverita duplicata* and *Natica canrena*, the larger predators in the fauna, but apart from this, possible predator cannot be related to prey. Each species could have its own unique way of attacking *Dentalium* and thus its preferred position for boring. Perhaps some of the scatter in circumferential position of the borings is due to the preference of one species of predator for boring ventrally. During ontogeny, the predator could also have changed its preferred position for drilling, though this seems unlikely.

SELECTION OF PREDATION SITE

Although borings may occur anywhere along the shell circumference, the dorsal side is preferred. The more significant preference seems to be laterodorsal about interspaces 2, 3, and 6, 7, of *D. (Dentalium) laqueatum*; this same polarity seems to occur in all rib-number variants of the species. In this position, part, if not most, of the shell of the predator gastropod would be near or above the sediment-water interface. More borings also are found on the observer's right side of the aperture. Although the shell of the naticid would not be likely to come in contact with the scaphopod tube, 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 tube, whereas 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. We have been unable to find any accounts of relationship of hole geometry to borehole position. The mechanics of naticid boring (Zeigelmeier, 1954; Fretter and Graham, 1962, p. 243-250) suggest that the anteriorward slope of the hole should be steeper. In general, the shape and movement of the odontophore (Carriker and Van Zandt, 1972b) should promote some slight asymmetry of the hole, regardless of the geometry of the prey shell. Allowing for this, the asymmetry of the hole would suggest that the predator crawled along the tube toward the apex.

In the present sea bottoms, naticids seemingly manipulate the valves of pelecypods to a preferred orientation before boring; observation is greatly hampered by the infaunal habit of the gastropods, and most of the information on life activities is anecdotal. If the predator is strong enough to move the prey, there need not be any correlation between life position of the prey and position of the borehole. One would expect that the long narrow tube of the scaphopod would be more difficult to manipulate in the sediment than a more globose pelecypod shell. Thus, the correlation between the borehole position and life position for scaphopods may be stronger than it is for pelecypods.

Most of the borings are dorsal, as might be expected. However, some borings are found in the ventral quadrant. We have noted that the holes in the ventral area have a smaller average size than those in the dorsal area. One would expect that a small predator, which could not manipulate the shell, might find it more difficult to bore upward from the ventral side. However, if specimens were exposed during a storm, they would be more subject to predation, particularly by small animals that could not travel quite so readily through sediment. The large number of broken shells and some worn fragments at the "mud lumps" suggest that from time to time the bottom may have been stirred by strong waves or currents.

A more speculative point is the relationship of prey size to borehole size. The mechanics of naticid predation have not been as exhaustively studied as have those of the commercially significant muricids (Carriker and Van Zandt, 1972b). Among the muricids, the larger the snail, the larger the prey, and the larger the animal overall, the larger its ABO (Carriker and Van Zandt, 1972a). Presumably, larger naticids bore larger holes than smaller ones. In general, the diameter of the

scaphopod where bored is related to the size of the hole and hence perhaps to the size of the foot of the prey. This relationship is irrespective of the total length of the prey. We infer that the naticid crawled along the scaphopod tube until it reached a point where the foot was conveniently situated, possibly extending part way around the circumference.

The number of individuals bored among scaphopods less than 20 mm long is significantly less than that among larger individuals. The smaller predatory gastropods probably preferred the small infaunal bivalves, which constitute the largest molluscan element of the "mud-lump" fauna, to small scaphopods. Several small-sized bivalve species common in the "mud lumps" have a high percentage of their valves bored. The low percentage of *Cadulus* specimens bored may be a result of the small size of this genus.

The longitudinal position of the borehole shows a much stronger locational preference by the predator than does the radial position. The position of borings averages nearly 45 percent of the distance between apex and aperture in the Washington collection and 54 percent in the Tulane collection. We suggest that this positioning is closely related to the anatomy of the scaphopod. That 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, 1964a; Trueman, 1968). The wiping of the captacula on the infolded edge of the mantle is further evidence that the mantle edge is not attached near the aperture. We do not know of any anatomic studies of *D. (Dentalium) laqueatum*, but the anatomy of *D. entalis* Linnaeus, studied by Morton (1959), may be representative of the group. Morton has indicated that most of the organs are in the middle third of the tube. The apical area is lined with mantle tissue, but other organs are not present.

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. 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. 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.

A few studies have been made of the position of naticid borings on prey, the latest being that by Berg

(1976). Geometry of the prey is often cited as having an influence on selection of the drilling site. Because scaphopod shells of varying size show little variation in the position of the hole, we conclude that the longitudinal position of the boring is related to the presence of soft parts. If the boring were related to the geometry of the shell, the radial position of the hole would be as constant as the longitudinal position. Because there is such a close relationship of the borings to the position of the organs inside the tube, we speculate that somehow the predator can sense, perhaps by slight vibration of the shell caused by retraction of the mantle, movement of the enclosed soft parts and that it can thus locate a suitable site for drilling. This speculation should be tested with other naticid prey, as Berg (1975, p. 421) suggested that "internal anatomy seems less important in determining borehole position."

OTHER CONSIDERATIONS

Examination of part of the collection of present-day scaphopods in the National Museum of Natural History, Washington, D.C., shows that predation is not distributed at random. Occasional specimens may be bored, but the predation rate is seldom higher than 1 percent. However, collections of recent *D. (Dentalium) laqueatum* show a high degree of predation, which at some localities approximates that found in the "mud lumps." We have found a good likelihood of a moderate to high degree of predation in a sample consisting of coarsely ribbed species. In contrast, smooth or very finely ribbed forms are almost never bored. Louie Marinovich (oral commun., 1978) has provided a striking example of another possible relationship. He has noted that nearly 50 percent of Pleistocene *D. neo-hexagonum* Pilsbry and Sharp at San Pedro, Calif., are bored. The sediment in which this six-ribbed species occurs is relatively coarse sand; judging from the literature, it is similar to the shell pavement seen in the "mud lumps."

We know of no studies of the relationship of ribbing in scaphopods to sediment size. Future studies might show a relationship between the coarsely ribbed taxa and a slightly coarser than normal sediment, relative to the finely ribbed or smooth form. A smooth tube should be best suited for penetration into sticky fine-grained sediment, whereas the external flanges of a strongly ribbed tube would aid in the penetration and anchoring of the scaphopod on a coarser grained, less well sorted sediment. Depth information is given with collections of modern scaphopods, but data are lacking regarding sediment size where such scaphopods have been dredged. The occurrence of naticid gastropods is at least related in part to sediment size of the substrate, as these

predators cannot move through sticky sediments. Boreholes may form a crude "tracer" for patches of coarse-grained sediment. If so, an abundance of borings at an outcrop could give some data on the original size composition of the sediment.

In a review of predation by gastropods through time, Sohl (1969, p. 725) noted that bored tests are known in "such diverse groups as the Foraminifera, Brachiopoda, Gastropoda, Pelecypoda, spirorbid polychaetes, echinoids, and ostracodes." To the best of our knowledge, the only report of gastropod predation on scaphopods was a brief mention of a single specimen from 283 fathoms that contained a naticid boring (Fankboner, 1970). This study documents that at some localities scaphopods may form a food resource and may indeed be subjected to significant predation by naticid gastropods.

The survey of fossil scaphopods indicates that they are not a newly acquired prey of naticids. We have not considered *Cadulus* and other members of the Siphonodentalidae in any detail in part because the small size of the individuals makes them more difficult to examine. Possibly in the Cretaceous, where we have observed a few bored *Cadulus*, this form was attacked because it is in the same general small size range as ostracodes, which also were bored.

Morphologic change within the Scaphopoda is not well known, but Paleozoic forms are all smooth or finely ribbed. Early Mesozoic forms are even less well known, but coarse-ribbed scaphopods do occur in the Cretaceous at about the same time that boring naticid gastropods appeared (Sohl, 1969). There is no obvious coevolution between prey and predator. One might think that, in the face of predation, the adaptation of relatively few coarse ribs would have died out rather than persisting. It may be worthwhile to examine the Mesozoic and Cenozoic record of the class from the standpoint of functional morphology to see when the coarse-ribbed forms first appeared and whether they have diversified through time.

One may summarize by noting that this study, like so many other scientific inquiries, answers certain questions but poses more interesting ones.

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PLATES 1-4

Contact photographs of the plates in this report are available, at cost, from the U.S. Geological Survey Library, Federal Center, Denver, CO 80225.

PLATE 1

Figures 1–4. General views of *D. (Dentalium)*.

1. Dorsal-side view of a seven-sided variant of *D. (Dentalium) laqueatum* Verrill, 4.5 cm in chord length; the borehole has a maximum length of 4.9 mm. × 5, USNM 780591a.
2. Left-side view of a six-sided variant, *D. (Dentalium) laqueatum* Verrill, that has a seventh intercalated rib, shown to the left appearing some distance below the broken apical area. × 5, USNM 780591b.
3. Left-side view of *D. (Dentalium) obscurum* Dall, a nine-sided variant, 3.1 cm in chord length; the borehole has a maximum length of 5.8 mm. × 5, USNM 780952a.
4. Part of a six-sided variant, *D. (Dentalium) laqueatum*, 4.5 cm in chord length, showing a complete boring, an incomplete boring, and, to the left, some damage by a boring sponge. × 15, USNM 780591c.

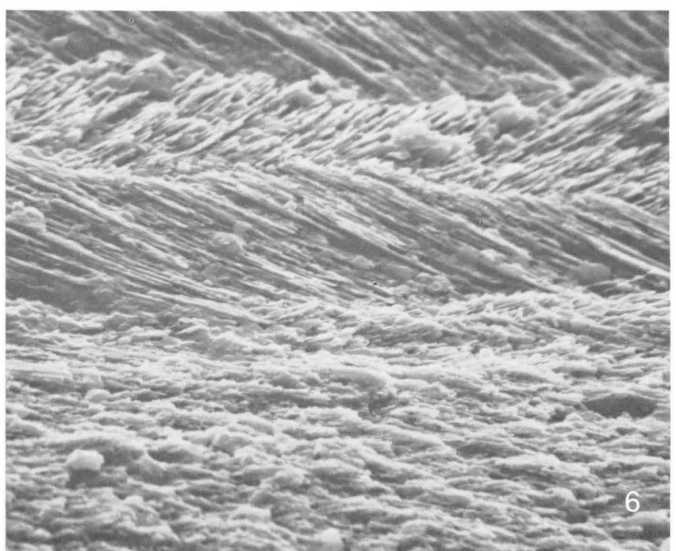
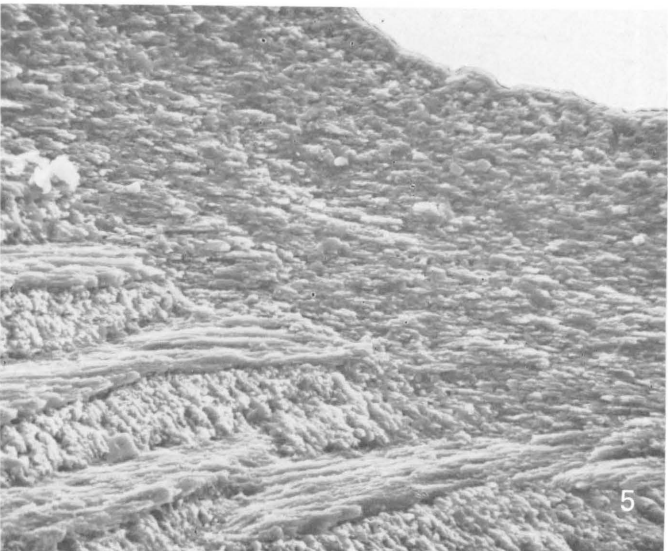
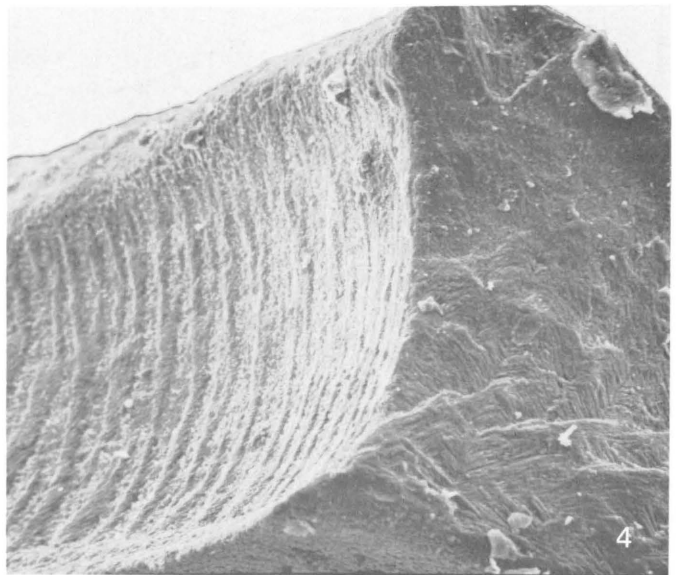
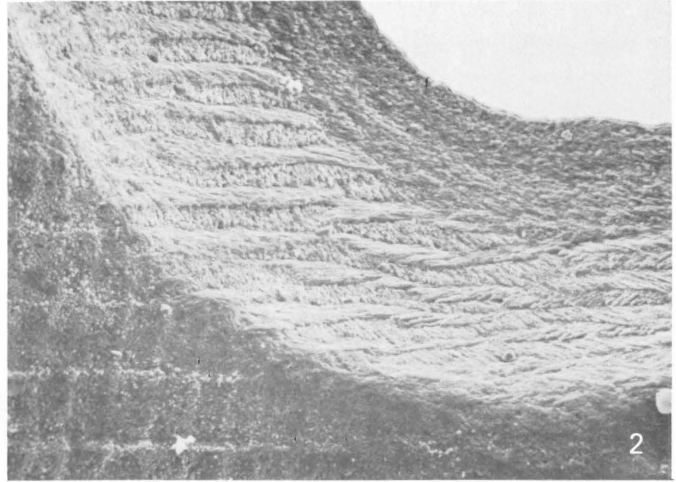
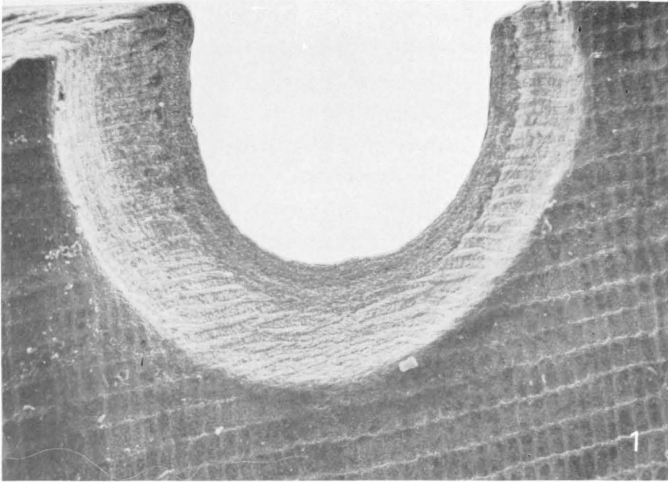


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PLATE 2

Figures 1-6. Scanning electron microscope photographs of a boring in a six-sided variant of *D. (Dentalium) laqueatum* Verrill, USNM 780591d.

1. Vertical view of "half hole" specimen, broken at the point of drilling. × 60.
2. Vertical view of the boring, showing the fine reticulate surface ornament extending to the margin of the boring without any etched zone. × 150.
3. Enlargement of the upper surface seen in figure 2, showing the relationship of crosslamellar structure to the ornament and emphasizing the lack of an etched zone. × 270.
4. Slightly oblique view, showing the steep but gently concave curved wall of the boring. × 150.
5. Detail at the inner margin of the boring. × 400.
6. Detail of shell structure of the fracture surface at the juncture of outer and inner shell layers shown in figure 4. × 1000.

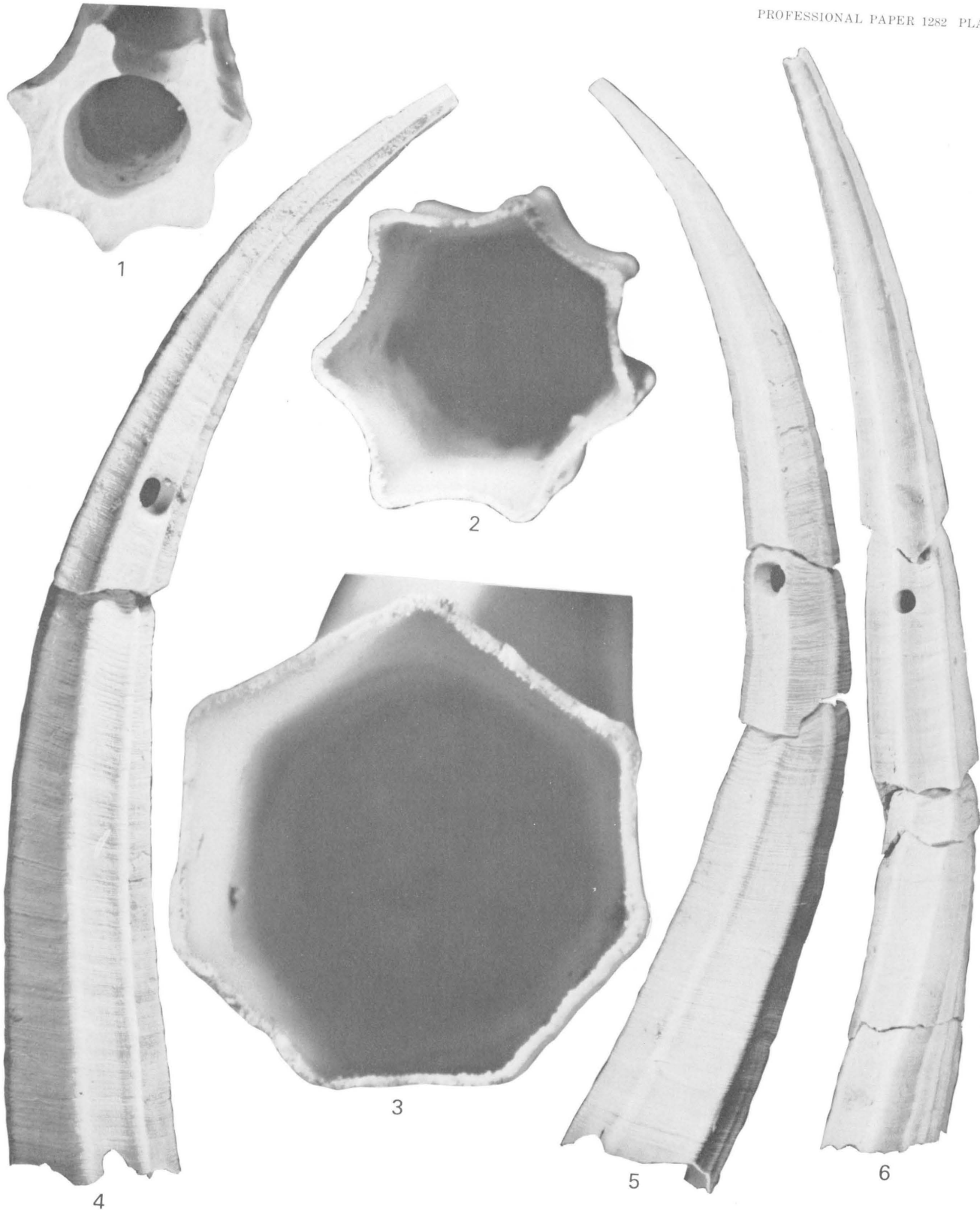


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PLATE 3

Figures 1-6. Broken and repaired shells and apertural views of *D. (Dentalium) laqueatum* Verrill.

1. A "half hole" between two ribs of a seven-sided variant. × 15, USNM 780591e.
2. Apertural view of a seven-sided variant broken at the apex; compare with the thickened ribs shown in figure 1. × 15, USNM 780591f.
3. Apertural view of a large seven-sided variant with reduced ribs, 4.9 cm in chord length. × 15, USNM 780591g.
4. Left-side view of a seven-sided variant, with a single break, 3.7 cm in chord length. × 5, USNM 780591h.
5. Right-side view of seven-sided variant with two breaks, 3.2 cm in chord length. × 5, USNM 780591i.
6. Slightly oblique ventral view of a seven-sided variant with four breaks, 5.0 cm in chord length; this is the only specimen that deviates from logarithmic curvature. × 5, USNM 780591j.



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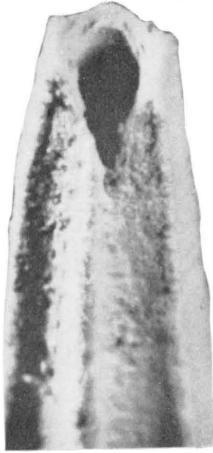
PLATE 4

Figures 1–3. Ontogenetic change in the apex of *D. (Dentalium) laqueatum* Verrill. All specimens $\times 15$.

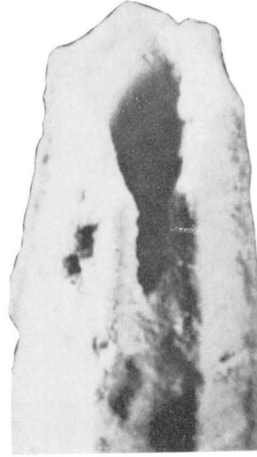
1. A small keyhole in a seven-sided variant, 3.6 cm in chord length; USNM 780591k.
2. A V-shaped reentrant in a six-sided variant, 5.1 cm in chord length; USNM 780591l.
3. A prominent slit in a six-sided variant, 5.3 cm in chord length; USNM 780591m.



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