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By MELBOURNE R. CARRIKER *and* ELLIS L. YOCHELSON

CONTRIBUTIONS TO PALEONTOLOGY

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Comparative morphology of specialized borings and their significance in the early fossil record

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RECENT GASTROPOD BOREHOLES AND ORDOVICIAN CYLINDRICAL BORINGS

By Melbourne R. Carriker[1] and Ellis L. Yochelson

ABSTRACT

A comparative study of Recent predatory gastropod boreholes and a review of gastropod boring activity shows that shell penetration has certain characteristics, in part due to morphology of boring organisms, in part due to boring behavior of the predators, and in part due to structure of the prey shell. These points are considered briefly. Recent gastropod boreholes exhibit a broad spectrum of geometric form and size, but are distinctive in a statistical populational sense in possessing smooth walls, beveled outer edges, decreasing diameters with depth, and a general circularity and perpendicularity. To clarify the geometry of the holes, terminology is introduced.

Cylindrically bored late Middle Ordovician brachiopods occur in collections from Ontario and Kentucky. The specimens from Kentucky provide new paleoecologic data on relative abundance of boring. One boring from the Pratt Ferry Formation of Cooper in Alabama and one from the Benbolt Formation of Cooper and Prouty in Virginia are also noted; these are the earliest reported borings of this kind (Porterfield Stage). All Middle Ordovician borings are new occurrences and all are similar to younger Paleozoic borings ascribed by previous workers to carnivorous gastropod attacks. Late Ordovician holes attributed to gastropods also have been reexamined.

The Middle Ordovician borings show many of the features of Recent gastropod borings but seem to differ from Recent holes in being bored at an oblique angle to the shell surface and in being irregularly chamfered rather than truly tapered. Ordovician borings appear to be exceedingly rare. There is no obvious relationship between these borings and any particular fossil gastropod.

The Ordovician holes need not have resulted from gastropod predation, for the physical evidence is equivocable. Several intrinsic features argue against such an early development of gastropod predation. As an alternative, it is suggested that these holes may be the result of activity of unknown and extinct soft-bodied organisms attaching to shells.

INTRODUCTION

The habit of boring by Recent carnivorous gastropods makes possible a complex mode of existence. Shells of the two most common genera of living borers or those of closely allied genera can be traced, with a high degree of confidence as to their phyletic relations, from the Recent into strata of Cretaceous age for the Muricidae and Jurassic for the Naticidae. Borings virtually identical with those made by modern borers are scattered but widespread in Tertiary and some Cretaceous faunules, along with representatives of these two families. Both typical muricid and naticid types of borings are known, and it is most reasonable to assume that gastropods were responsible for the holes; it is not germane to this particular problem to document the numerous occurrences of Cenozoic and Mesozoic borings. The Muricidae and Naticidae are unknown from strata of Triassic age, and presumably had not evolved prior to the Mesozoic.

Paleozoic shells that have cylindrical borings have been reported, the boring commonly being attributed to gastropod predation. If this interpretation is correct, it may be concluded that the peculiar specialized carnivorous habit evolved one or more times in the Paleozoic and completely independently of the Mesozoic to Recent predators. Further, this specialized method of feeding, if it is correctly ascribed to independently evolving gastropod stocks, becomes an interesting problem in evolution and paleoethology. This paper is concerned with Ordovician borings, both those reported in the literature and new material, and seeks to interpret the possible origin of the borings in the light of a comparative study of modern boreholes drilled by carnivorous gastropods. In the past two decades, knowledge of living predatory gastropods has increased significantly, and it is appropriate to reevaluate earlier statements as to the character of presumed early Paleozoic gastropod boreholes.

ACKNOWLEDGMENTS

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Zandt also photographed the modern boreholes illustrated in this paper. Live boring snails were airmailed to the senior author's laboratory: from England by D. A. Hancock, A. E. Urquhart, and D. P. Wilson; from eastern Canada by Neil Bourne; from Bimini, Bahamas, by Langley Wood; from Puerto Rico by Juan A. Rivero; from Japan by Akimitsu Koganezawa; from Korea by Yongbok Cho; from eastern Australia by D. F. McMichael; and in the United States from Washington by Cedric E. Lindsey and from Virginia by Michael Castagna. In addition, J. W. Blake, L. Wood, and the senior author collected live boring snails along the east coast of the United States from Massachusetts to Florida and on the west coast of Florida in the Gulf of Mexico. William J. Clench and Ruth D. Turner of the Museum of Comparative Zoology at Harvard University checked identification of species.

Study of early Paleozoic boreholes was also aided by many persons. Dr. G. Winston Sinclair, Geological Survey of Canada, generously made available specimens and unpublished observations of boreholes in Middle Ordovician brachiopods. Dr. K. E. Caster, University of Cincinnati, Cincinnati, Ohio, lent figured Late Ordovician specimens for examination and Dr. E. P. Eller, Carnegie Museum, Pittsburgh, Pa., lent Devonian and Ordovician figured material. Mr. Harvey Hambleton, Buffalo Science Museum, lent Devonian figured material.

Middle Ordovician fossils from Kentucky were collected with the assistance of D. F. B. Black, E. Cressman, J. Pomeroy, D. Wolcott, and J. Pojeta, Jr., U.S. Geological Survey, as part of a cooperative mapping project with the Kentucky Geological Survey. The Kentucky material was prepared jointly by Pojeta and Yochelson. Robert B. Neuman, U.S. Geological Survey, identified the brachiopods, and John Pojeta contributed data on distribution of pelecypods. Robert McKinney photographed the fossils illustrated in this paper.

TERMINOLOGY

To describe properly the geometry of Recent and fossil holes examined in this study, it has been necessary to define the range of representative shapes and of surfaces of these penetrations. The colloquial terms "bevel," "taper," "countersunk," and general descriptive adjectives employed in the earlier literature (Fischer, 1922; Bucher, 1938; Ziegelmeier, 1954; Carriker, 1955; Pilson and Taylor, 1961; Fretter and Graham, 1962; Carriker and others, 1963) have not been sufficiently precise to indicate the details of geometry. The most frequently employed words, "beveled" and "countersunk," are more or less synonymous; it is useful to treat them so in this paper and to restrict their application to a general description of the edge of the outer opening of a borehole.

Obviously, only living gastropods can be observed in the act of drilling. It is appropriate to emphasize that assignment of any fossil hole to the action of gastropod predation is probabilistic; for each occurrence one must evaluate this probability. Accordingly, a **gastropod borehole** is defined as an excavation of characteristic size and form drilled by a predatory snail in the calcareous exoskeleton of a prey organism by means of chemical weakening and radular abrasion of the prey shell for the purpose of obtaining food. The following additional definitions are used in this paper:

Axis, hypothetical central line of a cylindrical or conical-parabolic hole; in most holes this is a straight line, and in most gastropod boreholes, this is perpendicular to the shell surface.

Bossed bottom, center of bottom elevated in the form of a rounded protuberance or boss in an incomplete hole (fig. 2*I*); characteristic of naticid gastropod boreholes.

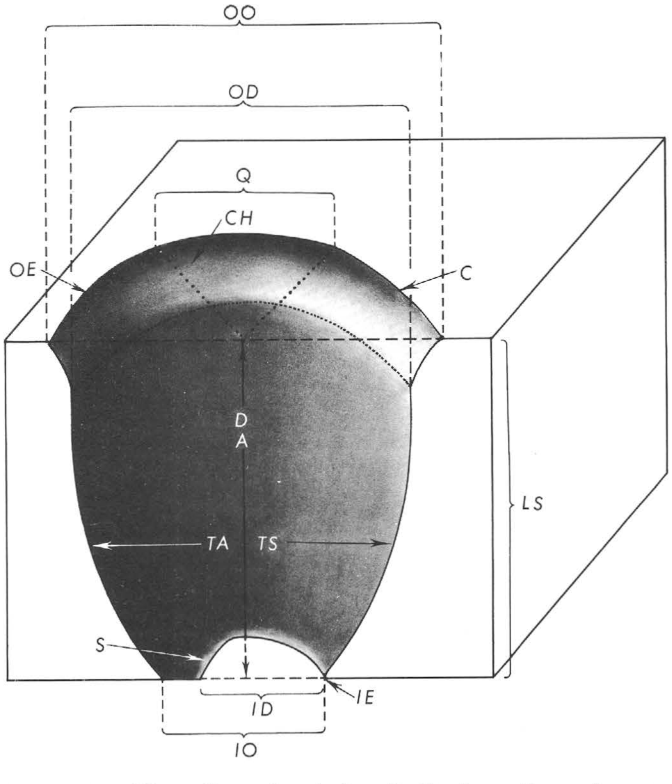

FIGURE 1.—Three-dimensional longitudinal section of parabolic countersunk hole to illustrate parts: A, axis; C, circumference; D, depth; CH, chamfer (the taper in one quadrant); ID, inner diameter; IE, inner edge (one-half removed); IO, inner opening (one-half removed); LS, longitudinal section; OD, outer diameter; OE, outer edge (one-half removed); OO, outer opening; Q, quadrant; S, shelf; TA, transverse axis; TS, transverse section.

Chamfer, an inclined surface through one quadrant of the edge of a hole; an incomplete "bevel." In a thick shell, the chamfer forms an angulation with the inner wall of the hole, but in a thin shell the chamfered surface may extend downward to the inner circumference.

Circumference, perimeter of a hole. This may be: circular in horizontal section giving rise to a cylindrical, conical, or parabolic form; oval, resulting in elliptical forms; or irregular, producing an anomalous form of holes (fig. 1).

Concave bottom, bowl-shaped bottom in an incomplete hole (fig. 2*H*); characteristic of muricid gastropod boreholes.

Conical hole, inner surfaces more or less straight in longitudinal section and inclined medially and symmetrically toward the inner opening of the hole. The overall form of the hole approximates that of a **truncated circular cone** if transverse sections are circular and the axis is vertical (fig. 2*B*) or a **truncated elliptical cone** if transverse sections are elliptical and the axis is inclined.

Countersunk, edge (synonymous with "beveled" and "tapered") a more or less uniform funnel-shaped enlargement of the outer opening of the borehole (fig. 1); this is an essentially uniform chamfer in all quadrants.

Cylindrical hole, inner surfaces more or less parallel in vertical section; general form of the hole approximates that of a cylinder (fig. *2A*).

Depth of hole, thickness of shell drilled; when the axis is vertical, depth and length of axis are equal (fig. 1).

Diameter, outer, inner, maximum linear distance across the center of the outer and inner openings of a hole, respectively (fig. 1).

Edge, circumference of hole and adjacent area modified by boring activity.

Flat bottom, relatively even and level bottom in an incomplete hole (fig. *2G*).

Inflated hole, enlargement of the diameter of parts of hole between the inner and outer openings.

Longitudinal section, a plane bisecting a borehole in any direction through the axis (fig. 1).

Oblique conical hole, a conical hole in which the axis is inclined to the outer shell surface (fig. *2E*).

Oblique cylindrical hole, a cylindrical hole in which the axis is inclined to the outer shell surface (fig. *2D*).

Oblique parabolic hole, a bowl-shaped hole in which the axis is curved and is inclined to the outer shell surface (fig. *2F*).

Opening, outer, the site at which perforation is begun, generally on the exterior of the exoskeleton of the prey; **inner,** the last part of the hole to be bored, generally on the inside of the exoskeleton and adjacent to the soft tissues of the prey (fig. 1).

Parabolic hole, inner surfaces concave or bowl-shaped in vertical section. The overall form of the hole approximates a **truncated spherical paraboloid** if horizontal sections are circular, or a **truncated elliptical paraboloid** if horizontal sections are elliptical (fig. *2C*).

Quadrant, approximately one-fourth of the circumference of a hole (fig. 1).

Sharp edge, edge of outer opening of hole not noticeably countersunk and approximating a right angle in cylindrical holes and an acute or obtuse angle in oblique holes.

Shelf, a ledge of shell material bounding and restricting the inner opening of a hole (fig. 1).

Transverse axis, any line throughout the depth of the hole parallel to the outer shell surface (fig. 1).

Transverse section, a section in the hole at any level parallel to the surface drilled and to a transverse axis (fig. 1).

RECENT GASTROPOD BORERS AND BOREHOLES

PREVIOUS LITERATURE

Several different sorts of etchings and borings occur in both Recent and fossil shells, but the result of gastropod boring is generally distinctive. Recent boring carnivorous gastropods are relatively well known, as several genera of Muricidae in oyster beds (Carriker, 1955; Hancock, 1959) and of Naticidae in clam bottoms (Giglioli, 1949; Sawyer, 1950) are commercially important predators. These two families exemplify separate types of the boring habit that evolved at least twice within the prosobranch Caenogastropoda or Monotocardia (Fretter and Graham, 1962). All muricid and naticid species examined to date are borers (Carriker, 1961). Several have been studied intensively (see review by Fretter and Graham, 1962). Some species in two other monotocardian families, Capulidae (Orr, 1962) and Cymatiidae (Dakin and others, 1952), and one pulmonate family, Oleacinidae (Wächtler, 1927; Degner, 1928) are said to bore holes in mollusks, but nothing is known about their boring mechanism. Typical gastropod boreholes are reported from predation by species of the Capulidae and Cymatiidae. Oleacinid holes are highly irregular jagged patches rasped in the shell; some of these holes are possibly bored to obtain calcium and others to consume the prey within. Boring cymatiids are carnivorous, and boring capulids take food from the food-gathering tracts of drilled ciliary feeding bivalve commensals.

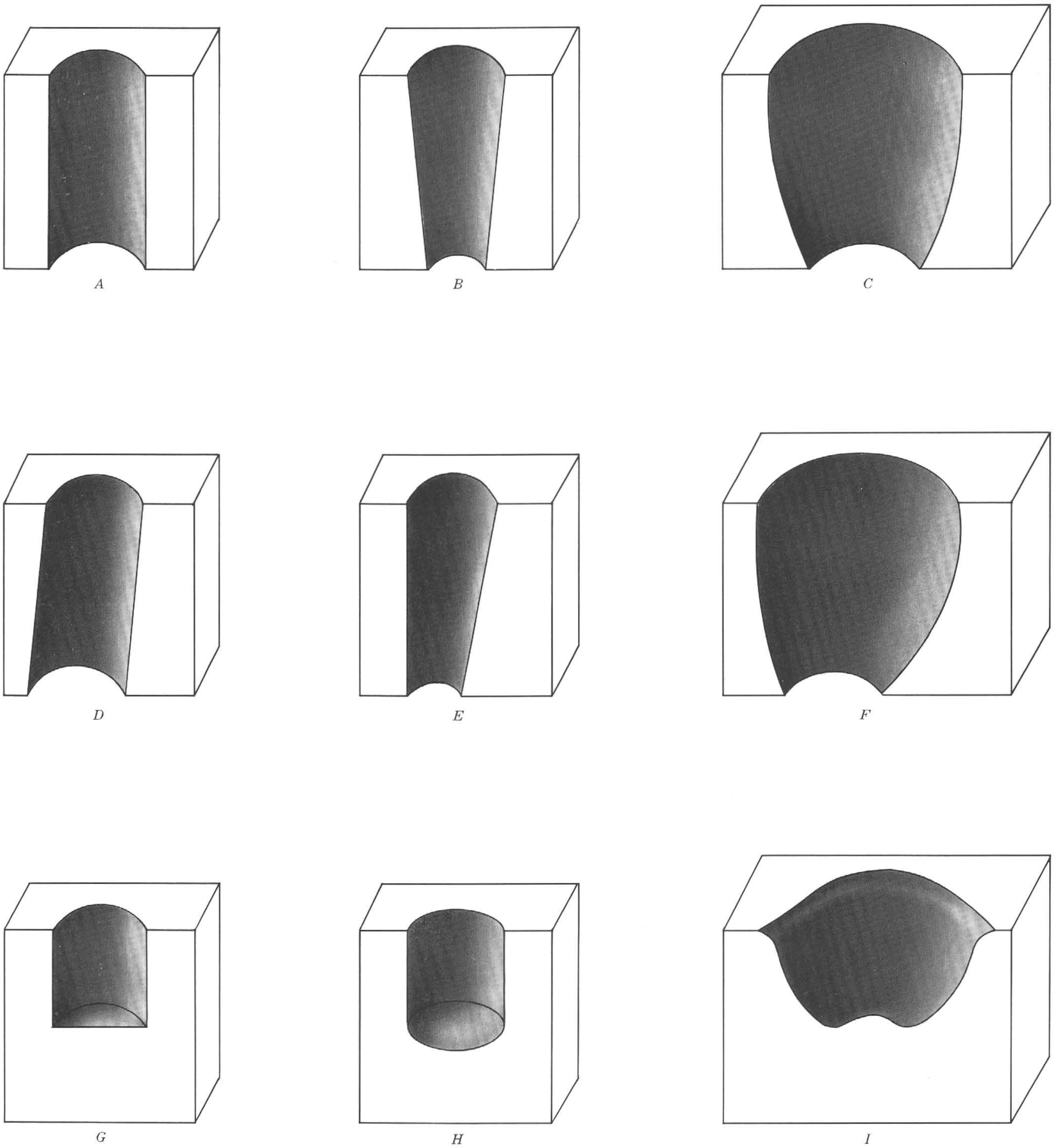

Figure 2.—Three-dimensional longitudinal sections showing idealized forms of holes. *A*, a cylindrical hole (a cylinder); *B*, a conical hole (truncated circular cone); *C*, a parabolic hole (truncated spherical paraboloid); *D*, an oblique cylindrical hole; *E*, an oblique conical hole; *F*, an oblique parabolic hole; *G*, an incomplete flat-bottomed cylindrical hole with sharp outer edge; *H*, an incomplete cylindrical hole with a concave bottom and sharp outer edge; *I*, an incomplete parabolic hole with bossed bottom and slightly countersunk outer edge.

There are conspicuous differences in the morphology of the boring mechanism of muricid and naticid snails (Fretter and Graham, 1962), but the end result of the boring activity is the same, in that a hole is drilled through the calcareous exoskeleton of the prey which permits the gastropod to insert its proboscis within the body of the victim and rasp out the soft parts. Prey of boring gastropods are mainly bivalves and barnacles (Carriker, 1955; Hancock, 1959; Fretter and Graham, 1962); several species of prey may be included in the diet of any one species of predator. Bored ostracodes, both fossil (Reyment, 1963) and Recent (Reyment, 1966), are known; they may have been attacked by immature carnivores.

Gastropod drilling consists of (a) a chemical phase in which an accessory boring organ, or demineralization gland, secretes an acid substance—as yet uncharacterized—which acts on the shell at the site of penetration (Carriker and others, 1963), and (b) a mechanical phase in which the radula rasps off the weakened shell as minute flakes which are swallowed (Carriker, 1961; Fretter and Graham, 1962). Radular teeth alone are ineffectual in removing firm untreated molluscan shell. The snail foot and shell do not rotate about the hole during boring, and the accessory boring organ is extended successively in the same position; only the radula moves freely about the borehole.

Degree of penetration of shell appears to be governed at least in part by the rate and depth to which the accessory boring organ secretion enters and weakens the crystalline shell structure, as shown by radiographs of boreholes (Carriker and others, 1963, figs. 5, 6). Alteration of shell involves differential pitting and intracrystalline dissolution of the inorganic component of shell (Carriker and others, 1963, figs. 25–30). Snails bore holes in calcitic or aragonitic shell of prey with equal facility. Excised accessory boring organs etch pure inorganic calcite and aragonite and human enamel and dentin (hydroxyapatite; Carriker and others, 1963).

The method of boring and, in general, the type of hole differ characteristically in the Muricidae (Carriker, 1943; 1961) and the Naticidae (Ziegelmeier, 1954) so far examined in the laboratory. In muricids, the accessory boring organ, withdrawn snugly within a sac in the midanterior part of the sole of the foot, is everted only in operation; in naticids, it lies under the distal tip of the proboscis that, as in muricids, remains inverted within the cephalic hemocoele of the snail except when exploring, drilling, and feeding. In muricids the accessory boring organ takes the form of a mushroom-shaped papilla, with a long thin-walled stalk; in naticids it is pad shaped and has a very short muscular stalk. In both families, the distal cap of the papilla consists of a tall complex secretory epithelium, strikingly different from other epithelia in the snail body (Fretter and Graham, 1962; Carriker and others, 1963). The secretion is exuded as a thin viscid layer over the epithelial cap, and this layer etches on contact of the cap with the shell. The diameter of this organ slightly exceeds that of the tip of the proboscis and approximates the diameter of the borehole made by it; during boring, it extends fully to the bottom of the hole.

METHODS OF STUDY

The present analysis of modern boreholes is based on a study of holes drilled by individuals of some 25 different species of muricid and naticid gastropods while in the laboratory. These species were obtained from nearly 20 different parts of the world. The details of the comparative morphology of drilling are still under study, and only a general summary is presented here.

Snails were isolated with appropriate live prey in perforated plastic containers. The snails and prey were maintained in high-salinity running sea water until boreholes were drilled. Vertical sections of boreholes were made by first cutting the shell with a small circular diamond saw and then grinding the section down to the borehole on a wet revolving silicon carbide abrasive disc of No. 400 grit. The polished cross sections were examined under a low-power binocular microscope.

RECENT BOREHOLES

Although there seems to be wide diversity among Recent gastropod boreholes, this diversity is in fact limited. When the two families of modern borers are considered separately, the amount of variation within each group is actually rather small.

Muricid snails commonly prey on epifauna and crawl toward them over the surface of the bottom, attracted by their ectocrines (Wells, 1958; Blake, 1960, 1961; Kohn, 1961; Wood, 1965). Though several genera of animals are preyed upon, there is a distinct preference for those living on hard bottom. After mounting the prey, the gastropod explores the shell surface with propodium and proboscis tip (Carriker, 1943). What constitutes a "suitable" drilling site is not known, and the distribution of boreholes on prey valves appears to to be random (Federighi, 1931; Carriker, 1955; Hancock, 1959).

Repeated laboratory observations show that after the animal mounts the prey, it wanders for several minutes to a half hour before choosing a boring site. In the laboratory, a snail in a dense mixed population of living and dead oysters will occasionally bore through a dead shell, from inside out (Carriker, 1955; Hancock, 1959), not able to distinguish clearly the living from the nonliving animals because of the close proximity of the two (pl. 1, figs. 5, 12; pl. 2, fig. 5) and the high concentration of ectocrines in the area.

After the boring site is selected, the snail removes periostracum and loose surface shell crystals at the boring site with the radula. It then commences boring by chemically weakening the shell and rasping it off with the radula. The snail adheres firmly with its foot to the surface of the prey shell and extends its proboscis to the borehole through a fleshy tube formed by overfolding of the anterior part of the foot. As the proboscis is withdrawn and returned to the cephalic hemocoele, the accessory boring organ, held within the foot over the hole, is everted by blood pressure into the partial hole and fills it closely and firmly. The long yielding cylindrical stalk permits extension of the distal secretory cap into the deepest boreholes drilled by these snails (pl. 1, fig. 24). Next, the radula is rotated on its axis as it scrapes, and thus effects roundness in the perforation; it grates principally at the bottom of the hole. This mechanical activity, combined with restriction of the secretory epithelium to the distal cap which contacts the shell mainly at the bottom of the perforation, makes possible the long cylindrical boreholes in thick shells which are diagnostic of muricids and the slightly parabolic holes in thin shells (pl. 1, figs. 9, 22–24; pl. 2, figs. 15, 19, 25). Incomplete holes possess a shallowly concave bottom (pl. 1, figs. 5, 12; pl. 2, fig. 5).

Rate of shell penetration ranges from 0.2 to 0.5 mm per day at summer water temperatures (Carriker, 1955; Fretter and Graham, 1962). Once the inner surface of the shell of the prey has been breached by means of a small aperture, boring is abandoned by some individuals; there is often left a characteristic crescent, circular, kidney-shaped or irregular shelf partly blocking the inner opening of the hole (pl. 1, figs. 5, 7, 10, 11, 16, 17, 20; pl. 2, figs. 20–22). For other individuals, the perforation is complete and results in a perforation with little shelf (pl. 1, figs. 2, 9, 14). There appears to be considerable specific and individual variation among boring snails in the matter of shelf formation, and insufficient observations have been made to determine whether this may be a species specific character. At least a few muricid species, for example *Thais haemastoma floridana* Conrad and *Murex fulvescens* Sowerby, penetrate bivalves at the line of contact of the two valves opposite the hinge (pl. 2, figs. 1, 2, 10). Because of the configuration of the valves along this line, the hole bored in these prey assumes an elliptical parabolic shape (pl. 2, fig. 10).

Naticid snails characteristically travel through clean to slightly muddy sand, both above and below the sediment-water interface; because of the obvious difficulty of moving in them, they avoid sticky, more compacted argillaceous sediments. When infaunal prey is located, also through recognition of their ectocrines (Kohn, 1961), the naticid burrows rapidly to its level, and commonly bores below the sediment-water interface. These gastropods are characterized by an exceptionally large flat foot which facilitates their movement within the sediment and with which they grip their prey tightly. The foot is fully extended and if large enough completely envelops the prey.

In boring, the midanterior region of the propodium retracts deeply, forming a groove into which the proboscis everts and is extended to the shell surface of the prey. During rasping, the proboscis and radula are rotated successively and precisely from one side to the other in such a way that shell weakened by secretion is removed most rapidly from the midradial region, and a characteristic central boss in incomplete holes is left (pl. 2, figs. 6, 8; Ziegelmeier, 1954; Carriker, 1961; Fretter and Graham, 1962). Between rasping periods, the ventral tip of the proboscis is advanced and the accessory boring organ is thus pressed into the incomplete borehole. Because the organ consists of a pad rather closely attached along its circumference to the ventral muscular wall of the proboscis, its secretory cap is extensible to the bottom of deep holes primarily by distension of the central region and not in the manner of that of muricids. This anatomical trait and distinctive manner of rasping account for the typical shallow spherical parabolic naticid borehole (pl. 3, figs. 4, 5).

Positions for boring among naticids seem to be related to the manner in which the prey is grasped, and holes thus are usually limited to a small area of prey valves when a population of borings is studied (Reyment, 1966). Limitations on grasping may also explain why one prey valve is bored more frequently than the other (Fretter and Graham, 1962). Boring rate for one species of naticid is given by Ziegelmeier (1954) as 0.6 mm per day.

Many ecological, physiological, and genetic questions still surround the problem of prey selection and thus of borehole formation by boring predatory gastropods. In addition to relative access and abundance of prey, there are such factors as the preference of the predator for certain prey species and attractiveness of early ontogenetic stages (Carriker, 1955; Wood, 1965). *Urosalpinx cinerea cinerea* (Say), for example, displays a preference for barnacles along the east coast of the United States, but as these prey species decrease in availability, it goes readily to oysters (*Crassostrea virginica*) and to edible mussels (*Mytilus edulis*) (Wood, 1965). In the laboratory of the senior author, *U. c. follyensis* Baker thrives on the unlikely diet of soft clams (*Mya arenaria*) left exposed out of sediment in their tanks, yet seldom drills *Anomia simplex*. Reasons for the immunity of this bivalve are unknown. *Murex fulvescens* Sowerby in the laboratory displays a preference for *C. virginica* over several other available prey (Wells, 1958). The larger the size of both individuals and species of snail predators, the larger the prey they seek. When it is within the morphological limits of predators to manipulate large-sized prey, available younger stages are selected over older ones, the preference being for the more actively metabolizing individuals (Carriker, 1955; Blake, 1960). Whether boring of ostracodes may be explained in these terms is not known, because predation of this group by boring snails has not been subjected to careful study in the modern environment.

Freshly drilled gastropod boreholes, though varying widely in size with the stage in the life history of individuals in a single predatory species and in form with different predatory species, may nonetheless be characterized by a number of common features.

Macroscopically the outer edge and interior surfaces of the hole appear smooth, but under appropriate magnification radular teeth marks are evident immediately after rasping. The inner edges of the holes may be sharp lipped, smooth, or jagged. The outer edges of the holes range from scarcely beveled to deeply countersunk. They are frequently discolored or bleached by action of accessory boring-organ secretion on pigmented shell and by removal of periostracum by the radula (pl. 1, figs. 4, 17, 22; pl. 2, fig. 14; pl. 3, figs. 5, 7). In light-colored shells, this discoloration is not always evident.

Boreholes generally penetrate the shell at right angles to the surface. In horizontal section, the holes may be circular, crescent shaped, heart shaped, or highly irregular, but most commonly they are circular. Both naticid and muricid boreholes are almost universally perpendicular to the external shell surface (Bucher, 1938). This feature may be explained by the radial symmetry of the extended accessory boring organ and by the perpendicular position of the longitudinal axis of its stalk to the ventral surface of the foot in muricids and to the ventral wall of the proboscis in naticids. Such circularity and perpendicularity are achieved particularly by naticids which bore relatively smooth-shelled bivalves. The symmetry of boreholes may be so warped by ornamentation, growth irregularities, and differences in hardness of prey shell that perforations may appear oval or even smoothly angular, as when muricids bore oysters (pl. 1, figs. 11, 19, 21; pl. 2, figs. 1–3, 7, 11–13; pl. 3, fig. 1; see also Fischer, 1922). Exaggerated external shell sculpture such as costae, concentric ridges, imbrication, fluting, and the like may be reflected on the side of the hole (pl. 1, fig. 21; pl. 2, figs. 10–13, 16; pl. 3, fig. 1; Fischer, 1922; Carriker and Boone, 1960). Occasional holes of muricids are bored slightly obliquely into the shell (pl. 2, figs. 5, 19) and, in rare specimens, direction of the axis of the hole will be shifted (pl. 1, figs. 10, 11), presumably either by exploiting some local weakness in the shell structure, or more likely, by abrupt shifting as soon as the inner surface of the shell is penetrated.

Boreholes generally decrease in diameter down the axis from the outer to the inner opening, a characteristic most clearly seen in deep holes in thick shells. Naticid holes show less diversity than those bored by muricids. The outer edge of naticid borings is gently countersunk, and the interior surfaces converge toward the center of the inner opening in graceful pronounced parabolic curves, a feature diagnostic of all holes of species of naticids so far examined (pl. 2, figs. 6–9; pl. 3, figs. 1–8; see also Reyment, 1966); this feature is the basis for designating the typical naticid borehole as a truncated spherical paraboloid.

On the other hand, muricid boreholes so far studied, although also variously countersunk, are considerably more diverse in vertical section (pl. 1, figs. 6–11, 24; pl. 2, fig. 25). The boreholes range from deep ones with nearly vertical walls which closely resemble complete cylinders, through truncated cones with a gentle convergence at the inner opening, as in those drilled by *Urosalpinx cinerea follyensis* Baker (pl. 1, fig. 22), to shallow holes in thin shell approximating truncated spherical paraboloids, as in those drilled by *Murex brevifrons* Conrad (pl. 2, figs. 17–25). Thus many muricid boreholes, especially in thin shell, bear a rough similarity to naticid holes (pl. 1, figs. 4, 15, 18, 25; pl. 2, fig. 14, 15). In the absence of the predator, boreholes of such species as *M. brevifrons* in thin shell (compare pl. 2, figs. 18, 19, with pl. 3, fig. 8) are difficult to identify as of muricid or naticid origin, except that the inner opening of naticid holes is generally centered and round (pl. 2, figs. 8, 9; pl. 3, figs. 1–8).

In shell composed of homogeneous material, holes are quite uniform (pl. 1, figs. 6, 9, 24). Some muricid boreholes in thick oyster shell may be characterized by an inflated barrel-shaped part where the diameter is noticeably greater than that at the outer and inner openings (pl. 1, figs. 7, 8, 10, 11; pl. 2, fig. 24); this irregularity may be explained by the presence of intermediate softer shell laminae. In some muricid species like *Murex brevifrons*, the snail often leaves a crescent-shaped thin shelf blocking part of the inner opening of the hole (pl. 2, figs. 20–22, 25). This apparently uneconomical behavior of boring, in which substantial "unnecessary" quantities of shell are removed from the outer regions of the hole prior to penetration of the smaller inner opening, is a reflection of the morphology and functioning of the parts involved. It indicates that, at least in these species, the proboscis can be extended and feed through holes of appreciably smaller diameters than the diameter needed to drill the hole.

Diameters of boreholes of different species of adult boring gastropods vary widely. Outer diameters in Carriker's collection range from 0.6 mm to 1.0 cm. Those of boreholes of newly metamorphosed boring snails or those newly emerged from egg capsules are 0.1 mm or less, and become progressively larger with the growth of the snail (Carriker, 1957). With increase in size, snails tend to attack larger prey, and thus there is a tendency for larger holes to occur in larger mollusk valves. Correspondingly, because of the size limitation of the snail and its accessory boring organ, very small boreholes, commonly less than a millimeter, are limited to relatively thin shell and small prey.

The form of the borehole is dictated by the anatomy of the boring organ, the behavior of boring, and the structure of the calcareous substratum; thus hole form is influenced largely by the genetics of the predator and the prey shell. Environmental influence on borehole form is brought about by ecological factors as they affect the nature and sculpture of the prey shell. Because of the range of variation in structure of the shell, it has not been possible to determine just how much inherent diversity of borehole form is produced by an individual snail. Given a substantial population of prey individuals with uniformly homogeneous valves, it should be possible to determine in the laboratory the range of form of borehole produced not only by an individual but by a species population as well. By varying such factors as salinity, temperature, turbulence, and turbidity, it would be possible to note the impact of these environmental factors on the rate and form of holes produced. An experimental and statistical approach to the study of gastropod borehole formation promises to be a rewarding one.

In summary, although Recent gastropod boreholes exhibit a broad spectrum of geometric form and size, characteristically they possess smooth walls, beveled outer edges, decreasing diameters with depth, and a general circularity and perpendicularity. Although it is not always possible to distinguish between those bored by naticids and muricids, they are distinctive in a statistical populational sense. Whereas typical naticid boreholes are broadly parabolic whether in thin or thick shell, those of muricids may appear parabolic in thin shell but in thick shell assume the characteristic cylindrical or nearly cylindrical form.

OTHER RECENT BORING ORGANISMS

An impressive number of major taxa other than gastropods are represented by species that have the capacity to decalcify calcareous structures. These species include algae, fungi, lichens, sponges, bryozoans, turbellarians, phoronids, polychaetes, sipunculoids, pelecypods, cephalopods, and barnacles; a useful summary of epibionic borers is given by Boekschoten (1966). Although a substantial number of references to decalcification are reported, in detail little is known of the biology of boring by these groups. Of those listed, so far as is known, only the turbellarians, gastropods, and cephalopods bore to obtain food. The remainder excavate primarily for shelter and in some instances possibly to derive shell nutrients. Shelter excavations do not commonly pass completely through the shell. In such taxa as boring polychaetes (Hannerz, 1956), bivalves (Yonge, 1955), and acrothoracican cirripeds (Tomlinson, 1953), the external opening in the shell is appreciably smaller than the cavern within which the animal is housed, and these dwellings can be distinguished readily from gastropod boreholes. Perforations of boring sponges may penetrate a shell completely, but their ramifying excavations within the shell often serve to identify their origin (Old, 1941; Warburton, 1958). Boreholes described for turbellarians (Woelke, 1957) are minute and oval in horizontal section (0.15×0.19 mm). Those of cephalopods (Pilson and Taylor, 1961) are irregularly oval and likewise minute; holes having about 2×3 mm outer diameters are reported for a large octopus with arm spread of 1.5 m.

Borings attributed to sponges, bryozoans, and cirripeds are well known in the fossil record of the Paleozoic. A few authors have suggested fossil algae as possible borers. A substantial literature has accumulated on fossil borings and borers. Although these occurrences are interesting in their own right, they need not be discussed further here. Attention here is focused only on those Paleozoic borings that earlier authors attributed to gastropod predation.

ORDOVICIAN CYLINDRICAL BORINGS

PREVIOUS LITERATURE ON PALEOZOIC BORINGS

Curiously, little has been written on cylindrical borings of Paleozoic age, though the occurrences are striking enough to warrant at least short notes. Clarke (1921, p. 80) who made the most extensive survey of "disease" among Paleozoic invertebrates simply mentioned that perforations "in ancient fossils are occasionally noticed." Moodie (1923) did not mention the subject.

Yakovlev (1926) described several perforated Permian brachiopods, and suggested *Naticopsis* as the predator. Hecker (1965, pl. 3, fig. 1) illustrated another bored Permian *Athyris* and, following Yakovlev, suggested that it was drilled by *Naticopsis*?. Brunton (1966) has reported extensive numbers of "neatly bored circular holes" in Viséan brachiopods at a locality in northern Ireland; some shells show as many as 44 borings. Although these borings are described as the result of gastropod predation, the large number of multiple borings reported argues strongly against such an interpretation. Clarke (1908, pl. 12) figured three bored Devonian brachiopods; only one of the holes is figured as showing tapered exterior edge.

Possibly the most comprehensive paper on these particular-shaped perforations is that of Fenton and Fenton (1931), who noted five Devonian localities where bored brachiopods have been found and also listed boring at two Upper Ordovician localities near Cincinnati, Ohio. They indicated that their Devonian material showed some holes that were not tapered, and included some that were bored on the interior and therefore presumed not to be the result of gastropod activity. For the Devonian borings considered of gastropod origin, *Diaphorostoma* or *Platyceras* were suggested as responsible for the predation.

Bucher (1938) questioned that the Late Ordovician borings described by Fenton and Fenton (1931) were caused by gastropods, but described other borings from the Upper Ordovician which he ascribed to carnivorous gastropods. He indicated that the only gastropod occurring in the same beds as the bored shells was a species of *Loxoplocus* (*Lophospira*).

Fischer (1962) discussed pre-Tertiary borings and concluded they need not be of gastropod origin. Fischer (1964) illustrated several Devonian fossils that had been bored; out of a large lot, some few showed cylindrical holes. Such activity was attributed by him to boring sponges. In Fischer's 1962 paper, Carriker was quoted, and in the 1964 paper a letter from Yochelson was included. Both Carriker and Yochelson, when cited, indicated that there was evidence of early Paleozoic gastropod borings, being influenced at the time of their remarks by Bucher's (1938) findings.

METHODS OF STUDY

All penetrated shells discussed in the literature presumably were collected free from weathered shale. In 1958, Dr. G. Winston Sinclair, Geological Survey of Canada, remarked to Yochelson that he had obtained bored shells from a residue of silicified fossils; this remark immediately suggested that bored specimens might be obtained in large numbers from limestone containing silicified shells. An excellent area in which to test this possibility is in Kentucky. Middle Ordovician limestones of Trenton age crop out over 4,000 square miles in the central Blue Grass area of Kentucky. About one-third of this region has been mapped geologically in considerable detail by the U.S. Geological Survey. Investigation of outcrops showed the presence of silicified fossils at many localities throughout the area, and scattered stratigraphically through the Lexington Limestone.

The lower two-thirds of the Lexington Limestone is divided, from the base upward, into the Curdsville Limestone Member, Logana Member, and Grier Limestone Member (Black and others, 1965). The upper one-third of the formation is divided into six intertonguing members; the formation has an average thickness of 310 feet. Black and MacQuown (1965) present a summary of recent interpretations of the stratigraphic relationships. Small fossil collections sent in previously by field geologists had yielded interesting and well-preserved brachiopods, but no bored specimens were noted.

During the 1965 field season, approximately 4 tons of limestone was obtained from the Lexington Limestone. Slightly more than half the material was from the Grier Limestone Member, most of the remainder being divided nearly equally between the Curdsville and Logana Members. The limestone was dissolved in hydrochloric acid (Cooper and Whittington, 1965). After the fossil residues were dried, well-preserved specimens were separated, and a special search was made for borings in representatives of all phyla. Each residue was examined at least twice, and, if borings were found, the residue was picked a third time.

Although collecting silicified fossils produces its own particular set of biases and problems, it also provides unique data. The silicified residue is, in effect, a sample of the sea bottom fully comparable with the modern ocean floor. It enables one to determine the fabric of the shells in the sediment, and it gives semiquantitative information, during an extremely short interval of geologic time, on the diversity of bentbonic animals that could be fossilized. In the central Kentucky area, interpretations of local paleoecology based exclusively on the silicified residues have almost always been in accord with the regional interpretation derived from geologic mapping and lithic studies. This study emphasizes only those localities that yielded bored shell and not all the localities from which silicified Ordovician fossils have been collected in Kentucky.

MIDDLE ORDOVICIAN BORINGS FROM KENTUCKY

Borings were found at eight localities in the Lexington Limestone. One collection (5022–CO) is from the Curdsville Limestone Member, two collections (6030–CO, D–1196) are from the Logana Member, and five collections (4868–CO, 4872–CO, 4956–CO, 5093–CO, and 5098–CO) are from the Grier Limestone

Member. Details of the locality and stratigraphic position are given in the register of localities.

Abundance of brachiopods in each collection was estimated and is tabulated below with the number of bored specimens obtained. The individual Curdsville and Logana collections were more than twice as large as the Grier Limestone collections.

Locality	*Number of bored shells*	*Estimated number of brachiopods*
4868	6	1, 000
4872	4	500
4956	6	250
5022	2	1, 000
5093	1	500
5098	[1]1	50
6030	1	1, 500
D-1196	3	10, 000

[1] Boring is in a pelecypod.

Some of the silicified shells from several localities, but particularly 5022-CO, are covered with a Leisegang structure, of the type informally known as beekite rings. The mode of origin of these rings is not known. They do form areas of weakness in the shell and may break free, the loss of such a plug forming a rudely circular hole. Where beekite rings are present, silicification is often erratic, so many specimens are partially silicified, as well as "beekitized." The nonsilicified part of the shell is lost during acid preparation, but the resulting hole is jagged and is easily distinguished from both those holes caused by the loss of a beekite ring and those bored through the shell.

The borings show some variation, and details from each locality are given below:

Locality 4868-CO

In this collection, six holes were observed. Four holes penetrate rafinesquinoid brachiopods; the other two are in fragments probably assignable to this group. On only one fragment can the bored valve be determined with certainty, and in this specimen the boring is the pedicle valve (pl. 4, figs. 1, 2). None of the borings seems to be near the hinge line. All holes are in relatively thin shells.

Because shell material is so fragmentary, only two of the holes are unbroken. The smaller hole (pl. 4, figs. 1, 2) is nearly circular and about 1.1 mm in diameter. It has a distinct chamfer on the exterior edge and is on the two adjacent quadrants toward the lateral and anterior margins. The quadrant nearest the hinge line has a sharp edge. The interior edge is sharp. The larger unbroken hole is distinctly elliptical in transverse section, with a maximum diameter of 2.3 mm (pl. 4, figs. 3, 4). The exterior edge is smooth along its circumference, except for irregularity near the hinge-line quadrant of the oval. Although this edge is fairly sharp, there is a suggestion of a slight chamfer in the quadrant toward the anterior margin. The interior edge has a strong chamfer on the quadrant toward the hinge line and directly below the external irregularity. The opposite quadrant has a sharp edge. Compared with other specimens, this shell fragment is thicker; the hole is distinctly oblique and appears to be from the interior toward the exterior.

The remaining four holes are all broken. They are rather large and nearly circular. The largest fragment is distinctly tapered from the exterior inward (pl. 4, fig. 5). Near one edge of the fragment there is a suggestion that the wall may be more nearly longitudinal to the shell surface than in the other parts; if so, this is another example of chamfer, rather than true uniform tapering, but the incomplete preservation makes this observation uncertain; the interior edge is sharp. The remaining three specimens show little of interest except that all have a sharp edge and give no indication of taper or chamfer on either the interior or exterior.

Locality 4872-CO

Five borings in four shells were obtained in this collection. Three of the borings are in *Sowerbyella,* two being in one pedicle valve and one in a second brachial valve. The one in the brachial valve is excavated near the margin and only partially preserved, but it appears to be circular in transverse section (pl. 4, figs. 12, 13). The hole shows distinct indication of a slight chamfer on the interior of the shell in the quadrant toward the lateral margin and even less chamfer in parts of the adjacent quadrants. The part of the exterior edge that is preserved is sharp.

A complete hole is in the pedicle valve near the axis of symmetry and close to the anterior margin (pl. 4, fig. 11). It is much smaller and is oval in transverse section, rather than circular. There is a wide chamfer on one exterior quadrant toward the lateral margin. The interior edge is masked by adhering silica. A second larger, partially preserved boring intersecting the anterior margin shows a wide chamfer. The interior edge of this hole seems sharp, though it too is incrusted with silica.

The two other holes are in indeterminate fragments, possibly *Heterorthina.* Both penetrate the brachial valve and are nearer to the anterior margin than to the hinge line. The larger hole is almost circular in horizontal section, with a maximum diameter of 3.0 mm (pl. 4, fig. 9). It shows a distinct chamfer only on the anterior marginward quadrant of the exterior edge; the rest of the exterior edge is sharp. The interior edge is sharp except for a narrow chamfer on the hinge-line quadrant, opposite from the chamfer on the exterior. The smaller hole is irregularly oval in transverse section, with a maximum diameter of 2.5 mm (pl.

4, fig. 10). There is a wide chamfer on the exterior quadrant toward the hinge line. The opposing quadrant has a sharp edge. The interior has a chamfer toward the anterior margin, and the quadrant toward the hinge line is sharp. The specimen is covered with beekite rings, which make difficult the observation of details of chamfer.

Locality 4956–CO

Four of the six bored shells in this collection are *Dalmanella;* the remaining two borings are in fragments probably belonging to that genus. Three of the fairly complete shells have borings in the brachial valves; one specimen shows two holes. The boring in the other complete shell is in a pedicale valve. The two fragments are too incomplete to determine which valve was bored. Three of the holes are complete, and one is broken on a short segment of the edge.

The largest complete hole has an elliptical transverse section but deviates only slightly from a circle (pl. 5, figs. 3, 4). It shows distinct chamfer on the interior edge of the quadrant adjacent to the axis of symmetry. The exterior edge is sharp except in the quadrants. The second complete hole is much smaller and is irregularly oval in horizontal section, with a pronounced chamfer on two opposite quadrants of the exterior edge (pl. 5, fig. 7). The interior edge is sharp. The third complete hole is a brachial valve that bears a series of small holes that riddle the shell (pl. 5, fig. 6). The holes are comparable in size to those drilled in the specimens of *Sowerbyella* from Canada. At least one of the small holes is at a strongly oblique angle to the shell surface, and several seem to show a slight chamfer on part of the exterior edge. These examples do not appear to be the result of loss of beekite plugs. At least six incomplete penetrations occur on the exterior.

The most complete of the three broken holes is bored in a brachial valve and is irregular in transverse section, with a straight edge for about one-third the circumference, the remainder being almost circular (pl. 5, figs. 5, 8). It shows chamfer on two opposing exterior quadrants, with irregularity of costae emphasizing one of the chamfers. The interior edge is smooth and sharp, but shows well the irregularity of shape, almost half the edge being straight rather than curved. A slightly smaller incomplete hole occurs at one broken edge of the shell. It shows a sharp interior edge, but a chamfer on one exterior quadrant. Another excavation on the shell seems to be an incomplete hole rather than the result of silicification.

A hole of somewhat larger diameter that seems to be circular in transverse section (pl. 5, figs. 1, 2) is in another shell fragment. The hole has a distinct chamfer on one of the preserved quadrants of the interior surface; the exterior edge is sharp. The boring in the last fragment is too incomplete to preserve any significant details.

Locality 5022–CO

Several specimens of *Dalmanella* at this locality bear holes, but these are also interpreted as loss of beekitized plugs rather than borings. Only one pedicle valve contains several holes of more certainly organic origin (pl. 5, fig. 9). The most conspicuous of these holes is elongate and nearly teardrop shaped in outline. Walls are straight, and there is no indication of chamfer. Another adjacent hole and one at the anterior margin are more irregular in transverse section, though they seem to be circular in longitudinal section. These holes are clearly the work of a different organism from that forming the more circular holes. They are included here because they are the only distinctly noncircular borings or excavations which penetrate the shell that were obtained in the Kentucky collections. Comparison with Recent holes suggests more affinity to the activity of polychaete worms than to that of either boring barnacles or boring sponges.

Locality 5093–CO

The one hole observed in fossils from this locality is bored in the brachial valve of an incomplete specimen of *Dalmanella* (pl. 5, figs. 10, 11). The hole is located posteriorly, somewhat nearer the hinge line than the lateral margin. It is nearly circular in transverse section. In spite of the thinness of the shell, there is a conspicuous chamfer on the interior quadrant toward the hinge line. The opposite quadrant has a sharp edge. The exterior edge is sharp and deviates from circularity at the hinge-line quadrant, the site of the interior chamfer. The hole is only slightly oblique in longitudinal section.

Locality 5098–CO

A boring oval-shaped in transverse section occurs in the left valve of a ctenodontid pelecypod, a representative of a new genus (pl. 5, figs. 12, 13). Maximum diameter of the hole is 2.6 mm; minimum diameter is 1.6 mm. Both interior and exterior edges are rounded, but the latter surface also shows a chamfer on the quadrant at the marginal end of the long axis. The walls are smooth but exceedingly irregular. Diameter of the hole changes several times through its width but trends toward increasing size inward.

Locality 6030–CO

A well-preserved silicified brachial valve of *Heterorthis clytie* (Hall) shows one fairly large hole and another larger hole (pl. 4, figs. 6–8). The smaller hole is about 7 mm from the hingeline and about 6 mm from the lateral margin. It is oval-elliptical in shape, with a maximum diameter of 2.8 mm and a minimum diameter of 2.3 mm. On the exterior of the shell, the edge is slightly irregular, costae protruding a short distance into it around most of the circumference. On the interior of the shell, the hole shows a distinct chamfer on each quadrant, though that on the narrowest edge of the ellipse is far steeper than that on the other three quadrants.

The second hole is about 1 cm from the hingeline near the center of the valve. It is nearly circular and is the largest hole observed in the Kentucky material, the diameter being 4.0 mm. On the exterior of the shell the edges are sharp for three-fourths of the circumference; this part lies in the area of shell where lirae are low. The remaining quadrant, that closest to the hingeline, deviates from the curvature of the other three and is also more irregular, some of the costae protruding a short distance into the hole. On the interior of the shell, this quadrant shows a wide, gently inclined chamfer; the shell here is thick. The wall of the opposite quadrant is vertical, and the remaining two quadrant walls are nearly vertical. The hole outline on the inner surface is distinctly elliptical, as contrasted with the more nearly circular shape on the exterior.

Locality D–1196–CO

Three bored specimens were obtained, all holes penetrating *Dalmanella.* The largest hole is in a brachial valve in the posterior part of the shell about equidistant between the hingeline and the lateral margin (pl. 4, figs. 14, 15). It is about 1.0 mm in diameter, but is slightly irregular in shape, particularly on the exterior. Extension of costae out over the hole accounts for much of the apparent exterior irregularity. On the interior, a conspicuous chamfer toward the hingeline quadrant extends laterally for nearly half the circumference; the remainder of the interior edge is sharp. The costal ends noted are preserved on the exterior of this chamfer. The hole shows clear evidence of pentration at a strongly oblique angle and suggests that this penetration was from the interior outward.

The other two holes are nearer the hinge line than the lateral margin. One is in a brachial valve, and the other is in a pedicle valve. Both holes are irregular in transverse section and may have been modified by subsequent diagenesis, but at least some of the irregularity may be ascribed to the ends of costae protruding into the hole. The hole in the pedicle valve has a maximum diameter of near 0.5 mm (pl. 4, fig. 18). There is a chamfer on the exterior quadrant toward the lateral margin and extending toward the hinge line; the extention of one costa inward emphasizes this chamfer. The interior edge is highly irregular and shows no chamfer.

The hole in the brachial valve is larger and quite irregular (pl. 4, figs. 16, 17). On the exterior quadrant toward the lateral margin, short extensions of costae seem to indicate a chamfer in that area. The interior edge appears sharp, though highly irregular. Although the organic origin of this hole may be less certain than that of the other two, the hole is far too large to have been caused only by the loss of an average-sized beekite plug.

MIDDLE ORDOVICIAN BORINGS FROM QUEBEC AND ONTARIO

In 1959, Dr. G. Winston Sinclair, Geological Survey of Canada, lent a collection of silicified Trenton age fossils, which contained bored brachiopods significantly older than the Late Ordovician borings of Bucher (1938). These fossils were collected from near the base of the Shipshaw Formation (Sinclair, 1953) on the right bank of the Shipshaw River, 1¼ miles below Chute aux Galets, Quebec, Canada.

More than 125 specimens of *Sowerbyella* were obtained at the locality. Nine of these are bored with cylindrical holes. Nine gastropods were also collected. These are provisionally identified as *Sinuites*?, bellerophontacean indeterminate (two genera), *Liospira, Trochonema*?, murchisoniacean indeterminate, and subulitacean indeterminate.

The nine bored specimens may be divided arbitrarily into three groups. Five specimens contain small holes about 0.5 mm in diameter. All openings are relatively near the hinge line and relatively near the axis of symmetry of the shell. Four of the holes penetrate the brachial valve and are nearly circular in transverse section (pl. 3, fig. 17). The fifth is in the pedicle valve and is oval in transverse section (pl. 3, fig. 18). In this hole, walls are longitudinal. The other holes may have longitudinal walls, but they are in a thinner part of the shell and hence more difficult to observe in the third dimension. No clear indication was seen of erosion around the edge of the holes, but one specimen seems to show a slight chamfer on the interior edge of the quadrant closest to the lateral margin, though silicification is coarse enough to cause uncertainty on this feature (pl. 3, figs. 12, 13).

In the second group, one fragment contains a hole drilled on the hinge line of a brachial valve but relatively far from the axis of symmetry (pl. 3, figs. 14, 16). It is somewhat larger than those noted above, being about 0.8 mm in diameter, and is very nearly circular in transverse section. The external edge is sharp, but the hole appears to have a chamfer on the interior of the valve. The chamfer is more pronounced on the quadrant adjacent to the axis of symmetry than on the rest of the edge. The opposite quadrant appears slightly jagged.

The third lot consists of three fragments bearing holes larger than 1.0 mm in diameter. Two holes are in the brachial valve, one is in the pedicle valve. The holes in two of these valves are near the anterior margin, and one may even have intersected the margin, though the incomplete nature of the fragment makes this uncertain. Because the perforations are broken, it is difficult to characterize their shape in transverse section, but they seem to deviate only slightly from circularity. In spite of incompleteness, all three holes show suggestion of boring at an oblique angle and only one quadrant of the hole is chamfered (pl. 3, fig. 15).

Subsequently, Dr. Sinclair found one bored *Hebertella* from the Ottawa Formation, 1.2 miles west of the Odessa interchange on Highway 401, Ontario. One hole comparable in size to the small group above penetrates the pedicle valve (pl. 3, fig. 19). It is nearly circular in transverse section. The exterior edge definitely appears to be slightly chamfered on two quadrants and is therefore an oblique hole. The interior edge is sharp. A second smaller hole almost at the hinge line of the specimen may be only an artificial break. Half a dozen specimens of the bellerophontacean gastropod *Carinaropsis* were collected at this locality.

MIDDLE ORDOVICIAN BORINGS FROM OTHER AREAS[1]

No attempt has been made to survey the shelled Ordovician invertebrates which have been gathered by American paleontologists during the last century or more; the very size of the collection in museums effectively defeats an attempt to search systematically for such a relatively rare feature as cylindrical holes. However, the descriptive work of Schuchert and Cooper (1932) and particularly Cooper (1956) provide an excellent sample of the brachiopod faunas. Because it was the aim of these works to illustrate brachiopod morphology, it is reasonable to assume that no bias either for or against bored shells would be present, provided the boring did not interfere with critical features of the morphology. Schuchert and Cooper (1932) illustrated several specimens which are excavated or incrusted by other organisms (for example on their pl. 18, fig. 33, and pl. 21, fig. 37) but no cylindrical holes are illustrated.

The 269 plates of brachiopods illustrated by Cooper (1956) show three specimens bearing cylindrical holes. The first, in *Glyptorthis concinnula* Ulrich and Cooper, (Cooper, 1956, pl. 43, fig. 43) may be an artifact and need not be discussed further. The second (Cooper, 1956, pl. 89, fig. 10) is reillustrated here on plate 3, figure 21. The boring is on the interior of a brachial valve of *Mimella globosa* (Willard) from the Benbolt Formation of Cooper and Prouty (1942). This hole does not penetrate the shell, but is eroded only to a shallow depth. The hole is circular and has a diameter of 2.4 mm. There is a central elevation as in an incomplete naticid gastropod boring, but this feature is more irregular both in shape and elevation above the lowest part of the hole than similar features in present-day shells. The excavation has a distinct chamfer on the quadrant toward the lateral margin, the remaining part of the edge being sharp and the walls being nearly longitudinal.

The third specimen (Cooper, 1956, pl. 38, fig. 19) is reillustrated here on plate 3, figure 20. This hole penetrates the pedicle valve of a silicified specimen *Taphrorthis peculiaris* Cooper from the Pratt Ferry Formation of Cooper (1956) and is thus the earliest known cylindrical hole. The hole is on the right lateral slope, a slight distance from the hinge line and midway between the lateral margin and the axis of symmetry. Its shape has been modified because of breakage toward the anterior shell margin, but it appears to be originally oval, with a maximum diameter of near 1.4 mm. The hole has a wide chamfer on the exterior hinge-line quadrant. The remainder of the intact edge appears to be sharp. The part of the interior edge that remains is sharp.

This sample of other brachiopod borings, although necessarily incomplete, does show several significant features. First, cylindrical boring does occur in brachiopods somewhat older than those in Kentucky. Second, if the assumption may be accepted that brachiopod workers did not select against bored shells, there is a further indication that such borings are rare. Third, two observed examples show asymmetry of the hole and obviously no preference for boring from the exterior of the shell inward, two features noted in the younger Middle Ordovician shells.

LATE ORDOVICIAN BORINGS FROM OHIO AND INDIANA

The two known literature reports of Late Ordovician predatory gastropods are by Fenton and Fenton (1931) and Bucher (1938). These papers, especially that of Bucher, are the basis for the general presumption of Ordovician gastropod predation. They are pertinent to this study in part because these authors influenced

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[1] After this paper was authorized for publication, Cameron (1967) reported borings in brachiopod shells of Trenton age. It is apparent from his descriptions and illustrations that the borings are like those we are describing from Trenton-age rocks in Kentucky. Cameron suggests that the holes are the result of activity of a carnivorous gastropod, possibly *Subulites*. We have not examined his bored shells or the field occurrence, but we see no reason to change our conclusion that these holes are not bored by gastropods.

the preliminary opinion of the writers quoted by Fischer (1962; 1964) regarding the occurrence of Ordovician carnivorous gastropods. Bucher's bored Ordovician shells were examined during 1959, and the data and notes assembled were then reviewed 6 years later in the light of new information from the Kentucky and Ontario borings. Most of the Late Ordovician specimens illustrated by Fenton and Fenton (1931) have been examined. These lots were supplemented by two Late Ordovician bored *Dalmanella* collected by John Pojeta, Jr.

Fenton and Fenton (1931, p. 526) report specimens of five species in four genera of brachiopods as drilled by gastropods. Three specimens illustrated by them are discussed below. *Rafinesquina* cf. *R. alternata* (Emmons) bears a single hole in the brachial valve along the axis of symmetry about 5 mm from the hinge line; it is refigured here (pl. 3, fig. 9). The hole is 4.5 mm in diameter and is nearly circular in transverse section on the exterior of the shell. In contrast to the drawing of it, this hole is not smoothly tapered around its circumference. The quadrant nearest the hinge line has a sharp edge and a nearly longitudinal wall. The quadrants to either side are strongly chamfered. Nearly half the hole can best be described as sloping gradually but irregularly inward. The impression is definitely that of erratic erosion of some sort, rather than chemicomechanial drilling. Dr. Norman F. Sohl, U.S. Geological Survey, had directed our attention to an excavation in a Cretaceous *Exogyra* made by the holdfast of a gorgonid coral which is similar in many respects to this hole.

The second hole illustrated by Fenton and Fenton is in *Sowerbyella rugosa clarksvillensis* (Foerste). This hole is in the brachial valve far out on the lateral margin and close to the hinge line. It is beveled on the interior. The third hole illustrated is in *Dalmanella meeki* (Miller). The hole perforates near the axis of symmetry about two-thirds of the way between the hinge line and the margin. It is apparently in the pedicle valve. The edge is sharp and does not show any chamfer. Neither of these two specimens is available for restudy.

Bucher (1938) questioned all five Ordovician occurrences. However, he inferred the presence of Late Ordovician predatory gastropods because of bored brachiopods collected near Fourmile Creek, south of Oxford, Ohio, from the Waynesville Shale. Six of his specimens were illustrated; 24 were available in his collection.

Ten borings in *Dalmanella* were fairly complete. Eight of these are into brachial valves. The remaining holes are in shell fragments, and no determination of the particular valve was made. Bucher's six illustrated specimens show that the position of the hole varies widely on the shell and that there is no systematic relationship between the size of the hole and the size of the brachiopod. One figured specimen bears two holes, and a second shell bored twice was not illustrated by Bucher. Both present writers independently observed that at least one shell showed clear evidence of boring from the interior outward. Yochelson observed that many of the holes lacked a distinct bevel and few were truly circular. Carriker confirmed these observations by detailed measurements and further observed that when the edge was not sharp only one or two quadrants commonly showed a chamfer. Many of the holes thus appeared to be drilled obliquely. When examined in detail, few of the specimens showed the typical cylindrical to slightly parabolic hole associated particularly with muricid gastropod predation.

Specimens were measured by Carriker in January 1959 with a micrometer ocular. The notation used is as follows:

$$\frac{\text{Outer diameter at maximum bevel}}{\text{Inner diameter at maximum bevel}} \times \frac{\text{outer diameter at minimum bevel}}{\text{inner diameter at minimum bevel}}$$

In this system, outer and inner refer to the shell surfaces of the bored brachiopods. The shell of these specimens is thicker than that of the Middle Ordovician material and is thus more readily amenable to this two-level form of size expression. At the time these specimens were examined, no distinction had been made between a bevel or uniform taper and a chamfer; as used here, the phrase "maximum bevel" almost certainly referred to a chamfered surface, but the specimens cannot now be reexamined. The measurements and comments are tabulated on the following page.

Measurements of holes bored in Dalmanella meeki *(Miller), from Bull Run tributary to Fourmile Creek, south of Oxford, Ohio*

Complete holes

Size (in mm)	*Comments*
$\frac{1.2}{1.2}\times\frac{1.2}{1.2}$	Definitely cylindrical; no beveling. Shell 0.4 mm thick at hole.
$\frac{1.8}{1.5}\times\frac{1.7}{1.5}$	Very slight beveling; maximum diameter corresponds to diameter of maximum beveled part of hole. This and preceding hole were both on same brachipod valve.
$\frac{1.5}{1.7}\times\frac{1.3}{1.3}$	No beveling visible from exterior, but slight beveling on interior of hole, to extent of 0.2 mm.
$\frac{2.3}{1.8}\times\frac{2.5}{2.0}$	Hole slightly oval; maximum dimensions at right angles to line of maximum bevel. Shell 0.5 mm thick at hole.
$\frac{2.3}{1.5}\times\frac{2.1}{1.6}$	Hole oval; line of maximum diameter 45° from line of maximum bevel. Shell 0.6 mm thick at hole; surfaces of hole very smooth.
$\frac{3.0}{2.3}\times\frac{2.5}{2.4}$	Hole bored slightly obliquely; wall opposite to maximum bevel outward, beveled inwardly by 0.15 mm on interior. Shell 0.4 mm thick at hole; surfaces of hole very smooth.
$\frac{2.1}{1.8}\times\frac{2.1}{1.7}$	Maximum diameter parallel to maximum beveling; shell 0.5 mm thick at hole.
$\frac{1.9}{1.4}\times\frac{1.6}{1.4}$	Hole oval and maximum diameter parallel to maximum beveling; shell 0.5 mm thick at hole.
$\frac{1.9}{1.4}\times\frac{1.9}{1.3}$	Hole almost round, maximum diameter parallel to maximum beveling; shell 0.3 mm thick at hole.
$\frac{1.6}{1.3}\times\frac{1.5}{1.3}$	Hole oval and bored obliquely into shell: shell 1.0 mm thick next to "umbonal" teeth where hole bored and 0.3 mm thick on opposite side.
$\frac{2.1}{1.9}\times\frac{1.8}{1.7}$	Hole very slightly beveled; not completely cleaned out of sediment, so thickness of shell could not be determined.
$\frac{2.5}{3.3}\times\frac{2.5}{3.2}$	Strongly beveled hole bored from inside out of shell; that is, beveling is inside valve; one wall almost straight and other sides beveled. Shell 0.5 mm thick at hole.

Broken holes

[Only outer/inner available diameters given because it is not known which is maximum]

Size (in mm)	*Comments*
1.5/1.5	½ of hole present; clearly straight walled.
2.5/?	⅓ of hole present; very large (diameter estimated).
2.2/?	⅓ of hole present; hole through very thin shell at edge of valve. Shell 0.4 mm thick at hole.
1.3/1.1	¾ of hole present; clean, smooth walled.
2.2/1.3	0.9-mm bevel on one side and straight walled on other.
2.0/1.7	½ of hole present; measurement made at right angle to bevel, strongly beveled at one side, maximum bevel of 0.5 mm.
2.0/1.8	½ of hole present; bevel on one side equaled 0.2 mm.
1.8/?	Only ⅓ of hole present; deeply beveled, but insufficient shell to take measurements.
2.2/?	On same shell as hole above; two borings in one shell.
2.7/?	⅓ of hole present, and walls present only slightly beveled. Diameter grossly estimated.
3.1/2.8	¾ of hole present; hole bored obliquely so one end has bevel on outer and other end has bevel on inner surface of shell. Shell 0.8 mm thick at hole.
1.8/1.5	½ of hole present; bevel mostly at one side of hole.
1.8/?	½ of hole present; so bored that presence of bevel cannot be determined.

Two bored specimens from the upper part of the Waynesville Shale, collected near the junction of Indiana State Roads 1 and 46, Cedar Grove quadrangle, Indiana, show the same sort of variations noted in earlier observations made of the Bull Run material. The smaller hole has an external diameter of 2.2 mm; it is near the anterior margin and near the axis of symmetry on the brachial valve of a *Dalmanella* having a length of 10.5 mm (pl. 3, fig. 10). The larger specimen has a diameter of 2.8 mm and is somewhat nearer to the lateral margin than to the hinge line of the brachial valve of a *Dalmanella* more than 18 mm long (pl. 3, fig. 11). Thus in spite of the slight difference in size of holes, the size of the bored shell varies widely.

Both holes are almost perfectly circular in transverse section. In the smaller hole, the walls are nearly longitudinal, but there is a slight suggestion of a chamfer on the quadrant toward the anterior margin. The opposite quadrant is sharp and has a nearly longitudinal wall. Part of the inner edge is sharp; the character of the remainder is lost because of flaking away of the shell. The larger hole is tapered throughout its exterior circumference, but the chamfer on the quadrant toward the anterior margin is more conspicuous than that on the others. In the interior of this shell, the edge is irregular but sharp on the quadrant toward the anterior margin, whereas the quadrant edge toward the hinge line seems slightly rounded.

John Pojeta, Jr. (oral commun., June 1966), indicates that about 5 percent of the shells at this locality show holes.

Although it is not the purpose of this paper to review the Devonian occurrences, most of the specimens illustrated by Fenton and Fenton (1931) were examined briefly. Three of their specimens have what appear to be simple abrasions of the shell, not necessarily of organic origin. Another partial penetration is most irregular at depth, much like the Ordovician *Rafinesquina* discussed earlier. The remaining nine available specimens, representing six species in four genera, all show relatively small holes approximately 1½ mm in diameter. There is no obvious relation between the size of the brachiopod and the size of the hole. Almost no taper or chamfer was observed. Rather, the outer edge is exceedingly sharp. One perforation is incomplete, and has a naticidlike boss at the bottom. Another shell shows two holes plus an incomplete excavation. The position of the hole on the shell varies widely, unlike present-day borings drilled by naticid predators. Most holes have nearly longitudinal walls, and in this feature these holes are more like the cylindrical ones of Recent muricid gastropods.

MOLLUSKS OF THE LEXINGTON LIMESTONE

Because gastropods have been indicated as possible predators and pelecypods may be possible victims, it is appropriate to include distributional data on these mollusks found at the Kentucky localities where bored shells have been collected, Cephalopod distribution is added, even though no fossil cephalopod has been seriously considered to be a borer; the holes described above are not like those excavated by Recent octopuses. The occurrence of two other classes of mollusks is noted simply for completeness. Bryozoan colonies constitute the principal remaining faunal element, but they do not bear on the question of the boring organism. Worm tubes, castings, echinoderm debris, and other rare fossils have been found at some localities, but again these organisms do not bear on the problem.

Although the occurrence of mollusks is to be counted in tens and hundreds, the abundance of brachiopods at most localities is to be counted in the thousands. In the field there was definite bias for selecting those blocks which it was hoped would yield silicified mollusks and against selecting many limestone blocks which showed only brachiopods on the weathered surfaces. Thus the abundance of mollusks indicated here is probably somewhat higher than actually exists.

An arbitrary scale of abundance is used: rare, 1–3; common 4–10; abundant, 11–25; very abundant, 26–100.

Gastropoda.—These were found at only one locality:

D-1196-CO

Cyrtolites aff. *C. retrorsus* Ulrich in Ulrich and Scofield (very abundant)
Carinaropsis cymbula Hall (rare)
Liospira aff. *L. decipens* Ulrich in Ulrich and Scofield (abundant)
Loxoplocus (*Lophospira*) sp. indet. (abundant)

Loxoplocus (*Lophospira*) is a moderately high-spired pleurotomariacean gastropod with a prominent slit in the aperture. It is closely related to the late Paleozoic *Worthenia. Liospira* is another pleurotomariacean, but it is lenticular, with a slit at the periphery; it is closely related to the late Paleozoic *Trepospira. Carinaropsis* is a remarkably broad, flattened bellerophontacean superficially resembling the Recent *Crepidula.*

Cyrtolites is commonly considered to be a bellerophontid, but it lacks a slit and possibly belongs to a different class of mollusks; it has a typical bellerophontiform shell.

Pelecypoda.—Pelecypods have been found at four of the eight localities as follows:

5022-CO

Cyrtodonta subovata Ulrich (common)
Vanuxemia gibbosa Ulrich (common)
cyrtodontid fragments indet. (abundant)
Lyrodesma cf. *L. acuminatus* Ulrich (rare)
Tancrediopsis sp. (abundant)

5093-CO

Modiolodon aff. *M. oviformis* (Ulrich) (common)

5098-CO

Cyrtodonta aff. *C. subovata* Ulrich (rare)
auriculate ctenodontid undetermined sp. A (abundant)
Ambonychia radiata Hall (abundant)
?*Nuculites* sp. (rare)

D-1196-CO

Modiolodon oviformis (Ulrich) (very abundant)
modiomorphid sp. (abundant)
Colpomya faba (Emmons) (rare)
Similodonta aff. *S. hermitagensis* (Bassler) (abundant)
Ctenodonta socialis Ulrich (very abundant)
?*Nuculites* sp. (rare)
?pterioid pelecypod (rare)
auriculate ctenodontid undetermined sp. B (rare)
Ambonychia sp. indet. (rare)

The fossil nuculoids probably were part of the infauna and had a habitat similar to that of Recent forms. These include ?*Nuculites, Ctenodonta, Tancrediopsis, Similodonta,* and the auriculate ctenodontid. The life habit of *Lyrodesma* was infaunal also. *Cyrtodonta* and *Vanuxemia* are judged to have been either surface dwellers or shallow burrowers. The remaining forms, *Modiolodon, Ambonychia,* pterioid, modiomorphid, and *Colpomya* are commonly considered to have lived as byssate epifauna.

Cephalopoda.—Fossils of this class were found at three of the eight localities. They have not been generically determined, but all are orthoconic nautiloids. Rather few genera seem to be present in the Lexington Limestone. The number of specimens at the three localities is as follows: 5093–CO, 1; 5098–CO, 8; D-1196–CO, 39.

Amphineura.—Isolated plates of amphineurans are rare but are widely distributed throughout the Lexington Limestone. None occur at the eight localities at which borings are found, and they are added here simply to complete the information on molluscan distribution. Recent amphineurans are herbivores or omnivores, and none is known to be a boring predator.

Monoplacophora.—In addition to *Cyrtolites,* which may be a coiled monoplacophoran, a few more typical patelliform shells have been found. These have been referred to *Archinacella.* None occur at localities where borings have been found. Although the life habits of living monoplacophorans are not well known, there is no reason to assume a boring habit for their ancestors. They are simply included, like the Amphineura, to round out the picture of the mollusks that occur in the Lexington Limestone.

PALEOECOLOGY AND PALEOETHOLOGY

Outcrops of the Lexington Limestone provide pertinent background data on the environment of boring.

The Logana Member is particularly interesting in this respect. The member is about 30 feet thick (Black and others, 1965, p. C16) and appears mainly as a shale in characteristic outcrops. Scattered through the shale is interbedded limestone commonly 3–4 inches thick, though several beds are almost a foot thick. The Logana Member thins eastward, and the upper part of it intertongues with the overlying Grier Limestone Member. The facies change and paleogeography of the central Blue Grass area indicate that the Logana was deposited in an area of quieter water, virtually parallel to the Grier Limestone Member. Little evidence is available on the depth of water, but there is no reason to assume depths of more than a few tens of feet for the Logana sea.

Shales of the Logana contain sparse fossil invertebrates, and some thin limestones are unfossiliferous calcisiltites. Other thin limestones are composed almost entirely of *Dalmanella* shells. In these beds, specimens are so numerous that it is appropriate to describe the rock as a coquina. Shells may be imbricated, but generally compose such a bulk of the rock that no arrangement can be seen. The fossiliferous limestone is interpreted as storm accumulations of shells gathered from local areas and accumulated in adjacent parts of the sea bottom which may have been in the direction of shallowing depth. In spite of presumed transport, rather few specimens show evidence of breaking or abrasion. Fossils in these limestone beds commonly are silicified, and samples have produced thousands of beautiful specimens; rare shells are pierced.

At several localities, the thicker limestones in the Logana have yielded a most unexpected fauna. Though the upper and lower few inches of the beds contain the typical *Dalmanella* coquina, the central part contains the large pelecypod *Modiolodon*. These pelecypods are closely packed in the rock, many being in presumed life position; most specimens have both valves together. A substantial number of gastropods and smaller pelecypods are in the interspaces between the larger *Modiolodon*. The insoluble residue contains much silt and some pyrite crystals; etching in hydrochloric acid produced an abundance of an oily scum.

The various features observed suggest obvious ecologic parallels between these *Modiolodon* beds and modern-day mussel banks. It is apparent that accumulations of *Dalmanella* shells were extremely close geographically to the *Modiolodon* mudflats. It is likely that both existed at the same time on slightly different parts of the sea bottom. No bored shells have been found at localities where the *Modiolodon* biocoenosis was found, but the one Logana locality that yielded pierced *Dalmanella* shells is less than 5 miles from such assemblages. This distance would seem a maximum between the biotope of the boring organism and the *Modiolodon* beds; it may well have been far shorter.

Modiolodon is at least superficially similar to Recent *Modiolus* in having a slightly inflated shell and presumably moderately thick soft parts. The genera are further similar in that *Modiolodon* has a thin shell. It is little more than twice as thick a shell as that of *Dalmanella*. In contrast to *Modiolodon*, *Dalmanella* is a small animal with a remarkably low ratio of volume of soft parts to shell. From the viewpoint of Recent predators, *Modiolodon* would have been an ideal prey. None of the hundreds of specimens obtained from the Lexington Limestone show evidence of boring. Bucher (1938, p. 5) indicates that none of the Late Ordovician pelecypods in the University of Cincinnati collection were bored; these are casts and molds which should show the mud filling of a hole.

Although animals do not necessarily act in what to humans is a logical manner, it is difficult to find any reason for the total neglect of *Modiolodon* as prey or indeed the neglect of all except one Lexington pelecypod. If one argues that predation may have been epifaunal, this hypothesis could have ruled out other pelecypods, but it does not apply to *Modiolodon*. There is no evidence to indicate that the *Modiolodon* beds were in brackish water, or that any physical barrier was present that separated them from the sites of *Dalmanella* accumulation. In fact, rare *Dalmanella* do occur in the *Modiolodon* beds. Even if the presumed carnivores were originally at the site of *Dalmanella* growth, currents or storms would have moved larvae, if not mature individuals, to the site of pelecypod growth. In such a choice environment, a modern predatory gastropod would have flourished.

The overlying Grier Limestone Member consists of about 135 feet of thin-bedded limestone (Black and others, 1965, p. C17). The Grier Limestone Member is interpreted from its texture, mineralogy, and fabric, as an extremely shallow-water deposit; it shows evidence of local high-energy deposition in the form of calcarenites composed mainly of crinoid ossicles. Scattered through the member are silicified zones that have yielded a fauna far more varied than that of the Logana. The fossils appear to have been shell heaps having a fabric even closer to that of present coquina beach rock than the Logana occurrences. There is evidence of size sorting of mollusks in that juvenile individuals are uncommon. Brachiopods are more varied in the Grier assemblages; in the collections obtained, brachiopods are more abundant in the Logana Member than in the Grier though, because so much of the Logana is unfossiliferous, it probably does not contain as many brachiopods as does the Grier. Pelecypods occur in the Grier, but *Modiolodon* is rare. The only generalization that may be made is that the localities where bored shells were found show indications of transport and mixing of biocoenoses. This same observation holds for the Curdsville occurrence.

Perhaps the presumed Paleozoic carnivorous gastropods were restricted to a diet of brachiopods, though the one bored Middle Ordovician pelecypod argues against this. Within the Brachiopoda, the evidence is strongly against any sort of specificity during predation. The lists compiled by Fenton and Fenton (1931) show 7 genera and 13 species of Devonian brachiopods that had been bored, and 4 genera of Late Ordovician brachiopods that they claimed had been penetrated.

Many of the Kentucky Middle Ordovician borings are in *Dalmanella*, but others are in *Rafinesquina*, *Sowerbyella*, and *Heterorthina*. One Ontario specimen is a bored *Hebertella*, and those from Quebec are in *Sowerbyella*. The boring from Alabama illustrated by Cooper (1956) is in *Taphrorthis*. If one predator were present during Middle Ordovician times, it would have preyed on five strikingly different genera. Living predatory gastropods considered at the generic level do prey on more than one genus and even more than one class at a locality, in the absence of preferred food, but there is at least more of a suggestion toward prey specilization than appears to be exhibited in the Middle Ordovician occurrences.

The number of penetrated shells is another factor to consider. The Kentucky material and that from Canada provide some quantitative approximation on ratio of bored to nonbored shells. Bucher (1938, p. 4) remarks that the five bored Ordovician specimens described by Fenton and Fenton are "all species of which hundreds, if not thousands of specimens were seen annually by the writer and his students in the field, in over twenty years, without a drilled one having been found." However, regarding one locality in Indiana, Bucher (1938, p. 6) remarked: "Here, *Dalmanella meeki* (Miller) forms regular banks in the Waynesville formation of the Richmond series. In a thin shale layer from which the shells could be withdrawn freely, about two dozen shells were obtained in a short time, each perforated by circular holes unmistakably like those produced by modern shell-borers."

The frequency of borings in Devonian shells is even less certain; one infers from Fenton and Fenton (1931) and the references they cite to illustrations of Clarke that all reports are of single occurrences. Inquiry for several years by Yochelson among paleontologists actively studying brachiopods resulted only in notification to him from time to time of an isolated bored shell. So far as known, there are no local concentrations of brachiopods bearing cylindrical perforations in the Paleozoic of North America, though data for the Ordovician are scant and data for the remainder of the Paleozoic are virtually nonexistent. Withal, fossils in the Cincinnati area have been assiduously collected for more than a century. For nearly four decades, mention of Late Ordovician gastropod predation has been available in the literature. The absence of any reports of accumulations of bored shells may be judged to have some significance.

It is well known that where predatory gastropods occur in modern commercial pelecypod beds, they are commonly present in abundance. The predators have a voracious appetite and are a menace to the prey populations. If the presumed Ordovician carnivore did attack brachiopods rather than pelecypods, it is difficult to understand why borings are not locally abundant. The frequency of boring is less than 1 percent at the Kentucky localities and not appreciably higher in Ontario. The Ordovician in Kentucky and Ohio is world renowned for the profusion of fossils, particularly brachiopods; the number of specimens available in some of the outcrops staggers the imagination. With such an abundant food supply available, one is hard pressed to understand why a carnivore would not thrive and undergo a population explosion within each stratum of shells.

It is evident that borings are not preferentially on either brachial or pedicle valves. There is no particular preference for the spot of penetration. Although Recent predators vary their point of attack, for Naticidae the distribution of holes is not as diverse as shown in these fossil samples. In itself this variation need not be significant, because Naticidae prey on the Recent infauna, and the articulate brachiopods are generally considered to have been exclusively part of the epifauna.

The transverse outlines of many Ordovician holes show some variation from circularity. The holes vary widely in size, and there is no obvious relationship between size of bored shell and size of hole. Even though conclusive evidence on form and inclination of these Middle Ordovician holes is hard to find, because of the thinness of the bored shell, there is indication in many shells of a chamfer limited to one or two quadrants rather than a true bevel. Many holes clearly have the axis oblique rather than perpendicular to the shell. Holes in the slightly thicker Late Ordovician shells illustrated by Bucher (1938) show diversity and asymmetry comparable to that of the Middle Ordovician material but, because of their greater shell thickness, asymmetry is more apparent. Indeed, the large proportion of inclined borings is one of the unusual characteristics of these Ordovician holes. The data suggest that these are cylinders of almost uniform diameter piercing the shell at an oblique angle.

A final observation may be made on boring direction and multiplicity of boring. Recent occurrences of multiple boring into one prey shell are known, as is boring starting on the inside of a dead shell. In a population sense, however, both these features are most atypical of Recent predation, and the frequency of each is exceedingly low. In contrast, in both the Middle and Late Ordovician material examined, the frequency of both features was higher by at least several orders of magnitude.

PALEOANATOMY AND SYSTEMATIC POSITION OF PRESUMED PREDATORS

It has been shown that the result of Recent naticid and muricid boring activity differs (p. B7). If any similarity of the Ordovician holes to Recent holes can be inferred, the holes are to be allied to those of the Muricidae rather than the Naticidae. It is generally accepted that the naticid stock is more primitive than the muricid stock. Certainly the accessory boring organ, the padlike feature of the Naticidae, is less elaborate than the elongate organ of the Muricidae. Yet something like this more elaborate organ must be ascribed to the hypothetical Ordovician borer.

For a gastropod to bore an oblique hole, theoretically, the accessory boring organ should be oblique. That is, one side would be padlike and short, as in the naticids and the opposite side would be extensible, about to the degree of the fully stalked muricid organ. Although it is impossible to say that this condition did not occur, it is contrary to the anatomy so far observed in any Recent gastropod borers.

It is to be emphasized that both the Naticidae and Muricidae are Caenogastropoda. None of the Middle Ordovician genera that have been tentatively assigned to the Caenogastropoda has a shell form remotely resembling that of the two Recent boring groups. Predation is limited to a few Recent Caenogastropoda. No Recent Archaeogastropoda, a more primitive group, are known which have a predatory habit.

Gastropods are extremely common in some parts of the Lexington Limestone, and several thousand specimens were obtained from the silicified residues. Although *Loxoplocus* (*Lophospira*) is the predominant form, a fair generic diversity occurs. Without exception, all genera found in the formation are those presumed to be Archaegastropoda (Diotocardia).

Genera presumed to be more advanced Caenogastropoda (Monotocardia) are known from slightly older rocks and from rocks of equivalent age in other areas. Although these more advanced gastropods may eventually be found in the Lexington Limestone, the large amount of material supplied indicates that if they were present at all, they could only have been exceedingly rare. No specimens of *Diaphorostoma* or *Platyceras* were found, and only two specimens of related *Strophostylus* were questionably identified. That genus might be a caenogastropod, though it too is considered to be an archaeogastropod.

The shell *Loxoplocus* (*Lophospira*) is similar enough to the shell of Recent pleurotomariacean gastropods to suggest that soft parts also were nearly identical. The Recent pleurotomariaceans are unusual in having two gills; further, these are aspidobranch gills which are relatively susceptible to fouling by sediment (Yonge, 1947). This delicate gill restricts mobility to firm bottoms. Presumably, restriction to a firm bottom also characterized the fossil pleurotomariaceans, though clearcut evidence is difficult to obtain. This restriction would cause difficulties in moving from one prey shell to another if the prey lived either directly on a soft bottom or attached to it by a pedicle.

Liospira, although low spired, is generally similar to other pleurotomariaceans, and the same difficulties would apply to it as a potential driller. *Sinuites* and *Carinaropsis* are bellerophontaceans, bilaterally coiled, but in other respects probably to be allied to the pleurotomariaceans.

Fenton and Fenton, (1931, p. 525) suggested that *Platyceras* or an allied genus might have been a borer. This suggestion derives from the presumed coprophagous habit of the group. Although this possibility cannot be ruled out for the Devonian boring, there is no proof to support the basic assumption. It is difficult to reconcile adoption to sedentary clinging and to stalking of prey in the same animals. In any event, this habit would not apply to the borings under consideration, for not only is *Platyceras* unknown in the Middle Ordovician, but *Cyclonema*, the precursor of this genus (Bowsher, 1955), is unknown in the area until rather late in the time of deposition of the Lexington Limestone.

Although *Naticopsis* was suggested by Yakovlev (1926) as a Permian predator, none of the Recent Neritacea show this habit, and again there is no basis for assuming predation by this group. Further, it is unknown until Devonian times. Regardless of whether one can assign habits to former living animals without presenting concrete evidence, Dr. Boris Licharev (written commun., 1965) who collected the material described by Yakovlev, notes that no *Naticopsis* occur at the localities where borings were found.

SUMMARY

Boreholes drilled by Recent predatory gastropods show only moderate variation in shape, but a wide variation in size and an even larger variation in position on the prey shell. When differences in the ethology and boring mechanisms of the two principal groups of Recent borers are considered, much of the apparent variety is shown to be the result of somewhat different modes of boring, coupled with strikingly different modes of hunting prey. If deep borings of naticids and muricids in thick-valved prey are studied separately, the characters of each can be demonstrated to be distinctive. Each type of borehole shows slight variation around a central form. A quantitative demonstration of shape variation has not yet been made, but it is qualitatively apparent that in a statistical sense there is little fluctuation from two idealized forms of holes. The almost cylindrical muricid hole and the conspicuously parabolic naticid hole are distinctive. Borings into thin-valved prey are less easy to distinguish, but with some difficulty the two forms of boring commonly can be differentiated.

By comparison with enough Recent borings, all the features shown can be matched in the Middle Ordovician borings. To do this, one must select Recent borings that deviate far from the two central forms. If the Middle Ordovician bored shells are all pooled and treated as one sample of bored shells, it becomes apparent that they differ in several particulars from the Recent borings.

First, there is more variation in horizontal section among the fossils than occurs even when the work of living maticids and muricids is lumped. Second, although a uniformly beveled edge is the norm in each modern group, it is the exception among these fossils; chamfer of one or two quadrants is closer to the norm in the fossils. Third, where an angle of boring can be obtained, it is characteristically oblique, whereas in the modern predation, holes are almost invariably at right angles to the shell surface. Fourth, chamfer in the interior, and therefore presumably boring from the interior, is common among those fossil shells that gave any indication of chamfer; boring through the interior of the dead shells does occur in the Recent, but it is rare.

The degree of predation should also be considered. Although there are some temperature and salinity barriers to carnivorous gastropods in modern environments, where predation occurs it characteristically does so on a large scale. On the basis of the reasonable assumption that the probability of bored shells being preserved as fossils is about as high as that of other shells, the degree of predation observed is remarkably low. With one exception, predation is confined to brachiopods. The only common factor between the Recent and Middle Ordovician predation is that of erratic distribution of the holes on the surface of prey valves, admittedly one of the conspicuous characters of Recent muricid epifaunal predation.

The identity of a gastropod predator and its functional anatomy should be considered. Within the Grier Limestone Member of the Lexington Limestone, *Loxoplocus* (*Lophospira*) is so abundant in one bed that it makes a useful local mapping unit. Yet at most localities where it occurs, there is no predation. This observation has some pertinence, for Bucher has (1938, p. 7) argued that because *Loxoplocus* (*Lophospira*) *perlamellosa* (Ulrich in Ulrich and Scofield) is the only gastropod in the bed that yielded late Cincinnatian bored dalmanelloids, it was the borer. The presumed anatomy of *Loxoplocus* (*Lophospira*) argues against this, as does the occurrence of borings in the absence of that subgenus. The only generalization that may be made is that no consistent outcrop occurrence between any family of Paleozoic gastropods and bored shells has been demonstrated.

CONCLUSIONS

These boreholes which date from the Middle Ordovician are almost certainly of biologic origin. That they are the result of gastropod predation, however, is an entirely different point. To have produced the type of inclined cylindrical hole most commonly observed in these fossils, a hypothetical gastropod predator would have required an accessory boring organ anatomically intermediate in form between that in the two predatory families known today. It would have had a preference for brachiopods having relatively small bodies, even though pelecypods containing larger bodies were present. The inexplicable point is that whether it preferred brachiopods or pelecypods, the unknown predator held predation and presumably reproduction to an exceedingly low level in the face of an abundant food supply.

We conclude that the morphology of the holes does not give unequivocable support to gastropod predation as their cause. Gastropod predation can be accepted as the explanation for selected borings in fossils of the later Mesozoic. Fischer (1962) is justified in concluding that the available evidence is too equivocal to suggest that this habit occurred independently 200 million years earlier. On balance, our observations as interpreted here indicate to us that the Ordovician borings were not the result of activity by an unknown gastropod.

The primary purpose of this paper is to record information on Recent and Ordovician holes so that each reader may justify for himself the validity of the Ordovician-gastropod-predation hypothesis. Nevertheless in rejecting this particular hypothesis, there is some need to offer an alternative origin for these enigmatic holes.

It is generally recognized that the paleontologist, except under the most unusual circumstances, deals only with a small part of the former biota. Vast numbers and varieties of soft-bodied organisms which must have existed have left virtually no trace of their occurrence. Speculation about them is based almost entirely on what can be observed today.

One of the characteristics of attached soft-bodied animals and plants is a basal stalk which typically is cylindrical. When these organisms settle, their base of attachment is a circle when viewed from above. If the substrate is at a slight angle, the base of attachment is an oval, essentially along an oblique plane through a cylinder.

It is suggested that an unknown species, or several species, of a soft-bodied organism was responsible for the Middle Ordovician holes. As does any other living creature, this form had ecologic preferences and limitations that restricted it. Presumably, it preferred areas where brachiopods were abundant or areas where brachiopod shells commonly formed the substrate. The position of a hole in a shell would be nothing more significant than the place where a larval stage first settled. Apparently the shell simply provided a hard substrate. and it was not a critical matter whether the interior or the exterior of a shell was facing upward.

We must further assume that individuals could have secreted a body fluid at the base which dissolved and removed the shell under the attachment area. Thus the holes would have been primarily chemical in origin rather than chemicomechanical. There would be a basis for the low frequency of the holes were this secretion only a pathologic condition in an otherwise normal sessile organism. If the substrate shell was tilted, etching into it might have automatically resulted in obliquity. Erratic secretion from part of the base, or death of the organism after the thin shell substrate was penetrated, would explain some of the irregularity observed in a few holes.

Ascribing the Ordovician cylindrical holes to a stalked sessile soft-bodied organism in a sense is substituting one theory for another. No modern organisms are known that penetrate shells in the manner described above. This tentative hypothesis may be completely false. However, it is the only logical one we can suggest that fulfills the requirements of producing rare cylindrical holes that penetrate from either the interior or exterior of a shell and follow either a straight or an oblique course.

REGISTER OF KENTUCKY LOCALITIES

4868–CO	Valley View quadrangle, Jessamine County. Roadcut in southwest quarter of quadrangle, running from Trinity Church to Antioch Church, 1 mile southwest (along the Kentucky River) of the northern termination of Kentucky Route 595 at the Kentucky River (bench mark 567). Grier Limestone Member of the Lexington Limestone.
4872–CO	Same locality as above. 23 ft above 4868–CO; Grier Limestone Member of the Lexington Limestone.
4956–CO	Salvisa quadrangle, Mercer County or Anderson County. Roadcut on west side of the Kentucky River at bridge crossing of the central Kentucky Parkway on the north side of the parkway. Kentucky coordinate system: North Zone, east 1,835,050 ft and north 173,600 ft. 137 ft above contact of Tyrone and Lexington Limestones; 85 ft above base of Grier Limestone Member.
5022–CO	Keene quadrangle, Woodford County. Quarry and roadcut, first outcrop southeast of crossing of Kentucky Route 33 (Ford Mills Rd.) and Clear Creek. Kentucky coordinate system: North Zone, east 1,857,000 ft and north 162,600 ft. Float from lower 22 ft of Curdsville Limestone Member of the Lexington Limestone.
5093–CO	Frankfort West quadrangle, Franklin County. Devils Hollow Road, lat 38°11'38½"; long 84°53'13". Macedonia Bed in lower part of Grier Limestone Member of the Lexington Limestone.
5098–CO	Valley View quadrangle, Jessamine County. Roadcut along stream immediately across (northwest) of the Kentucky River from north termination of Kentucky Route 595, in the southwest quarter of the quadrangle. 40–45 ft above the base of Grier Limestone Member of the Lexington Limestone.
6030–CO	Frankfort East quadrangle, Franklin County. Glenns Creek Road at county lines; in excavation just north of main gate of Old Crow distillery. 29–32 ft above contact of Tyrone and Lexington Limestones; lower part of Logana Member of the Lexington Limestone.
D–1196–CO	Frankfort East quadrangle, Franklin County. Along Interstate Highway 64, on east side of Kentucky River, just below bridge abutment and about 0.8 mile north of Glenns Creek. Recollection of April 1965. Top of Logana Member, Lexington Limestone.

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[Italic page numbers indicate major references]

PLATES 1–5

PLATE 1

[All figures × 5]

FIGURE 1. Boring by *Eupleura caudata* (Say), from lower Chesapeake Bay, Va.

Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; cylindrical borehole with negligible bevel. OD (outside diameter) 1.5 mm, ID (inside diameter) 1.1 mm. USNM 673535.

2–11. Borings by *Eupleura caudata etterae* Baker, from Chincoteague Bay, Va.

2. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; cylindrical borehole with slight bevel. OD 1.4 mm, ID 0.9 mm. USNM 673536.
3. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; parabolic borehole with sharp edge. OD 1.5 mm, ID 0.7 mm. USNM 673537.
4. Boring in *Balanus venustus niveus* Darwin from Bogue Sound, N.C.; parabolic borehole with countersunk edge. Note irregularity of the surfaces of the hole imposed by the sculpture of the barnacle valve. OD 1.4 mm, ID 0.9 mm. USNM 673538.
5. Borings in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C., from inside the valve in the area of the adductor muscle scar outward toward a live oyster attached to the outside of the oyster valve being bored. Snails were crowded in observational aquarium; only one of the four holes is complete. Range of OD 1.6–2.3 mm. USNM 673539.
6. Longitudinal section of boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; hole is slightly inflated in parts of the shell consisting of chalky calcite and constricted at the outer and inner openings where the shell is of a hard translucent nature. OD 1.3 mm, ID 0.7 mm, MD (middle diameter)1.6 mm, depth 1.8 mm. USNM 673540.
7. Longitudinal section of boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; a boring similar to that in fig. 6 except that the inner and outer strata of translucent calcite are thicker. The inner opening is narrowly constricted by a wide shelf. OD 1.3 mm, ID 0.8 mm, MD 1.6 mm, depth 1.5 mm. USNM 673541.
8. Longitudinal section of boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; the two strata of soft chalky calcite at the inner end of the hole have been excavated slightly more than the remaining translucent shell. MD 1.6 mm, ID 0.9 mm, depth 2.4 mm. USNM 673542.
9. Longitudinal section of boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; in homogeneously translucent calcite, a uniform nearly cylindrical borehole with a slight inflation at the inner end. OD 1.1 mm, ID 0.9 mm, MD 1.2 mm, depth 1.5 mm. USNM 673543.
10. Longitudinal section of boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; hole is an oblique paraboloid. Drilling was first carried out at right angles to the shell surface and then veered to one side to effect entrance into the mantle cavity of the prey. OD 1.3 mm, ID 0.6 mm, depth 1.6 mm. USNM 673544.
11. Longitudinal section of boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; markedly stratified structure of the shell contributes to the irregularity of the surface of the hole. As in fig. 10, the hole was first bored perpendicular to outer shell surface, possibly until preliminary penetration was effected and then in the direction of the oyster mantle cavity. OD 1.2 mm, ID 0.5 mm, MD 1.6 mm, depth 1.6 mm. USNM 673541.

12. Boring by *Ocenebra erinacea* (Linné) from Plymouth, England.

Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; incomplete hole bored on the inside of the oyster valve. OD 1.4 mm. USNM 673545.

13. Boring by *Ocenebra japonica* (Duncker) from Puget Sound, Wash.

Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; typical slightly parabolic muricid hole, appearing slightly naticid in shape because of the thin shell of the prey. OD 1.1 mm, ID 0.6 mm. USNM 673546.

14–21, 24. Boring by *Urosalpinx cinerea follyensis* Baker from Chincoteague Bay, Va.

14. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; hole is characterized by wide inner opening and slightly irregular sides. OD 1.9 mm, ID 1.2 mm. USNM 673547.
15. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; edge of outer opening conspicuously countersunk, slight shelf in inner opening. OD 2.0 mm, ID 1.0 mm. USNM 673548.
16. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; cylindrical hole with countersunk outer edge, shelf at inner opening, opening to one side. OD 2.1 mm, ID 0.9 mm. USNM 673549.
17. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; hole with conspicuous crescent-shaped shelf. OD 2.0 mm, ID 1.6 mm. USNM 673550.
18. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; parabolic hole with irregularity on one side, resembling a naticid borehole. OD 2.3 mm, ID 1.4 mm. USNM 673551.
19. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; hole irregularly elliptical parabolic. OD 1.4×2.0 mm, ID 0.6×0.9 mm. USNM 673552.
20. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; oblique, spherical, parabolic hole with small inner opening to one side. OD 1.3 mm, ID 0.4 mm. USNM 673552.

PLATE 1—Continued

FIGURE

21. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; highly irregular form of parabolic hole probably resulting from heterogeneity of structure and form of shell. OD 1.3 mm, ID 0.9 mm. USNM 673553.

24. Longitudinal section of boring in aragonitic shell of snail *Murex fulvescens* Sowerby from Beaufort Inlet, N.C.; the hemogeneity of the shell material permitted drilling of the smooth-surfaced nearly cylindrical hole. OD 1.6 mm, ID 1.2 mm, depth 2.5 mm. USNM 673554.

22, 23. Boring by *Urosalpinx cinerea follyensis* Baker from Wachapreague Bay, Va.

22. Boring in small thin-shelled rapidly growing *Crassostrea virginica* (Gmelin) from Cape Cod, Mass.; oyster shell at site of perforation is composed of hard translucent calcite, hole is elliptical parabolic. OD 1.7×2.0 mm, ID 1.0×1.2 mm. USNM 673555.

23. Longitudinal section of boring illustrated in fig. 23. Depth of hole 0.6 mm. USNM 673555.

25. Boring by *Urosalpinx cinerea* (Say) from Burnham-on-Crouch, England.

Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; spherical parabolic hole, predominantly so shaped because of location in thin-shelled oyster valve. OD 1.2 mm, ID 0.6 mm. USNM 673556.


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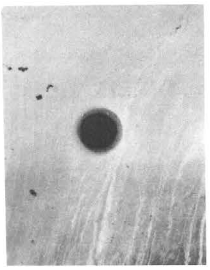
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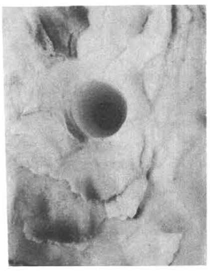
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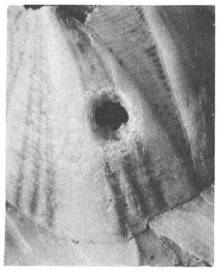
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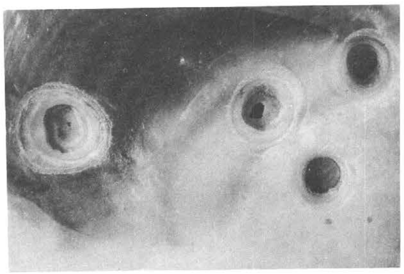
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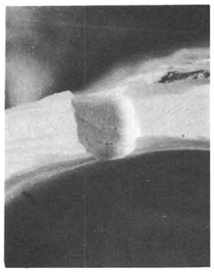
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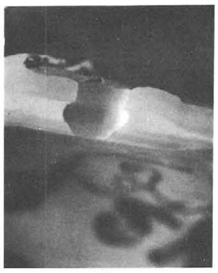
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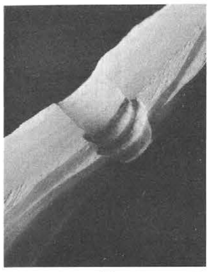
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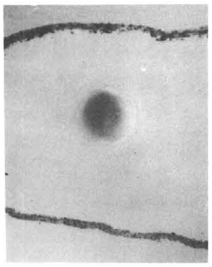
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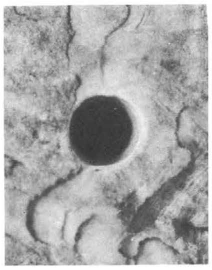
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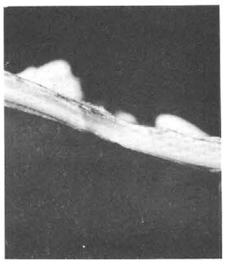
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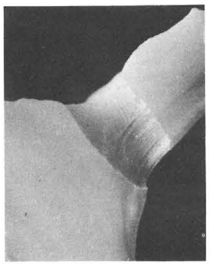
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GASTROPOD BORINGS IN RECENT SHELLS

PLATE 2

[All figures × 5]

FIGURES 1–4. Borings by *Thais haemostoma floridana* Conrad, from Bogue Sound, N.C.

1. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; hole drilled typically at the juncture of the valve edges. Drilling frequently proceeds into the opposing valve, leaving a slight concavity before the snail extends its proboscis into the cavity of the bivalve to feed. MD 1.6 mm. USNM 673557.

2. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; hole similar to that in fig. 1 but larger. MD 2.0 mm. USNM 673557.

3. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; hole is highly irregular as a result of the structure and configuration of the oyster shell in the vicinity of the borehole. OD 1.6×2.0 mm, ID 0.8×1.2 mm. USNM 673558.

4. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; hole was drilled at the edge and juncture of the two valves of the oyster, but "misdirected" into the lower valve for some distance (shown here) before the snail turned into the cavity of the oyster to feed. MD 1.6 mm. USNM 673559.

5. Boring by *Thais haemastoma* Linné from Bimini, Bahamas.

Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; incomplete hole bored obliquely from inside the oyster valve. A small live oyster growing on the outside of the bored valve probably stimulated selection of the site by the snail. OD 1.4×1.6 mm, ID 1.1 mm. USNM 673560.

6–9. Borings by *Polinices duplicatus* (Say) from Cape Cod, Mass.

6. Boring in *Mya arenaria* Linné from Cape Cod, Mass.; incomplete spherical parabolic hole with central boss in the bottom. OD 2.1 mm. USNM 673561.

7. Boring in *Mya arenaria* Linné from Cape Cod, Mass.; irregularity of shell surface causes irregularity on the edge of the hole. OD 2.3 mm. USNM 673562.

8. Boring in *Mya arenaria* Linné from Cape Cod, Mass.; the borehole is almost through the shell and emphasis of rasping in the interradial region has left the central boss. OD 2.7 mm. USNM 673563.

9. Same specimen as in fig. 8 but showing the spherical parabolic borehole complete. OD 2.4 mm, ID 1.5 mm. USNM 673563.

10. Boring by *Murex fulvescens* Sowerby from Beaufort Inlet, N.C.

Boring in *Mercenaria mercenaria* (Linné) from Bogue Sound, N.C.; hole is drilled typically at juncture of two valves. Note persistence of shell pattern at the bottom of the elliptical parabolic hole, probably indicating differences in hardness. OD 3.6×7.2 mm. USNM 673564.

11–14. Borings by *Murex florifer arenarius* Clench and Perez Farfante from Alligator Harbor, Fla.

11. Boring in *Chione cancellata* (Linné) from Bogue Sound, N.C.; incomplete hole reflecting the costa over which it was drilled. OD 2.3 mm. USNM 673565.

12. Boring in *Chione cancellata* (Linné) from Bogue Sound, N.C.; illustrates effect of the cancellate sculpture of the substratum on the form of the hole. OD 1.9 mm, ID 1.0 mm. USNM 673566.

13. Boring in *Chione cancellata* (Linné) from Bogue Sound, N.C.; this clam is larger than that in fig. 12, but the effect of the sculpture of the shell on the hole is still evident. Hole is deeply inflated. OD 1.6×2.3 mm, ID 1.2 mm. USNM 673567.

14. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C. Note that a hole bored by this snail in smooth shell resembles the spherical parabolic hole of naticids. OD 2.0 mm, ID 1.2 mm. USNM 673568.

15. Boring by *Murex pomum* Gmelin from Alligator Harbor, Fla.

Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; hole is spherically parabolic, and the steepness of the curve of the sides is intermediate between the typically naticid boreholes. OD 2.0×2.0 mm, ID 1.2×1.5 mm. USNM 673569.

PLATE 2—Continued

FIGURE 16. Boring by *Bedeva haleyi* (Angas) from Port Jackson, Australia.

Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; the irregular sculpture of the surface of the oyster shell produced a somewhat disfigured borehole. OD 1.0 mm, ID 0.8 mm. USNM 673570.

17–25. Borings by *Murex brevifrons* Lamark from Puerto Rico.

17. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; incomplete elliptical parabolic hole with concave bottom. OD 3.4×3.9 mm, ID 2.3×2.7 mm. USNM 673571.

18. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; elliptical parabolic hole with pronounced shelf. OD 2.8×4.1 mm, ID 1.2×2.0 mm. USNM 673572.

19. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; oblique nearly spherical parabolic hole. OD 2.9×3.1 mm, ID 1.6×1.8 mm. USNM 673573.

20. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; oblique elliptical parabolic hole with pronounced shelf. OD 3.9×4.3 mm, ID 1.0×2.6 mm. USNM 673574.

21. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; nearly spherical parabolic hole with conspicuous crescentic shelf. OD 3.7×3.9 mm, ID 1.7×2.3 mm. USNM 673575.

22. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; elliptical parabolic hole with slightly crescentic shelf. Hole bored between two high ridges, which are out of focus in photograph, on the surface of the shell of the oyster. OD 3.9×4.8 mm, ID 1.4×2.5 mm. USNM 673576.

23. Boring in *Crassostrea virginica* (Gmelin) from Bogue Sound, N.C.; hole drilled at juncture of upper valve, to the right, and lower valve, to the left. The snail "mistook" the inner valve for continuation of the upper valve and bored into it a short distance, shown by the small circular hole at bottom, before discovering oyster flesh between the valves to the right (between large intermediate level oval boring and small circular boring beneath). OD 3.5×3.6 mm. USNM 673577.

24. Longitudinal section of boring in *Crassostrea virqinica* (Gmelin) from Bogue Sound, N.C.; the section was ground slightly off center to emphasize the alternation of chalky and translucent strata of the oyster shell and the deeper excavations by the snail into the chalky strata. MD 3.0 mm, depth 6.3 mm. USNM 673578.

25. Longitudinal section of boring in *Crassostrea virqinica* (Gmelin) from Bogue Sound, N.C. This hole is typical for the species; it illustrates the slightly oblique spherical parabolic shape with conspicuous shelf, inner opening to one side of center, and gentle countersinking of the outer edge. The perforation was made almost entirely in translucent calcite; to the right of the hole is seen stratification of chalky and translucent shell. OD 4.7 mm. ID 1.8 mm, depth 2.2 mm. USNM 673579.


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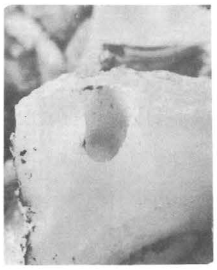
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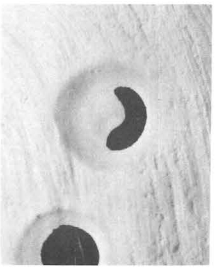
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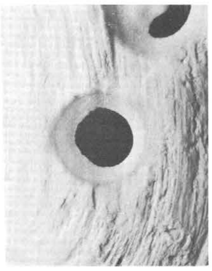
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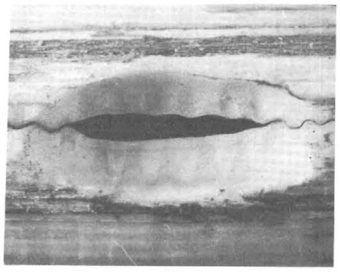
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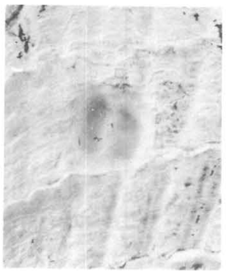
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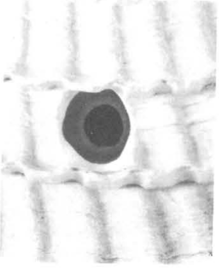
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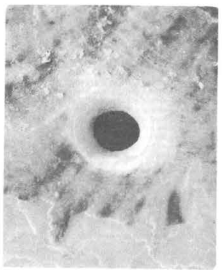
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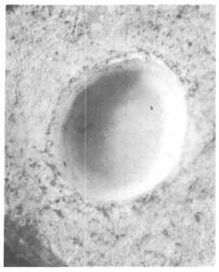
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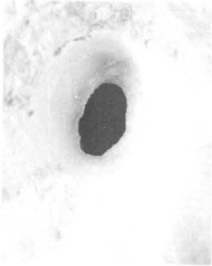
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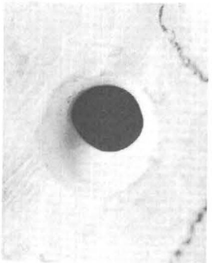
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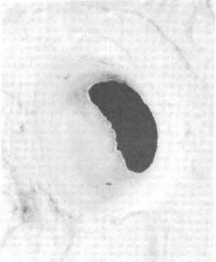
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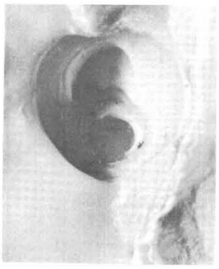
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GASTROPOD BORINGS IN RECENT SHELLS

PLATE 3

[All figures × 5, except figs. 9 and 21 which are × 2½ and figs 13 and 16 which are × 10]

FIGURES 1–6. Borings by *Lunatia heros* (Say) from Cape Cod, Mass.

1. Boring in *Mya arenaria* Linné from Cape Cod, Mass.; note persistence of valve sculpture and central boss at the bottom of the hole. OD 5.0 mm. USNM 673580.
2. Boring in thin-shelled *Mya arenaria* Linné from Cape Cod, Mass.; note irregularity of inner opening, due perhaps to thinness of the shell. OD 6.4 mm, ID 4.7 mm. USNM 673581.
3. Boring in moderately thick shell of *Mya arenaria* Linné from Cape Cod, Mass. OD 6.6 mm, ID 3.4 mm. USNM 673582.
4. Boring in *Mercenaria mercenaria* (Linné) from Cape Cod, Mass.; illustrates the classical form of the spherical parabolic naticid borehole in a prominently ridged valve. The beveling of the hole includes the shell ridges OD 4.4 mm, ID 2.8 mm. USNM 673583.
5. Boring in thick-shelled *Mya arenaria* Linné from Cape Cod, Mass.; a typical spherical parabolic naticid borehole in smooth shell. Note the gentle beveling of the outer edge of the hole. OD 5.0 mm, ID 3.6 mm. USNM 673584.
6. Longitudinal section of boring in *Mya arenaria* Linné from Cape Cod, Mass.; illustrates the graceful parabolic curve of the typical naticid borehole. OD 5.9 mm, ID 3.4 mm, depth 1.2 mm. USNM 673585.

7. Boring by *Lunatia triseriata* (Say) from Cape Cod, Mass.
Boring in *Mytilus edulis* Linné from Cape Cod, Mass.; shows the beveling of the edge of the outer opening as a result of rasping of the periostracum. OD 1.6 mm, ID 1.1 mm. USNM 673586.

8. Boring by *Natica severa* (Gould) from Korea.
Boring in *Mercenaria mercenaria* (Linné) from Bogue Sound, N.C.; interior surface of hole is very smooth; outer edge is moderately beveled; outer opening is circular and inner opening is elliptical. In this hole the parabolic form changes from spherical to elliptical inward. OD 3.3×3.3. mm, ID 1.6×1.9 mm. USNM 673587.

9. Boring in *Rafinesquina* cf. *R. alternata* Emmons from Waynesville shale, from cuts 14 and 15 on Big Four Railroad, east of Weisburg, Ind.
Boring in brachial valve; this is the original drawing of fig. 1E of Fenton and Fenton (1931). Carnegie Museum of Pittsburgh no. 9833/7094.

10, 11. Boring in *Dalmanella* from Waynesville shale, near junction of Indiana State Roads 1 and 46, Cedar Grove quadrangle, Indiana.

10. Boring in brachial valve. USNM 155010.
11. Boring in brachial valve. USNM 155011.

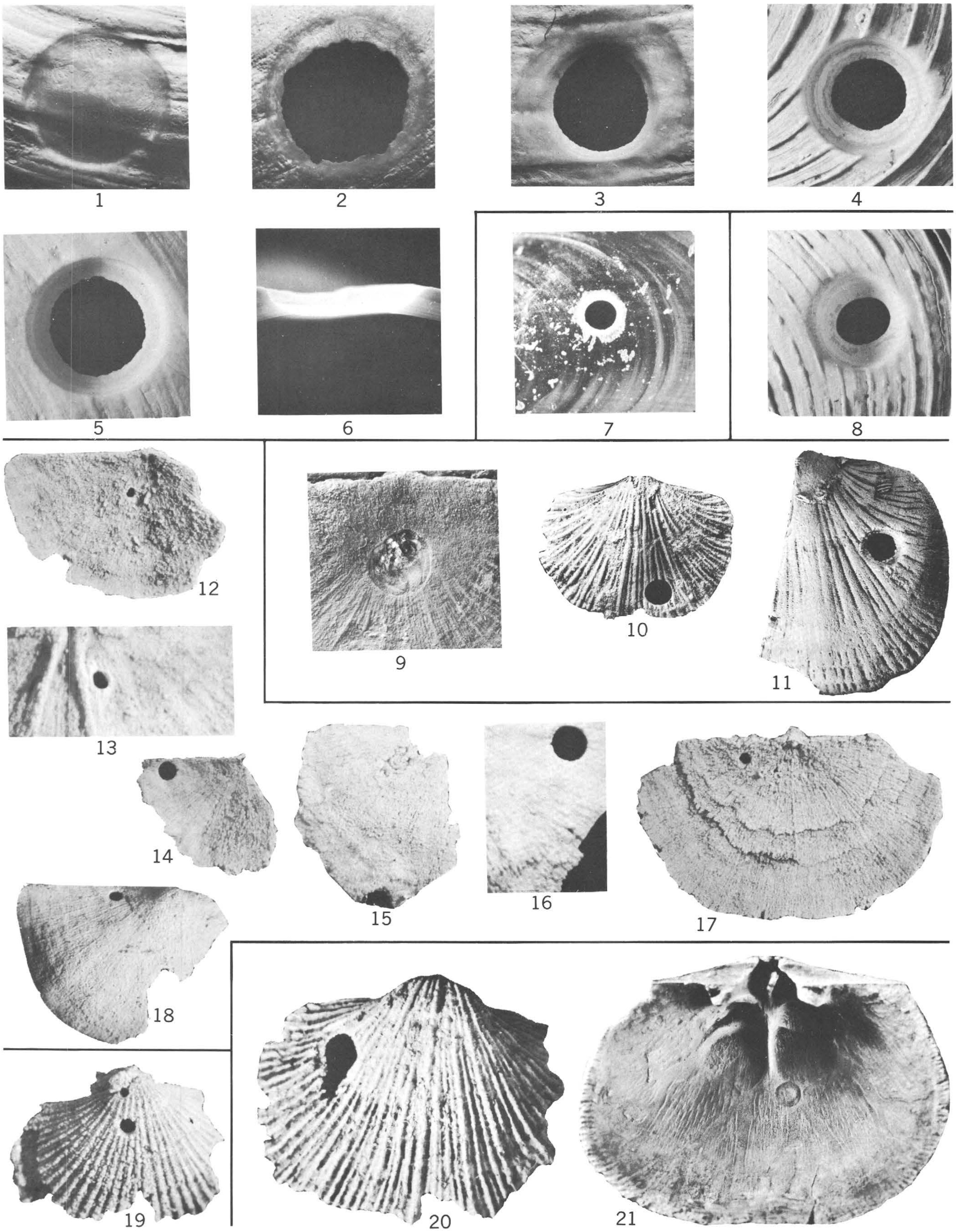
12–18. Borings in *Sowerbyella* from the Shipshaw Formation, 1¼ miles below Chute aux Galets, Quebec.

12. Small boring in brachial valve. USNM 155012.
13. The same specimen from the interior, enlarged.
14. Intermediate size boring in brachial valve. USNM 155013.
15. Broken boring on edge of brachial valve. USNM 155014.
16. The same specimen as fig. 14 from the interior, enlarged.
17. Small boring in brachial valve. USNM 155015.
18. Small boring in pedicle valve; distinctly oval in outline. USNM 155016.

19. Boring in *Hebertella* from Ottawa Formation, 1.2 miles west of Odessa interchange on Highway 401, Ontario.
Small boring in pedicle valve; the smaller hole above may be artificial. USNM 155017.

20. Boring in *Taphrorthis peculiaris* Cooper from the lower one-third of Pratt Ferry Formation of Cooper (1956), 0.2 mile south of Pratt's Ferry, Blocton quadrangle, Ala.
Boring in pedicle valve; the lower half of the hole is broken. This specimen is figured by Cooper (1956) as pl. 38, fig. 19. USNM 117984b.

21. Boring in *Mimella globosa* (Willard) from the Benbolt Formation of Cooper and Prouty (1943), from the roadside ¼ mile southwest of New Bethel Church, Hilton quadrangle, Virginia.
Incomplete boring in interior of brachial valve; this specimen is figured by Cooper (1956) as pl. 89, fig. 10. USNM 117038b.



GASTROPOD BORINGS IN RECENT AND FOSSIL SHELLS

PLATE 4

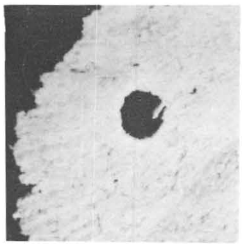
[All figures × 5, except fig. 7 which is × 1; figs. 14 and 15, × 2; and figs. 12 and 14, × 10]

FIGURES 1–5. Borings in brachiopod shells from the Grier Limestone Member of the Lexington Limestone, in Kentucky at locality 4868–CO.
  1. Part of pedicle valve of *Rafinesquina*? USNM 155018.
  2. Interior of same specimen as fig. 1.
  3. Part of fragment, probably from a rafinesquinoid brachiopod. USNM 155019.
  4. View of same boring from other side; the specimen is too worn to determine interior and exterior.
  5. Exterior of part of fragment of *Rafinesquina*?; the specimen is too worn to determine which valve is bored. USNM 155020.

6–8. Borings in brachiopod shell from the Logana Member of the Lexington Limestone, in Kentucky at locality 6030–CO.
  6. Part of interior of brachial valve of *Heterorthis* into which two holes were bored. USNM 157854.
  7. Exterior of same specimen, natural size.
  8. Exterior of specimen showing both borings.

9–13. Borings in brachiopod shells from the Grier Limestone Member of the Lexington Limestone, in Kentucky at locality 4872–CO.
  9. Part of brachial valve exterior of *Heterorthina*?; silica adheres to left side of the hole. USNM 155021.
  10. Fragment of brachial valve exterior of *Heterorthina*?. USNM 155023.
  11. Pedicle valve exterior of *Sowerbyella;* two borings occur in this valve. USNM 155024.
  12. Part of brachial valve interior of *Sowerbyella,* enlarged. USNM 155022.
  13. Exterior of same specimen as fig. 12; a bryozoan colony adheres to the specimen and was trimmed from the photograph.

14–18. Borings in *Dalmanella* from the Logana Member of the Lexington Limestone, in Kentucky at locality D–1106–CO.
  14. Interior of brachial valve. USNM 155025.
  15. Exterior of same specimen as fig. 14.
  16. Interior of brachial valve. USNM 155026.
  17. Exterior of part of same specimen as fig. 6, enlarged.
  18. Exterior of pedicle valve; the holes to the right and below are probably artificial. USNM 155027.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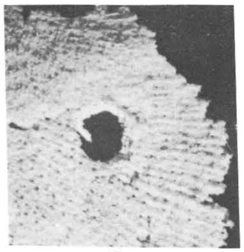
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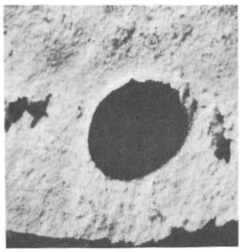
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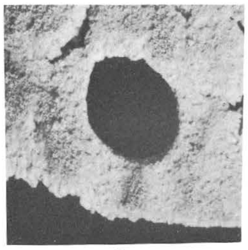
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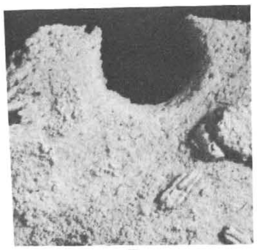
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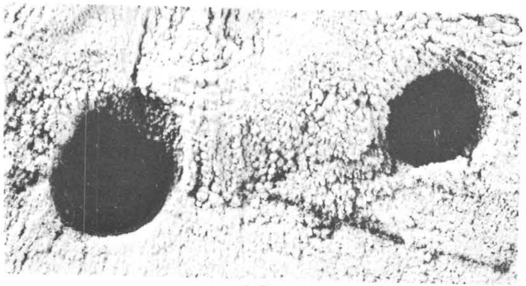
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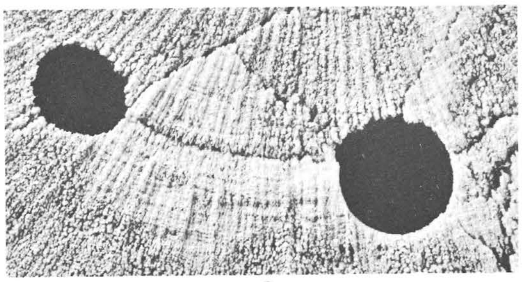
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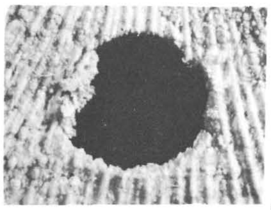
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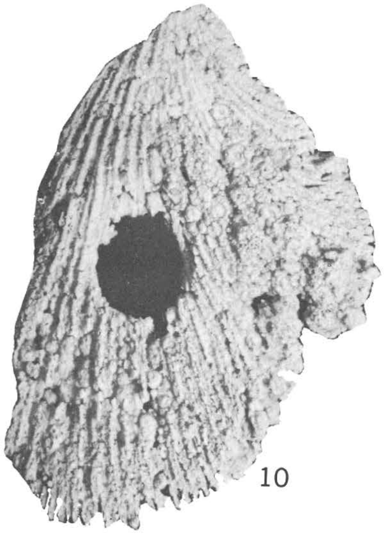
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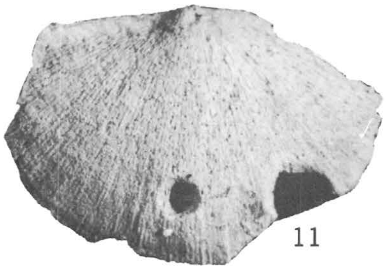
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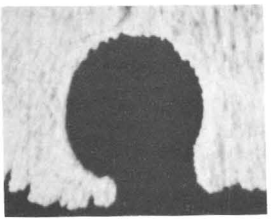
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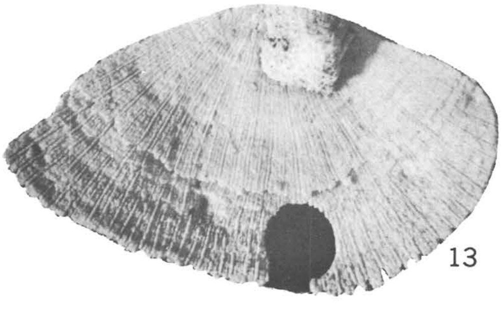
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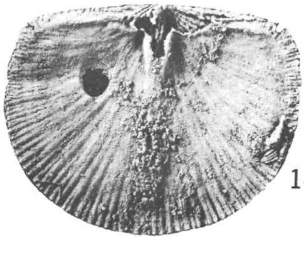
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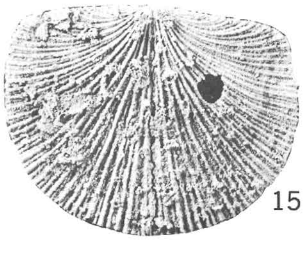
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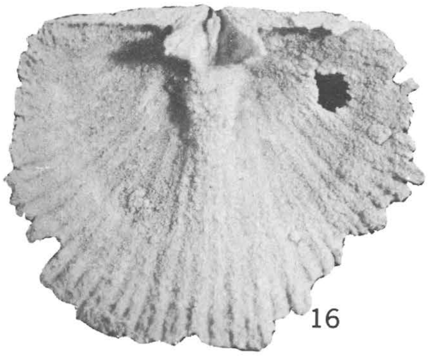
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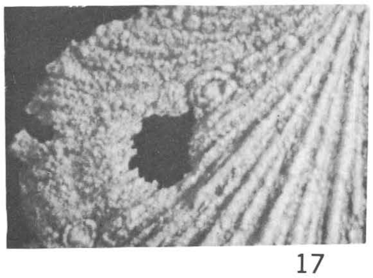
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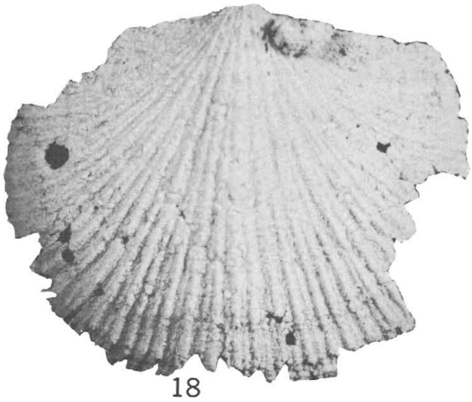
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GASTROPOD BORINGS IN FOSSIL SHELLS

PLATE 5

[All figures × 5, except fig. 11 which is × 10]

FIGURES 1–8. Borings in *Dalmanella* from the Grier Limestone Member of the Lexington Limestone, in Kentucky from locality 4956–CO.

1. Exterior ot a fragment. USNM 155028.
2. Interior of same specimen as fig. 1; the specimen is too incomplete to determine which valve is bored.
3. Fragment of brachial valve exterior. USNM 155029.
4. Interior of same specimen as fig. 4.
5. Brachial valve interior; this view shows two holes. USNM 155030.
6. Fragment of pedicle valve; almost all the holes appear to be organic in origin, rather than the result of breakage. USNM 155031.
7. Fragment of brachial valve exterior. USNM 155032.
8. Exterior of same specimen as fig. 5; a third hole may be seen near the midline.

9. Boring in *Dalmanella* from the Curdsville Limestone Member of the Lexington Limestone, in Kentucky from locality 5022–CO.

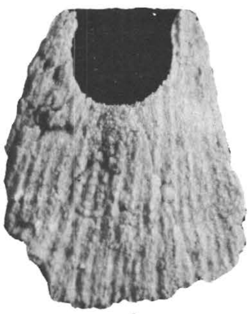
Pedicle valve exterior with several elongate borings or burrows. USNM 155033.

10, 11. Borings in *Dalmanella* from the Grier Limestone Member of the Lexington Limestone, in Kentucky from locality 5093–CO.

10. Brachial valve exterior. USNM 155034.
11. Interior of same specimen as fig. 10, enlarged; the shadow to the upper right is caused by part of the crural process.

12, 13. Borings in a ctenodontid pelecypod from the Grier Limestone Member of the Lexington Limestone, in Kentucky from locality 5098–CO.

12. Left valve exterior. USNM 155035.
13. Interior of same specimen as fig. 12.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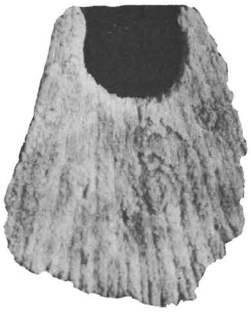
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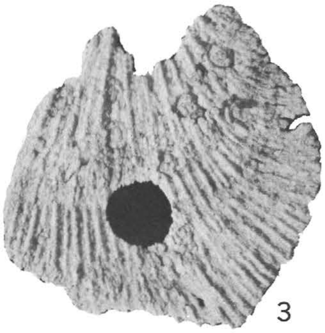
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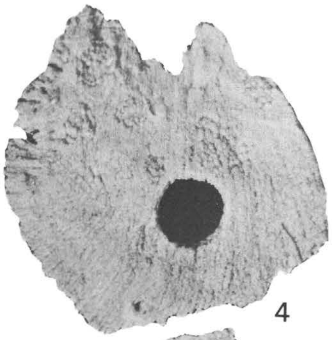
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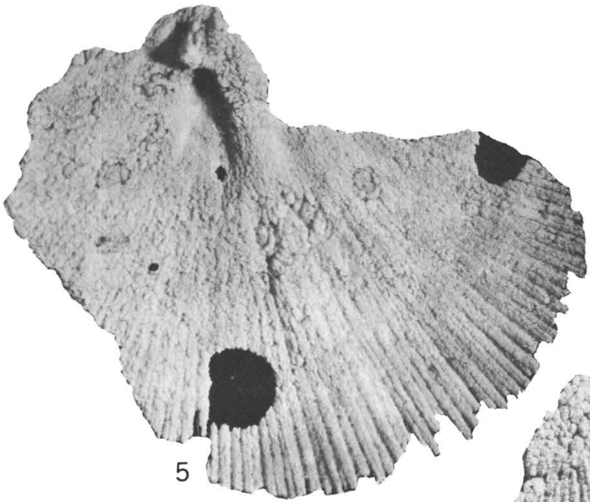
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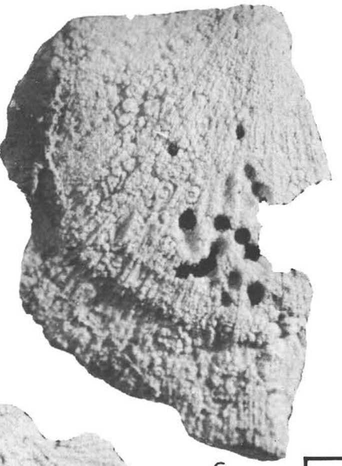
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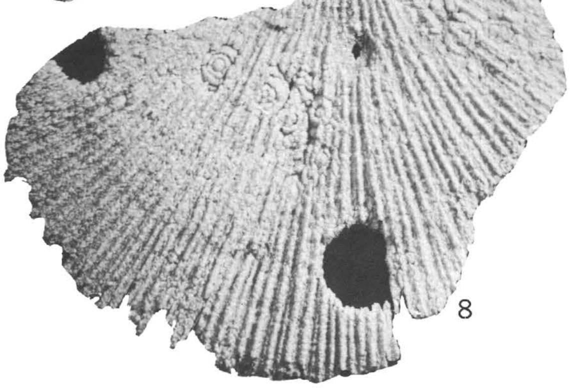
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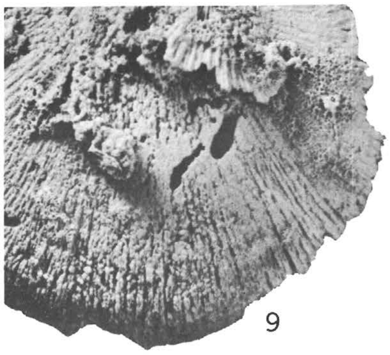
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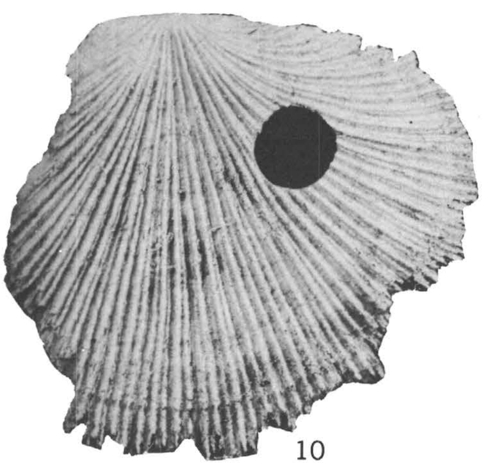
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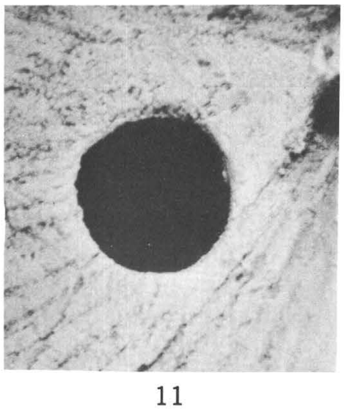
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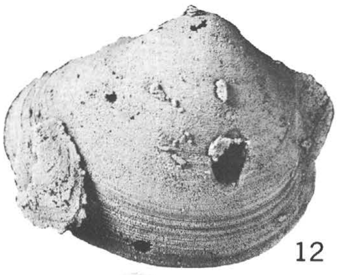
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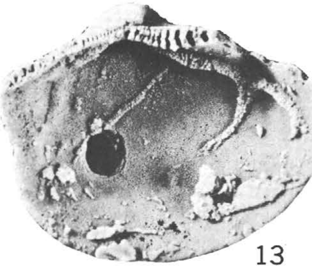
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GASTROPOD BORINGS IN FOSSIL SHELLS

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