ENDOSIPHUNCULAR STRUCTURES IN ORDOVICIAN AND SILURIAN CEPHALOPODS

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CONTENTS

INTRODUCTION

The following series of three short papers describing unusual endosiphuncular structures in some Ordovician and Silurian cephalopods was compiled during a number of short working sessions in the winter seasons 1972-73 and 1973-74. The first paper describes the development of the endosiphoblade pattern during ontogeny in an Ordovician endocerid from Colorado. The second paper deals with an unusual cone-in-cone structure in the endosiphotube of an Ordovician endocerid from Manitoba. The third paper describes presence of a set of radiating blades in the siphuncle of a Silurian huroniid from Ontario.

All photographs were prepared by Michael Frederick of the University of Kansas Paleontological Institute; the text-figures were prepared from our sketches by Roger B. Williams, of the same institution, who also helped to assemble the plates.

1. ORDOVICIAN ENDOCERID FROM COLORADO

ABSTRACT

An endocerid siphuncle of uncertain generic affinities has an unusual arrangement of endosiphuncular blades. During ontogeny these develop from a biradiate to a triradiate pattern and then again to a biradiate condition at maturity. Further, the blade pattern is oriented asymmetrically with regard to the dorsoventral plane of the siphuncle.

INTRODUCTION

The specimen described here was collected by Rex E. Crick in 1972 on Cripple Creek Road in Helena Canyon, Fremont County, Colorado. It comes from a dolomite bed in the Lower Ordovician Manitou Formation, 10 cm above its base.

The formation here rests unconformably on Precambrian granite.

We are indebted to Dr. R. H. Flower for fruitful discussions.

MORPHOLOGIC DESCRIPTION

The specimen (no. 73310, Museum of Invertebrate Paleontology, University of Kansas), is part of a silicified endosiphuncle with a nearly perfect circular cross section. It is 212 mm long, having a maximum diameter of 19.5 mm at the adoral end, tapering first slowly to 17 mm at 85 mm from the adoral end, then more rapidly to 6.5 mm at the adapical end.

The surface of the endosiphuncle is crossed at regular intervals of approximately 6 mm by oblique ridges which have been called "septal ridges" by Flower (1968, p. 28) (Pl. 1, fig. *1a*). These septal ridges formed in areas where the holochoanitic septal necks turned outward on meeting the preceding septum (Fig. 1). They therefore indicate the site of the septal foramen and the angle of the septal ridges indicates the slope of the septa in the vicinity of the siphuncle. At the adoral end of the specimen the septal ridges lie at an angle of 30 degrees to the longitudinal axis of the siphuncle. This angle decreases to about 20 degrees at the adapical end.

The zone where the septal ridges are closest to the adoral end of the endosiphuncle indicates the ventral side of the endosiphuncle. The fact that the septal ridges are clearly visible on the ventral side indicates that the siphuncle was not fully marginal, but situated a short distance from the ventral side of the shell wall. By extrapolating the slope of the septal ridges (and thus of the septa), it can be estimated that the diameter of the conch at the adoral end of the siphuncle was in the vicinity of 115 mm and that, therefore, the ratio of diameters of conch to siphuncle was of the order of 6:1.

The endosiphuncle consists of an outer layer of cryptocrystalline silica seen as a thin light-colored ring in Plate 1, fig. *1c, 1d,* and *1j.* It varies from 1 to 1.5 mm in thickness.

Inside the outer layer much of the endosiphuncle is filled with crystalline quartz and these infillings are arranged in definite patterns. In the middle part of the siphuncle they are formed in the shape of three sectors separated by relatively wide void spaces. The quartz crystals point from the walls of these spaces toward the interior of
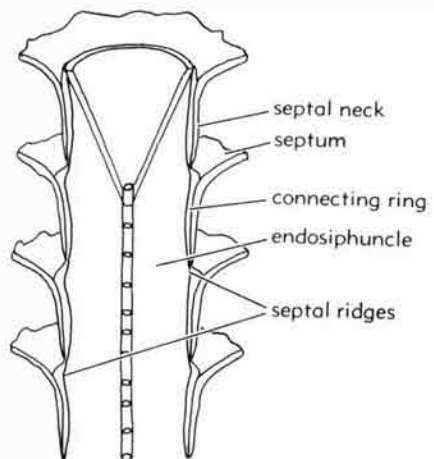

Fig. 1. Lateral section of an endoceroid siphuncle illustrating the position of septal ridges in relation to septa, septal necks, connecting rings, and endosiphuncle.

the sectors, leaving a small open space in the center of each sector (see Pl. 1, fig. *1g*). In the adapical as well as adoral parts of the specimen the quartz fills the entire siphuncle with the exception of a thin median void space (see Pl. 1, fig. *1b, j*).

By analogy with other endocerids, it is concluded that the radially oriented void spaces inside the endosiphuncle are spaces left by diagenetic removal of endosiphoblades and we, therefore, refer to them as *blade spaces*. Discussion of the detailed spatial configuration of the blade spaces and their development throughout ontogeny follows.

For a length of 13 mm measured from the apical end, the endosiphuncle is filled completely with quartz, with the exception of a central void thought to represent the original endosiphotube (Pl. 1, fig. *1b*). There is no evidence of blade formation in the first 24 mm.

At a distance of 25 mm from the apical end, a biradiate blade space pattern is first observed. The blade spaces seem to be an extension of the central void shown in Plate 1, fig. *1b*, although it is difficult to be sure about this, due to poor preservation. A section (Pl. 1, fig. *1c*) 26 mm from the apical end shows more clearly the initial biradiate pattern. At the center of this pattern the endosiphotube can be seen, filled with siliceous material as are the blade spaces. The blade spaces are not arranged in the dorsoventral plane. The blade space D lying close to the dorsal side of the siphuncle points at an angle of 37° to the left of it; the opposite blade space forms an angle of 55° with the dorsoventral plane of the endosiphuncle. It is here designated VL_1.

The initial stages of a triradiate pattern appear 36 mm from the apical end (Pl. 1, fig. *1d*). Blade space D lies here 27° to the left, VL_1 at 45° to the right, and a new blade space here designated VL_2 is seen to grow outward from the junction of VL_1 and D at 37° to the left of the dorsoventral plane. VL_1 and VL_2 form angles of 162° and 143° with D.

A natural break, 48.5 mm from the apical end (Pl. 1, fig. *1e*), shows the triradiate pattern fully developed. Blade space D is now aligned with the dorsoventral plane. VL_1 and VL_2 form angles of 64° and 49° with the dorsoventral plane. VL_1 and VL_2 form angles of 116° and 131° with D. VL_1 and VL_2 form an angle of 113°, the greatest

angle to be attained by the two ventrolateral blade spaces. The largest angle attained by the ventrolateral blade spaces and the alignment of blade space D with the dorsoventral plane suggest that the triradiate blade pattern reaches its most perfectly symmetrical arrangement 48 to 50 mm from the apical end of the specimen.

A natural break at 85 mm from the apical end (Pl. 1, fig. *1f*) shows the triradiate blade space pattern, similar to fig. *1e*. Blade space D is again aligned with the dorsoventral plane; VL_1 and VL_2 form nearly equal angles of 36.5° and 34° with the dorsoventral plane. VL_1 and VL_2 here form a common angle of only 70.5°, considerably less than in fig. *1e*. In accordance with the last measurement, VL_1 and VL_2 form angles of 143.5° and 146° with D.

In a section at 104 mm from the apical end (Pl. 1, fig. *1g*) the triradiate pattern is again observed with D aligned with the dorsoventral plane, and VL_1 and VL_2 forming angles of 23° and 31.5° with the dorsoventral plane. VL_1 and VL_2 form angles of 157° and 148.5° with D. Blade space D, after having begun 37° in a position to the left of dorsal side (Pl. 1, fig. *1c*) and then aligning with the dorsoventral plane (Pl. 1, fig. *1e*), is now beginning to veer toward the right at approximately 107 mm from the adapical end (not illustrated). An extension of this reorientation of D is shown in the following section (Pl. 1, fig. *1h*). Here, blade space D is 21.5° to the *right* of the dorsoventral plane. VL_1 and VL_2 are 25° and 22° to the right and left, respectively, of the dorsoventral plane. VL_1 and VL_2 form an angle of 47°. VL_2 is almost aligned with D as it forms an angle of 179.5° with D. VL_1 forms an angle of 133.5° with D.

The section 118 mm from the apical end (Pl. 1, fig. *1i*) shows D and VL_2 in alignment, each forming angles of 19.5° with the dorsoventral plane. VL_1, which is approximately one-half its former length, forms an angle of 26° with the plane. VL_1 and VL_2 form an angle of 45.5°. VL_1 and VL_2 form angles of 154° and 180°, respectively, with D.

The most adoral section, at 194 mm from the apical end (Pl. 1, fig. *1j*) shows again the biradiate structure similar to that seen in early ontogenetic stages (Pl. 1, fig. *1c*), with one significant difference: blade space D is situated to the right of the dorsoventral plane at an angle of 46.5°.
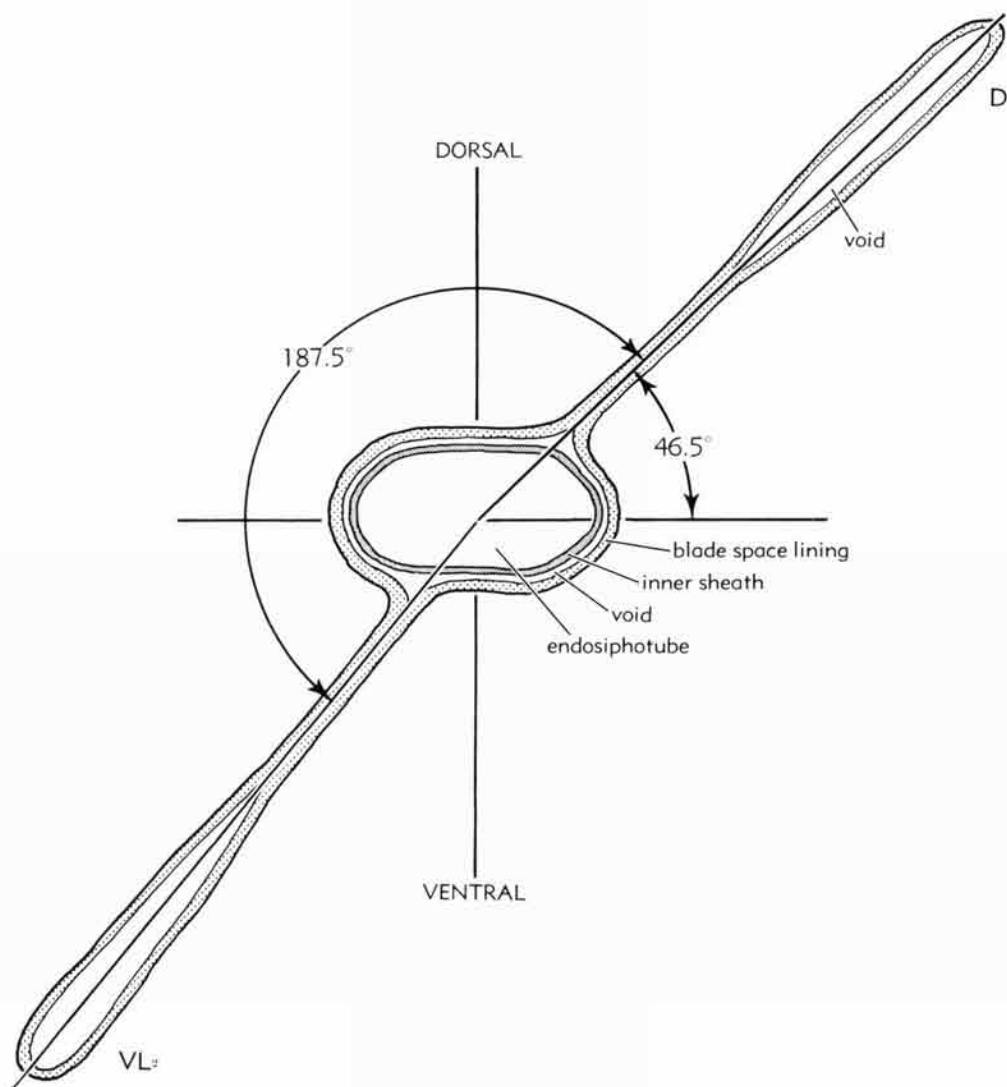
FIG. 2. Illustration based on Plate 1, fig. 1j, depicting the encasement of the endosiphotube by two successive and independent sheaths of siliceous material.

VL_2 forms an angle of 39° with the dorsoventral plane and an angle of 187.5° with D. VL_1 has disappeared. The endosiphotube appears at the junction of the two blade spaces encased in a sheath of siliceous material 0.2 mm thick, which in turn is surrounded by another sheath of material 0.4 mm thick. The latter can be seen to be wholly separated from the inner sheath and is formed of the same material that lines the blade spaces in this section (Fig. 2; Pl. 1, fig. 1j).

The crystalline quartz between the blade spaces is assumed to occupy space which was taken up originally by endocones. Although no traces of endocones are preserved, a conical space 10 mm long and 3.3 mm wide adorally (Pl. 1, fig. 1k) is interpreted by us to be the impression of the last endocone. This conical space continues adapically into a small tube (Pl. 1, fig. 1j), which we consider to be part of the endosiphotube as shown in Plate 1, fig. 1b, 1c. From the adoral end the endosiphotube can be followed for a distance of 5 mm from the bottom of this conical space, but is lost due to silicification of the endosiphuncle until it appears in figs. 1b, 1c.

SUMMARY

Our interpretation of the endosiphuncular structures described above is the following. The endosiphuncle begins and continues for a distance of 25 mm with the usual endosiphuncular structure of a central endosiphotube surrounded by endocones. This condition is inferred, as endocones are not actually preserved. In the next 11 mm, 25 mm to 36 mm from the apical end, a biradiate endosiphuncular blade system develops, presumably for the support of the endosiphotube. Blade D, lying closest to the dorsal side, is to the left of the dorsoventral plane while its counterpart, VL_1, in the ventrolateral area is to the right of the dorsoventral plane. At a point 36 mm from the apical end a third blade, VL_2, develops to the left of the dorsoventral plane in the ventrolateral area and a triradiate blade system is established. Blade D remains to the left of the dorsoventral plane. In the next 14 mm, 36 to 50 mm from the apical end, VL_2 becomes fully developed and D aligns with the dorsoventral plane. At this point a triradiate blade system is fully developed. In the next 56.5 mm, 50 to 106.5 mm from the apical end, blade D remains in the dorsoventral plane while the angle formed by VL_1 and VL_2 decreases to 54.5°. Approximately 107 mm from the apical end reorientation and alignment of D and VL_2 with one another begins. Blade D moves 21.5° to the right of the dorsoventral plane and VL_2 adjusts 1° to the right in the direction of the dorsoventral plane forming an angle of 22° with the dorsoventral plane (Pl. 1, fig. *1h*) and near alignment with D (179.5°). In the next 11 mm, 107 to 118 mm from the apical end, VL_1 is reduced to approximately one-half of its original length while D and VL_2 continue in alignment. Approximately 102 to 125 mm from the apical end the triradiate blade system is terminated by the disappearance of VL_1 and a biradiate blade system is reestablished. The endosiphotube is again visible at the juncture of the blades of this system (Pl. 1, fig. *1j*) 194 mm from the apical end. Here, the blade system bears resemblance to the initial biradiate condition (Pl. 1, fig. *1c*), except that the blade positions are reversed. Blade D (Pl. 1, fig. *1j*) lies 46.5° to the *right* of the dorsoventral plane while its counterpart (Pl. 1, fig. *1c*) lies 37° to the left of that plane. Blade D has now moved through a total angle of 83.5° from the left to the right of the dorsoventral plane in approximately 170 mm (Pl. 1, fig. *1c-j*).

The siliceous material forming the sheaths surrounding the endosiphotube and endosiphuncular blades (Fig. 2; Pl. 1, fig. *1j*) is thought to be diagenetic replacement of a late ontogenetic structure as it is not observed in earlier stages. It was obviously originally comprised of solution-resistant material and successfully resisted removal until later diagenetic stages caused its recrystallization. The functions of these sheaths are interpreted by us to be those of further support and protection of the endosiphotube and endosiphuncular blades.

As explained in the descriptive section of this paper, endocones were not found within the endosiphuncle; however, a conical space (Fig. 1, *1k*) 10 mm from the adoral end is interpreted by us to be the impression of the last, most adoral, endocone. We suggest that endocones did exist within the endosiphuncle in the following manner: 1) prior to the development of the biradiate blade structure the endocones surrounded the endosiphotube (Pl. 1, fig. *1b*) in the usual configuration; 2) during development of the biradiate blade systems (Pl. 1, figs. *1c, 1j*) endocones were formed on either side of the blades; and 3) during existence of the triradiate blade system (Pl. 1, fig. *1d-i*) endocones were formed in the three sectors between the blades.

DISCUSSION

Dewitz (1880) introduced the term *Endosiphoscheide* (= endosiphoblade) in a description of the endosiphuncular structures of *Endoceras commune*. Dewitz considered the blades to be organically secreted membranes extending from the posterior portion of the fleshy sipho, which in part reached the wall of the siphuncle.

Dawson (1881) mentioned the occurrence of a similar structure in *Piloceras amplum* Dawson: "The lower part of the shell is divided by a vertical partition crossing its longer diameter."

Holm (1885, pl. 3) described two- and three-pronged endosiphoblades in *Endoceras gladius* Holm (=*E. belemnitiforme* Holm).

Foord (1888) described an endosiphoblade in *Piloceras sp.* in which a longitudinal septum stretches from "the lower part of the siphuncle between the wall of the latter and that of the sheath into which the endosiphon opens." Foord described the endosiphon as having probably penetrated the septum, stating, however, that poor preservation did not allow accurate observation.

Holm (1895) discussed the function of thin bladelike membranes spread in longitudinal direction of the siphuncle as serving to sustain the endosiphuncle in the middle of the endosiphotube.

Ruedemann (1905) first introduced the terms endosiphuncle and endosiphotube. He also described, in a specimen of *Cameroceras brainerdi* Ruedemann, the existence of a set of trifid endosiphuncular blades from which were suspended the endosiphocoleon and endosiphotube.

Ulrich, *et al.* (1944) described a siphuncle of *Endoceras? baylorense* from the El Paso Limestone of West Texas which is remarkably similar, externally and internally, to the specimen described here. The surface of the siphuncle "bears low rounded annulations which slope strongly apical from the ventral to the dorsal side. In the adoral end of the holotype there is a central circular depression, about 6.5 mm in diameter, that may represent an endocone. At a transverse break in the adapical half of the holotype there is exposed a structure that divides the siphuncle into three subequal parts, and two of the paratypes show a similar structure." *E.? baylorense* exhibits a similar external morphology and, at one point in the siphuncle, a trifid blade pattern similar to that present in the endocerid from the Manitou Limestone.

Flower (1955) illustrated various cross sections through endosiphuncles showing variation in the shape of cones, position of tubes, and number and arrangement of blades. He mentioned that "the number and arrangement of the blades may be uniform through the length of the endosiphuncle. In some endoceroids there is unquestionably a marked variation from early to late stages which clearly marks an ontogenetic progression." He further referred to a Canadian genus (then awaiting description) with a pair of dorsolateral blades which moved in ontogeny from a dorsal to a relatively lateral position. Here, as in all previous work, no mention is made of changes during ontogeny from biradiate to triradiate systems, nor, as in the specimen described here, back to the biradiate condition. Flower supports the view that blades are features of early growth stages which disappear in later stages. He explained the absence of endocones in the most adapical part as a result of rapid growth in the early stages of the endosiphuncle. Flower explained the blades "as slight differentiation and discoloration of calcareous material filling the siphonal tissues, located at regions where this tissue was strengthened to support the endotube, and to maintain it in a normal and regular position. . . ."

Flower (1968) described a siphuncle of *Rossoceras lamelliferum* Flower containing a triradiate blade system, which is somewhat modified as compared with our specimen. The middorsal blade is analogous but the pair of lateral blades are curved downward. Flower notes that the siphuncle originally contained numerous repeatedly bifurcated blades. As a result of alteration, recrystallization obscures most of the blade pattern, commonly leaving vestiges of the pattern of middorsal and lateral blades.

This discussion of endosiphoblade structures shows the opinion expressed by Mutvei (1964) who interpreted the blades as "postmortem fracture lines" to be untenable.

2. ORDOVICIAN ENDOCERID FROM MANITOBA

ABSTRACT

A Lower Ordovician endoceratid, *Cameroceras,* is described, having a rare endosiphuncular, imperforate, cone-in-cone structure. Unlike most endoceroids, this specimen possesses successive imperforate endocones whose apices cross the endosiphotube. There is no evidence that these apices were ever pierced. This specimen is discussed and compared with other genera exhibiting similar endosiphuncular structures.

INTRODUCTION

The specimen of *Cameroceras* discussed in this section was collected by Curt Teichert, in 1955, from the Dog Head Member, Red River Formation, Upper Ordovician, in the general vicinity of Selkirk, Manitoba, Canada. After sectioning the specimen, it was found that endocones and an unusual cone-in-cone structure were preserved in part of the siphuncle. In view of the rare occurrence of this type of endosiphuncular structure, we believe it to be worthy of description and closer discussion.

Rocks of Ordovician age in southern Manitoba were first described by Whiteaves (1880). The terms Dog Head Member and Red River Formation were proposed by Foerste (1928). Species of *Cameroceras* Conrad are common fossils in the Dog Head Member, but little significant work

has been published on Red River cephalopods since Foerste's publication (1929). Especially the study of the Endoceratidae has been neglected, but it seems that among named forms, the affinities of our specimen are closest with *"Endoceras" manitobense* Foerste (1929, p. 149) and it is here tentatively identified as *Cameroceras* sp. *cf. C. manitobense* (Foerste).

In 1897, J. F. Whiteaves compiled the then known information concerning the fauna of the Red River Formation and his list was published by Dowling (1900). It contained the names of four species of *"Endoceras"* (=*Cameroceras*) from the Dog Head Member, but none of these seems to be applicable to the specimen under consideration.

MORPHOLOGIC DESCRIPTION

The specimen is a conch fragment about 80 mm long, with a dorsoventral diameter of 55 to 56 mm and a lateral diameter of about 70 mm. By reconstructing two of the partially destroyed camerae, it can be determined that seven camerae existed in a conch length of 92 mm. The camerae vary in length from 11 to 13 mm. All camerae are filled with fine calcareous sediment which is thought to have entered through breaks in the shell wall. On the dorsal side, the shell wall varies in thickness from 1.0 to 1.5 mm. On the ventral side, where it is less well preserved, the shell wall is abnormally thickened in two places, attaining a thickness of as much as 3 mm. The conch is flattened on the ventral side, the flattened area being about 30 mm wide.

The dorsal half of the conch is heavily encrusted by a coral, tentatively identified as *Calapoecia canadensis* Billings, 1865 (Pl. 2, fig. 1) (see Cox, 1936, p. 7). This coral forms a layer which is 6 to 7 mm thick in the dorsal area and tapers to a thickness of 1 to 2 mm on each side from the dorsal to the lateral areas. It must have encrusted the conch fragment after the latter was embedded in sediment because it is absent from the ventral part of the conch. From the distribution of the encrusting coral it may be concluded that the conch fragment did not come to rest in

the living position, but was tilted sideways by 25 degrees.

The siphuncle lies at a distance of 7 mm from the ventral side of the conch and has a flattened side, which, although it is in the same area of the conch as the flattened area of the shell wall, is not oriented parallel to it. The diameter of the siphuncle is 22 mm in the lateral and 18 mm in the dorsoventral plane. The ratio of diameter of conch to diameter of siphuncle is 3:1. The septal necks are remarkable in their uniformity, with each neck being slightly deflected inward at its distal end. They are holochoanitic.

The siphuncle is almost entirely filled with sparry calcite, individual crystals varying from 1 to 3 mm in size. It contains no sedimentary matrix. Preserved in the sparry calcite are some remnants of endocones, which are about 0.5 mm thick. Due to recrystallization, the attachment of the endocones to the siphuncle wall cannot be seen. At the apical end of the specimen, one endocone fragment 25 mm in length completely surrounds an axial cone-in-cone structure formed by successive endocones. Upon first observing this structure it appeared to represent an endosipho-tube, as commonly found in endocerids. However, acetate peels and photographs showed that the apices of the endocones are not pierced by an

endosiphotube (Fig. 3; Pl. 2, fig. 2). The area between the fragmental endocone, the siphuncle wall, and the cone-in-cone structure was once presumably occupied by other endocones.

The section of the endosiphuncle exhibiting the cone-in-cone structure is 24 mm long and 1.8 mm in diameter. On either side of the axial structure a zone about 1 mm wide exhibits successive layers of endocones (Fig. 3). There are ten such cones in a length of 24 mm. The walls of the cones vary in thickness. The distances between successive tips of cones are also variable; measured from proximal to distal end they are 1.3, 2.0, 1.4, 0.5, 2.4, 2.5, 1.5, 2.4, and 2.5 mm.

DISCUSSION

The literature contains few descriptions of endosiphuncular structures comparable to those

FIG 3. Schematic illustration depicting the interrelationships of continuous imperforate endocones in *Cameroceras* sp. *cf. C. manitobense* Foerste, ×10.

described here. Collins (1967) discussed endosiphuncular structures in various species of endocerids and distinguished two groups of diaphragms found in endosiphotubes: 1) diaphragms unrelated to endocones which he termed "simple diaphragms," 2) diaphragms which were clearly extensions of endocones, which he named "complex diaphragms." It should be noted that the complex diaphragms are imperforate and in the specimens studied by Collins endocones with perforated apices alternate with endocones whose apices are pierced.

The use of the term "complex diaphragm" (Collins, 1967) to describe an "imperforate endocone crossing the endosiphuncular space" lends additional complexity to an already complex endosiphuncular terminology. In an attempt to preserve a simple terminology, we prefer to speak of perforate (pierced) and imperforate (unpierced) endocones. In the case of perforate endocones, successive perforations from the endosiphotube which may or may not be traversed by secondary diaphragms. In imperforate endocones tips are narrowly rounded, forming "complex diaphragms" in the sense of Collins (1967). In his restudy of *Lobendoceras emanuelense* Teichert & Glenister, from the lower Ordovician of Western Australia, Collins (1967, fig. 4) described "sporadically preserved endocones" and seven diaphragms crossing the endosiphotube, with no observed connection between the endocones and diaphragms. Further, the apex of each endocone was pierced by an endosiphotube.

Kobayashi (1947, pl. 6, fig. 1 & 2), illustrated a specimen of *Penhsioceras* (?) sp., from an unknown locality, presumably of Early Ordovician age, with five imperforate endocones, each pair separated by several perforated endocones. In the area of perforate endocones the endosiphotube is crossed by diaphragms unrelated to endocones. The important difference from the specimen de-
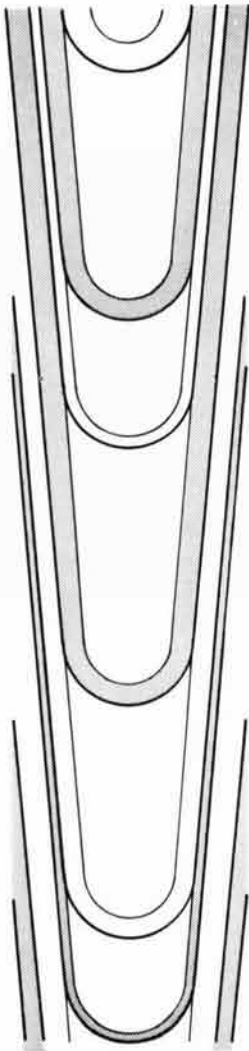
scribed here is that not all endocones are imperforate.

In a restudy of *Manchuroceras wolungense* from the Lower Ordovician of Manchuria, Kobayashi (1935, pl. 3, fig. 4, 5; pl. 4) illustrated a siphuncle that contained many endocones connecting with rather flat partitions, which cross the endosiphotube. Many of these do not align with endocones and many endocones are pierced. Kobayashi did not state whether he regarded the endocones as imperforate or perforate.

Flower (1961, pl. 1, fig. 1-4, 6, 10, 11; pl. 4, fig. 8) presented good illustrations of cone-in-cone structures in fossils he called "Things," from the Chazyan of New York. Collins (1967) refigured Flower's "Thing 1," but did not recognize the basic cone-in-cone structure. In general, it would appear that Flower's "Things" are the only known fossil cephalopods with structures that closely resemble those described here. We here accept Collins' (1967) interpretation of them as endocerid siphuncles.

Flower (1964) illustrated several specimens of endocerids which have similar cone-in-cone structures. Two of these belong to *Bisonoceras* from the first piloceroid zone of the El Paso Group (Lower Ordovician), new Mexico, exhibiting cone-in-cone structures preserved in the proximal section of the siphuncle (Flower, 1964, pl. 5, fig. 12, 14). Elsewhere within the siphuncle, they are destroyed by recrystallization. In *Dartonoceras gracile,* also from the El Paso Group, endocones are imperforate (Flower, 1964, pl. 5, fig. 16). In addition, two unnamed specimens of endocerids from the first piloceroid zone, El Paso Group of New Mexico, have a cone-in-cone structure near the point where the endosiphocone begins (Flower, 1964, pl. 4, fig. 10 & 12).

Much more must be learned about these structures before a functional interpretation can be made. For endocerids having endocones with perforate apices it is reasonable to assume that the resulting endosiphotube contained a thin fleshy strand. In endocerids having endocones with imperforate apices such a structure could not have existed, indicating a rather different organizational plan. In general, then, the endosiphotube could not have performed any important functions, and that closing it off by diaphragms or leaving endocones unpierced was an advantage to the metabolism of the animal.

3. SILURIAN ACTINOCERID FROM ONTARIO

ABSTRACT

An actinocerid cephalopod described by Foerste and Savage (1927) as *Armenoceras severnense,* from Silurian beds near Hudson Bay, possesses a system of longitudinal, radially arranged endosiphuncular blades, in addition to the normal endosiphuncular canal system, typical for actinocerids. The species is here transferred to the genus *Huroniella* and similar endosiphuncular structures are noted in other huroniids.

INTRODUCTION

From time to time illustrations of actinoceroid cephalopods have appeared in the literature suggesting presence of radially arranged, longitudinal blades in their siphuncles, but these features have never been discussed or described in detail. One such specimen was described by Foerste and Savage in 1927 under the name of *Armenoceras severnense.* These authors noted the presence of "vertical plates" in the siphuncle of the holotype of that species, but regarded these as the result of weathering.

Through the efforts of Dr. R. L. Langenheim we were able to borrow the specimen described by Foerste and Savage, which is in the collections of the Geology Department of the University of Illinois, and we are greatly indebted to him for making this interesting specimen available to us for study.

For reasons explained below we are reassigning Foerste and Savage's species to the genus *Huroniella* Foerste. A morphologic description and discussion of the endosiphuncular structures follow.

MORPHOLOGIC DESCRIPTION

HURONIELLA SEVERNENSE (Foerste & Savage)

Plate 2, fig. 3; Plate 3, fig. 1-5

Armenoceras severnense Foerste & Savage, 1927, p. 69, pl. 69, fig. 4A,B.

External morphology: The holotype and only known specimen is a fragment of an actinoceroid siphuncle that has been well described by Foerste and Savage as follows:

Specimen 42 mm. long, consisting of 4 segments of a siphuncle, enlarging from a lateral diameter of 28 mm. to 30 mm. in a length of 22 mm. Three segments occur in a length equal to this diameter. The ventral side of the upper two segments shows areas of contact with the ventral wall of the conch. These areas are 20 mm. wide and 7 mm. in height, their lower margin presenting a lunate outline which fails to reach the top of the underlying segment by a height of nearly 3 mm. The segments slope in a dorsal direction at an angle of 10 degrees with the horizontal. The outer zone of contact between the septa and the overlying segments of the siphuncle present concave vertical outlines, the upper margins of which rise on passing from the dorsolateral to the ventrolateral sides of the segments; on the dorsal side of the segments this concave vertical zone probably disappears entirely. In a corresponding manner, the annulations characterizing the individual segments occupy the entire height of these segments dorsally, but only their upper portion ventro-laterally. The septal neck at the base of the specimen is estimated at 16 mm. in diameter. Along the inner contact zone, the septum was in contact with both the segment above and that beneath.

The septal necks are clearly visible in places. They are of the recumbent type, with the tips pointing obliquely adorally. The septal necks are similar, if not exactly like, those of *Huroniella persiphonata* (Parks, 1915; see also Teichert, 1933, p. 122, fig. 4).

The presence of shell material on the ventral side of the siphuncle indicates a near-ventral position of the siphuncle. Although the siphuncle does not exhibit flattening usually encountered with a marginal siphuncle, it does show a restriction of the external ridges to the upper portion of each segment ventrolaterally. Dorsally these ridges occupy the length of each segment.

The segments have an outline that is typical of *Huroniella*. The adnation areas are funnel-shaped. The free part of connecting ring is considerably expanded, especially in the adoral part. In several places connecting rings have been removed by weathering.

Internal morphology: Internally the siphuncle is partially filled with crystalline calcite. Preserved within the crystalline mass and discernable by the effects of different stages of crystallization are central canal, radial canals, septal necks, and a system of longitudinal, radially arranged blades.

The central canal is centrally situated and is approximately 5 mm in diameter. Branching from the central canal at regular intervals, one set in each segment, are the radial canals. These canals can be traced toward the connecting ring on a path curved adapically. The canals can be traced to within 1-1.5 mm of the connecting ring where they presumably enter the perispatia, which, however, are not preserved. They strongly resemble the canals of *Huroniella persiphonata* as figured by Teichert (1933, p. 122, fig. 4).

In addition to the typically actinoceroid canal system the siphuncle contains a set of longitudinal blades that radiate inward from the connecting ring (Pl. 2, fig. 3; Pl. 3, fig. 3). At the connecting ring the blades are 0.3 to 0.5 mm thick and are spaced at distances of approximately 1 mm. In transverse section the blades are somewhat sinuous. On the exterior of the connecting rings the edges of the blades appear as weak longitudinal ridges.

Ventrally these external longitudinal ridges are absent, but the internal blades are seen to be present in areas exposed by removal of the connecting ring. The absence of the ridges here is believed to be a function of the marginal orientation of the siphuncle.

Foerste and Savage (1927, p. 69) did observe "vertical plates which radiate outward from the subcentral parts of the siphuncle," but ascribed them to weathering action.

It is not clear how this system of radial blades is morphologically related to the endosiphuncular canal system. Additional specimens for serial thin sectioning will be needed to solve this question.

Occurrence: Severn River (about 25 miles from its mouth), Ontario; Attawapiskat Limestone, Middle Silurian.

Depository: No. X-761, Paleontological Collection, University of Illinois.

DISCUSSION

The most remarkable feature of *Huroniella severnense* is the combination of an endosiphuncular canal system of the actinoceroid type and a system of longitudinal radially arranged blades. The existence of radial blades in siphuncles of actinoceroids was first observed in the Silurian *Huronia vertebralis* by Stokes (in Bigsby, 1824), who misinterpreted the specimens as corals because of the similarity of the radial blade system to coral septa (Fig. 4). However, by 1840 he had realized the cephalopodean nature of these fossils (Stokes, 1840).

These features seem to have received little or no attention for several decades, although Barrande (1874, p. 667) mentioned and described them in his discussion of *Huronia*, which he regarded as a subgenus of *Orthoceras*.

Parks (1915, p. 27), in discussing *Huronia septata* from the Shammattawa River, found that "the interior of the siphuncle shows about 20 longitudinal plates, radiating from a central endosiphuncle, which, however, is inferred but not observed. The internal support for radiating tubuli is very different from that of other species, in which it seems to take the form of annular membranous or calcareous expansions." In his restoration of the vertical median section of this specimen (pl. 5, fig. 8) Parks refers to vertical radiating lamellae. Foerste and Savage (1927) refigured the holotype of *Huronia septata*, clearly showing the radial lamellae in the siphuncle, but did not discuss them in the text (Foerste and Savage, 1927, pl. 12, fig. 2).

It is of interest to note that radial blades are also present in the siphuncles of the late Paleozoic genus *Rayonnoceras*. When Croneis (1926, p. 344) described this genus and its type species, *R. solidiforme*, he noted that "the nummuli are strongly corrugated longitudinally, except on the ventral side, four to five corrugations occurring in a space of 1 cm." These corrugations bear a strong similarity to the external longitudinal ridges present on *Huroniella severnense*.

Foerste and Teichert (1930, pl. 49, fig. 1; pl. 50, fig. 1) illustrated a specimen of *Rayonnoceras girtyi* exhibiting the characteristic external longi-
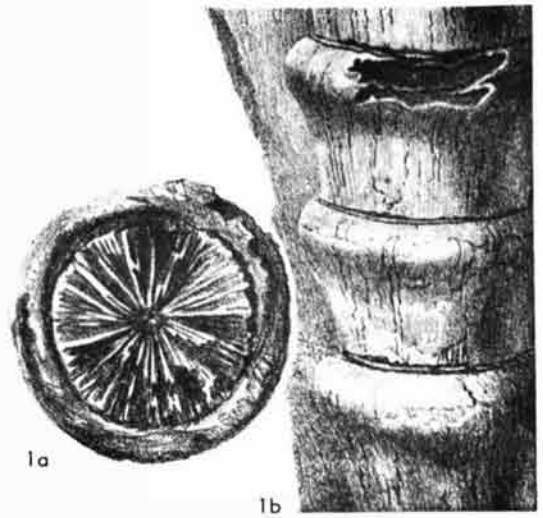
Fig. 4. Radial lamellae in the siphuncle of *Huronia vertebralis* Stokes from Silurian. Drummond Island, Michigan; *1a*, adoral view; *1b*, lateral view of siphuncle segments. ×1 (from Bigsby, 1824).

tudinal ridges of *Rayonnoceras*. The ridges of *R. girtyi* appear eight to 10 in a space of 2 cm. as in *Huroniella severnense*.

Turner (1951, pl. 3, fig. 4) illustrated a cross-sectional view of the siphuncle of *Rayonnoceras windmorense* and noted the existence of a "pinnate arrangement of rayonnets." In his discussion of *R. cantonense* (p. 186) Turner noted "the adapical surface of the siphuncle carries 15 radial grooves."

Schmidt (1956, p. 59, pl. 4, fig. 4b) recognized the existence of radial blades in a specimen of *Rayonnoceras giganteum:*.

Although the existence of endosiphuncular radiating blade systems can be proven in some groups of cephalopods and external longitudinal ridges on the siphuncle segment in others, only *Huroniella severnense* possesses both these distinguishing structural phenomena. *H. severnense* is further unique in that the relationship of the endosiphuncular radiating blade system to the external longitudinal ridges is such that the latter is an extension of the former.

CONCLUSIONS

It is interesting to note that systems of radial lamellae were developed repeatedly and independently in the siphuncles of several groups of cephalopods:

1) the huroniids among the Actinocerida in the Silurian;

2) the intejoceratids among the Endocerida in the Ordovician;

3) numerous, though by no means all, families and genera of the Oncocerida.

The structures of the second and third groups were briefly described by Teichert (1964, p. K42-43), whereas in the first group the endosiphuncular lamellae hitherto have been either disregarded or were interpreted as diagenetic in origin.

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EXPLANATION OF PLATES

PLATE 1

Endocerid, gen. *et* sp. indet., from Manitou Formation, Helena Canyon, Fremont Co., Colorado. (No. 73310, University of Kansas, Museum of Invertebrate Paleontology.)

FIGURE

1a. Lateral view of siphuncle exhibiting adapically sloping septal ridges, ×1.

1b-1j. Transverse sections, oriented dorsal side up, all ×2; *1b,* 13 mm from apical end showing central void; *1c,* 26 mm from apical end showing initial biradiate blade pattern; endosiphotube seen at junction of two blade spaces; lighter outer ring is silicified outer layer; *1b,* 36 mm from apical end showing initial triradiate blade pattern; *1c-g,* 48.5, 85, and 114 mm from apical end, exhibiting triradiate blade pattern; *1h,* 122 mm from apical end, showing triradiate blade pattern illustrating the initial stage of shifting of D 21.5° to right of dorsal, VL_s and D form an angle of 179.5°; *1i,* 128 mm from apical end, triradiate blade pattern continued; D removed 19° to right of dorsal; VL_s and D now aligned at 180°; *1j,* 192 mm from apical end showing a return to biradiate blade pattern; D is 46.5° to right of dorsal; VL_s and D form an angle of 187.5°.

1k. View of adoral end of siphuncle, exhibiting the impression of the last existing endocone.

PLATE 2

Cameroceras, Huroniella
(KU = University of Kansas, Museum of Invertebrate Paleontology)

FIGURE

1-2. *Cameroceras* sp. cf. *C. manitobense* (Foerste), from Red River Formation, Manitoba (KU 65926). ——*1.* Longitudinal median section showing arrangement of cone-in-cone structure in the near ventral siphuncle, ×1. White material on dorsal side is an encrusting colony of *Calapoecia canadensis* Billings,——*2.* Invagination of imperforate endocones. The offset of the cone-in-cone structure in the upper one-third of the siphuncle is a diagenetic feature, ×4. (Enlargement of part of Pl. 2, fig. 1.)

3. *Huroniella severnense* (Foerste & Savage), Attawapiskat Limestone, Ontario (University of Illinois, Department of Geology, no. X-761). Adapical view illustrating central canal and radiating longitudinal blades, ×2.5.
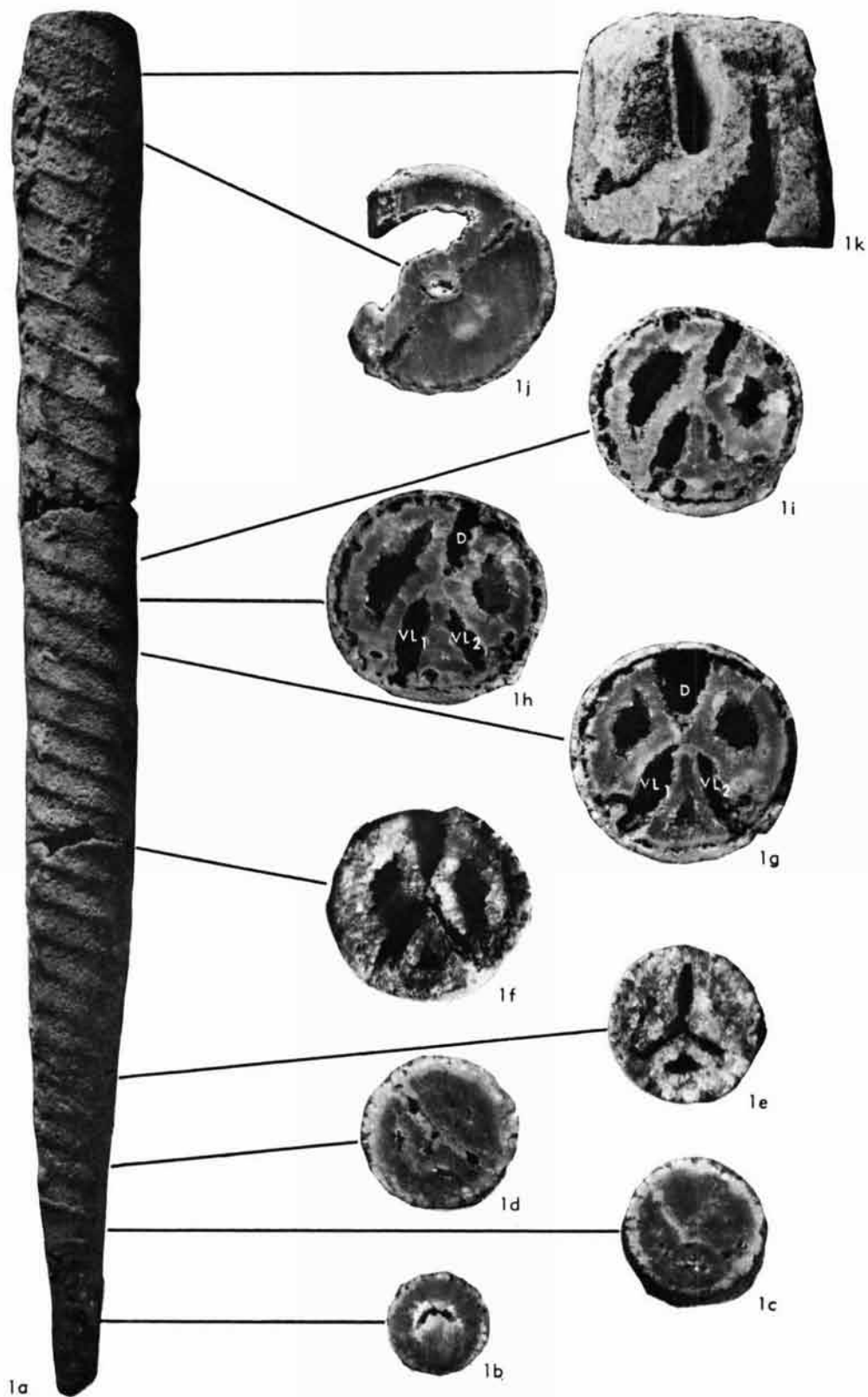
PLATE 3

Huroniella severnense (Foerste & Savage), University of Illinois, Department of Geology, no. X-761.
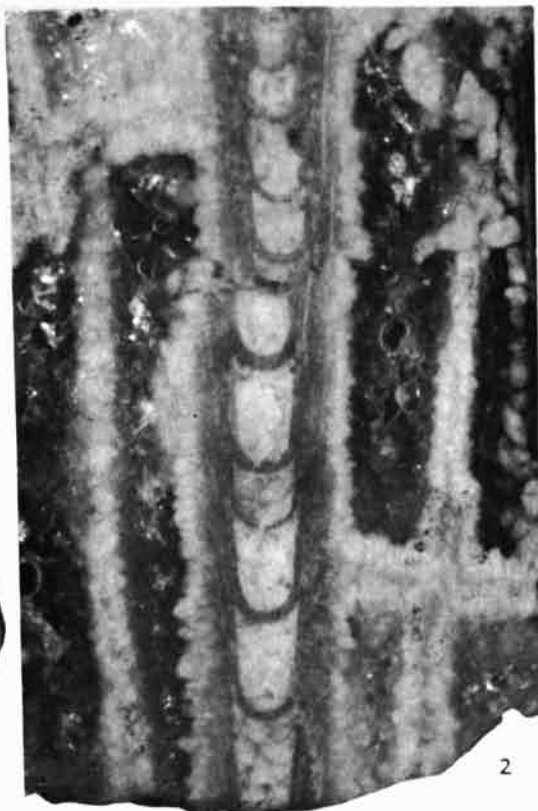All figures ×2.

FIGURE

1. Lateral view exhibiting longitudinal ridges on connecting rings.

2. Lateral view of side opposite to that shown in Fig. 1. Portions of shell wall attached to ventral side.

3. Adoral view showing attachment of longitudinal radiating blades to connecting rings.

4. Longitudinal median section showing central canal and radial canals.

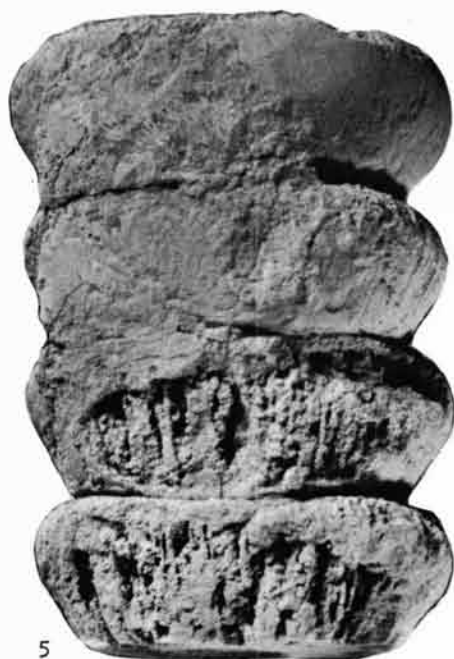*5.* Ventral view showing longitudinal radiating blades; portion of shell wall preserved on upper two segments.