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A BELEMNOID FROM THE LATE PERMIAN OF GREENLAND

BY

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WITH 6 FIGURES IN THE TEXT AND 2 PLATES

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ABSTRACT

Belemnoid remains collected in the Permian of East Greenland by Danish expeditions under the leadership of Dr. LAUGE KOCH are referred to *Dictyoconites groenlandicus* FISCHER, n. sp. The material studied includes well preserved rostra, fragmentary phragmocones, and arm hooks. Ontogenetic studies indicate rostral development from a needle-shaped body through a smooth, more or less cylindrical *Atractites* (*Ausseites*) like stage to the clavate, costate and sulcate type characteristic of *Dictyoconites*.

INTRODUCTION

Among the voluminous Permian material collected by the Danish Greenland expeditions led by Dr. Lauge Koch there appear the fragmentary remains of belemnoids in various samples from the so-called *Posidonomya* beds. These fossils were not referred to the belemnoids, though Rosenkrantz (1930) called attention to the resemblance of some of these, namely arm hooks, to dibranchiate cephalopod remains of the Triassic.

A survey of the Greenland material sent to the Peabody Museum has yielded hundreds of fragmentary specimens from the Gael Hamkes Bay region, mostly rostra, but including parts of phragmocones, one or more proostracal fragments, and numerous arm hooks or onychites. Most of this material appears to be referable to one species, here described as *Dictyoconites groenlandicus* n. sp. Other records of Paleozoic belemnoids are De Koninck's tentative and doubtful report of a belemnoid from the Devonian (1843) and Flower's description (1945) of a belemnoid which, according to its label, was collected years ago by Ulrich in a probably Mississippian boulder in Pennsylvanian shale in John's Valley, Oklahoma.

Detailed morphologic investigations were prevented by the scarcity of well preserved specimens. It is certain that future collecting in Northeast Greenland will yield more excellent material, and will add much to our knowledge of this interesting form, and of Aulacoceroids in general.

The writer is indebted to Dr. Carl O. Dunbar for the loan of the material, and for stimulation and advice. Dr. N. D. Newell suggested the study and supplied a guiding hand through much of it, and Dr. A. K. Miller contributed encouragement and rare and useful literature. To these I wish to express my sincere gratitude.

OCCURRENCE

The belemnoids occur in the *Posidonomya* beds of northeastern Greenland, a series of black, pyritic shales and limestones up to 80 m thick. For the stratigraphic relations of this unit the reader is referred to MAYNC (1942). Suffice it to say here that the *Posidonomya* beds represent a facies which interfingers with dolomites and limestones of Zechstein age as well as with the *Cyclolobus*-bearing *Martinia* beds. The *Posidonomya* beds are therefore dated as Upper Permian.

ROSENKRANTZ (1930, p. 354) says of the *Posidonomya* beds at Hird Bay:

. . . "Apart from fish remains there were found only one species of *Posidonomya*, one gastropod, one orthoceratite, and some mysterious hook-formed fossils, much resembling decapod hooks (particularly *Phragmoteuthis* from the Trias)".

NIELSEN (1935) in describing the *Posidonomya* beds at Godthaab Gulf states on page 18:

"These limestone bands . . . in addition to the *Posidonomya*-orthoceratite fauna . . ." On page 20: "In several places the whole surface of one of the two lower limestone beds can be seen to be covered with long acute Tetracorals(?) all pointing in the same direction. These Tetracorals(?) were also occasionally found singly, but seem to be absent from the uppermost limestone band of the fish zone."

And on page 88: "The peculiar hooks discovered by ROSENKRANTZ (1930, p. 354) in the Permian at Hird Bay and compared by him to the Triassic *Phragmoteuthis*, occur now and then in great abundance in company with an orthoceratite shell in such a way that their possible association cannot be rejected (according to a discussion with ROSENKRANTZ)."

ALDINGER (1934) notes of the fauna of the *Posidonomya* beds:

". . . dass Kalkbänder und Konkretionen in den Schiefern neben Fischen und *Posidonomya* noch Orthoceraten (ROSENKRANTZ 1930, p. 354), Nautiliden und (?)Tetrakorallen enthalten . . ."

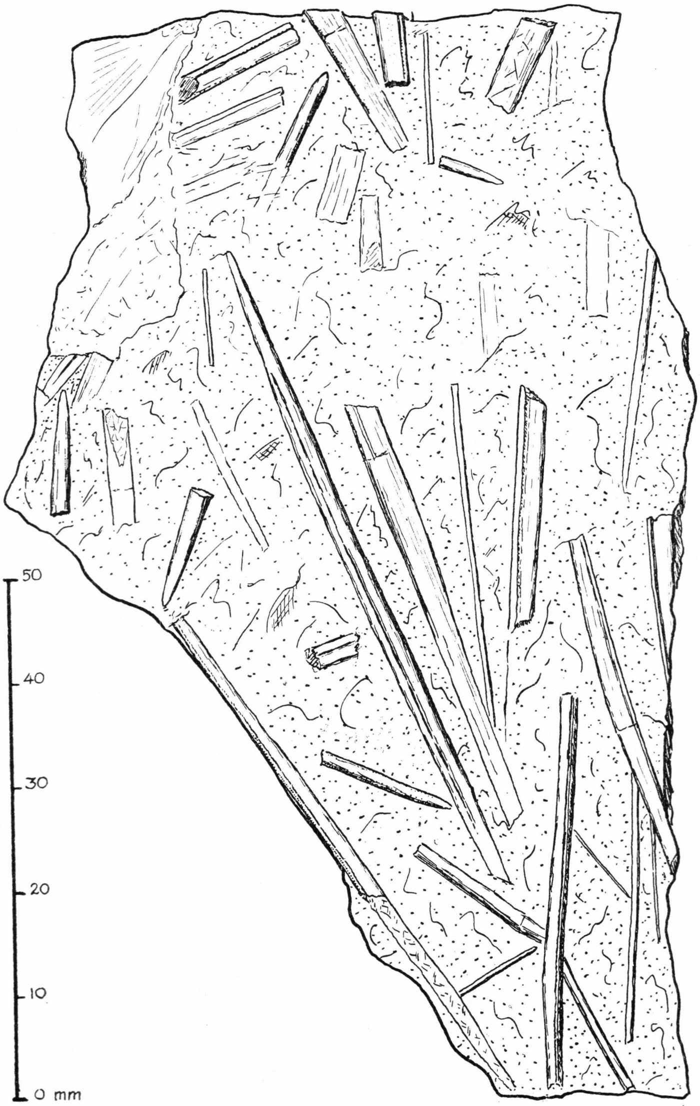

Fig. 1. Limestone slab with rostra of *Dictyoconites groenlandicus*, ranging from nepionic to gerontic. Loc. N. 10, R 14—15, *Posidonomya* zone.

Study of the material at hand suggests that the hooks are, as ROSENKRANTZ intimated, the arm hooks of belemnoids, that the orthoceratites found in association with them are at least in part belemnoid phragmocones, and that the (?)tetracorals of NIELSEN are belemnoid rostra, the radial-lamellar structure of which simulates the radial septation of the former.

The material studied comes from the lands around Gael Hamkes Bay, partly from Clavering Island to the north, and partly from the Cape Stosch region of Hold-with-Hope to the south.

The best specimens were found in a limestone block labelled L.K.38. This yielded a number of fragmentary rostra with well preserved surface features. Some of the fragments include parts of the alveole and the enclosed portions of the phragmocone. Associated delicate shell fragments with traces of septation and what may be cameral deposits probably represent the crushed extra-alveolar portions of phragmocones; two small pieces appear to be proostracal fragments. A streak of brown argillaceous material was found to be full of belemnoid arm hooks (onychites). The associated fauna consists of *Posidonia* sp., radiolaria, and tiny gastropods. A block of similar lithology, collected at Hird's Fox Farm on Clavering Island (no. 17, leg. KOCH, NOE-NYGAARD, 17th July, 1930) shows similar arm hooks, associated with one of much greater size and different shape, and with *Posidonia* sp. Another limestone specimen, collected by STAUBER and labelled SI Permian I, is full of badly recrystallized rostra. Black micaceous radiolarian shales collected by MAYNC on the Fish Fossil River (R 2468) in the southern part of Clavering Island contain juvenile rostra in addition to the ubiquitous *Posidonia*; a piece of black, argillaceous, micaceous, siliceous limestone found in the same area (A 98) shows a poorly preserved rostrum, 70 mm long, with both ends missing. A rather similar piece of limestone from the Fish River on Clavering Island (Elvsborg), labelled 2505, contains abundant small nacreous fragments of phragmocones, which resemble those from loc. L.K. 38. Large blocks of brown argillaceous limestone from the Cape Stosch area, labelled N 10, R 14, 7—21—37, and N 77—R 14—15, June 1937, are crowded with broken and partly silicified rostra in all stages of development, associated with *Posidonia* and fish remains (Fig. 1).

MORPHOLOGICAL NOTES

The belemnoid skeleton is generally subdivided into two main portions, the *phragmocone sensu lato* and the *rostrum*. The former is composed of an outer shell, the *conotheca*, also known as the *velamen triplex* (MÜLLER-STOLL, 1936), and an inner, chambered portion, the *phragmoconus sensu stricto*. The outermost layer of the conotheca, termed the *stratum callosum* by MÜLLER-STOLL, is extended orad in a dorsal, or in some cases both a dorsal and a ventral, lobe or tongue, the *proostracum*. The rostrum generally shows concentric layers, alternatingly clear and pigmented due to differences in conchiolin content. These MÜLLER-STOLL has named *laminae pellucidae* and *laminae obscurae*, respectively. The rostra of some belemnoids, including the form at hand, carry one or more pairs of longitudinal lateral furrows. These were called Asymptotenfurchen by von BÜLOW, in analogy to the asymptotic zones of the conotheca, but it has been pointed out that these two sets of features may not be equivalent; therefore the term *sulci geminati*, proposed by MÜLLER-STOLL, is here used.

Table 1 compares the various layers of the belemnoid and the pelecypod skeleton, based mainly on homologies by MÜLLER-STOLL (1936), and partly on homologies by NAEF (1922), and NAEF, POMPECKJ, and SCHINDEWOLF (1933).

Table 1.

Pelecypods	Belemnoids	
periostracum	rostrum	
ostracum (prismatic layer)	stratum callosum	velamen triplex or conotheca
light interlayer	stratum album	
outer laminated layer	stratum profundum	
inner laminated layer	phragmoconus	

DESCRIPTION

Family **Aulacoceratidae** (Bernhard).

Genus **Dictyoconites** Mojsisovics.

Dictyoconites groenlandicus Fischer, n. sp.

Plates 1 and 2, Text Figures 1 to 6.

Exterior of the ephebic rostrum, (Fig. 2).—The rostrum is slender and gently clavate (Plate 1, figs. 1—3; text-fig. 2). From its apical, more or less bluntly pointed end it slowly swells orad to the middle region, somewhat short of the alveole, then gently tapers orad to a "neck" beyond which the gradually expanding phragmocone causes the adoral portion of the rostrum to re-expand before wedging out. In cross-section the apical tip is more or less circular; orad the rostrum tends to become increasingly elliptical, higher than wide, up to the central portion; from this to the thin orad "neck" the rostrum loses its ellipticity and becomes sub-triangular, to become nearly circular at the extreme orad end, where it conforms to the shape of the phragmocone. A fragment of this region indicates that the rostrum is here slightly higher than wide, and overlaps the phragmocone farther on the dorsum and venter than on the sides. There appears to be no sharply defined adoral edge; rather, the rostrum becomes reduced to a delicate brown layer with indefinite margins.

No complete rostra have been found. Fragments vary in size up to 70 mm in length and 5 mm in diameter. One specimen represented by several well preserved fragments (Plate 1, fig. 2) measures 2.5 mm dorso-ventrally at its thin adoral neck, and 4 mm through its central portion. The holotype (Plate 1, fig. 1) is a part of an ephebic rostrum from loc. L. K. 38. It measures 45 mm in length, and 0.5 to 1.0 mm of the apical tip as well as most of the alveolar portion of the rostrum are lacking. At 10 mm from the apical end this rostrum shows a diameter of 2 mm, 30 mm from it a maximum diameter of 3.6 mm dorso-ventrally and 3.4 mm laterally. At the adoral end the diameter is 3.0 mm.

A reconstruction has been attempted in text-fig. 2, assuming an ephebic rostrum 70 mm long, 3.5 mm high at its adoral end, 2.5 mm high

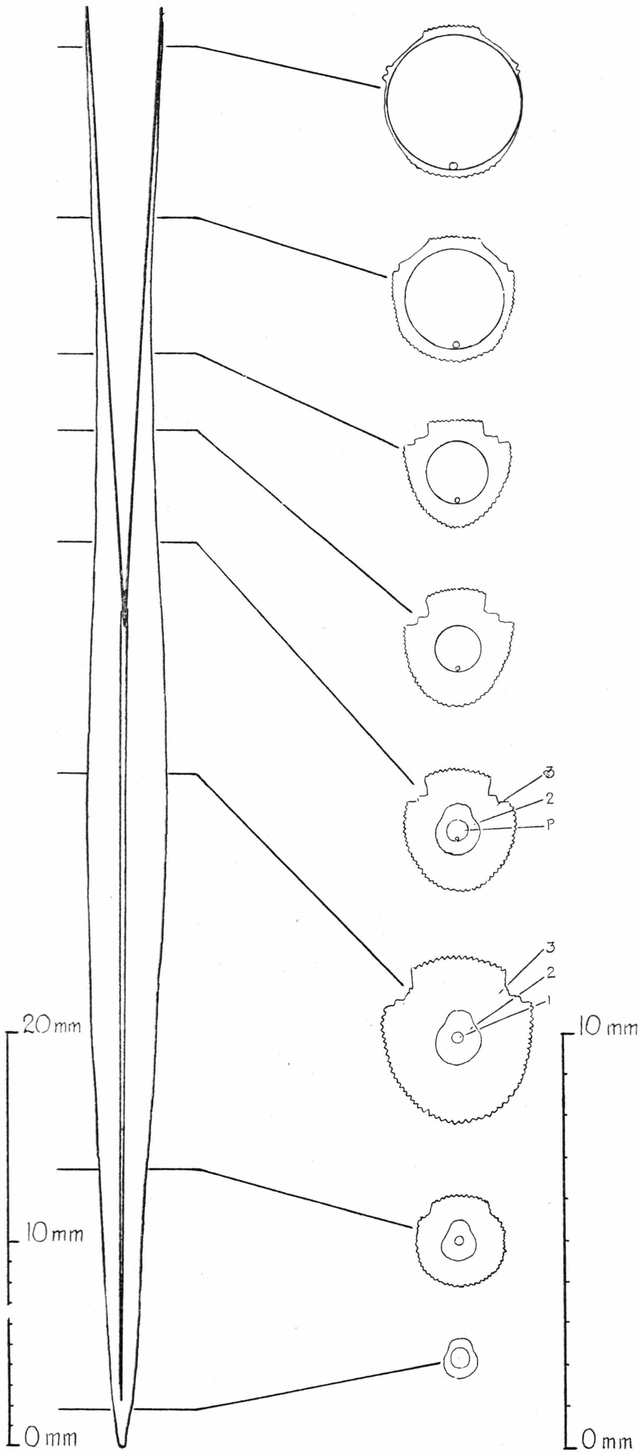

Fig. 2. Reconstruction of an ephebic rostrum of *Dictyoconites groenlandicus*. Longitudinal section at left, representative cross-sections at right. 1, nepionic deposits; 2, neanic deposits; 3, ephebic deposits; p, phragmocone.

at its adoral neck, and 3.7 mm high in its thick central portion. For such a rostrum the length of the alveole is estimated at about 30 mm.

The rostrum is ornamented with fine longitudinal costae (Plate 1, figs. 1—6). These begin near the apical end, about 5 mm or more orad of the latter on the dorsum and venter, and 2.5 mm to 5 mm orad of it on the slightly flattened sides, the regions of the sulci geminati discussed below; there is thus left a smooth apical tip, which appears to be equivalent to the Endstachel described in *Aulacoceras* (von Bülow 1915). The rostral costae are largest in the adapical and central regions; orad they become fine and very sharp, to be lost where the rostrum becomes reduced to a periostracum-like layer over the conotheca. In this zone they appear to extend farther orad on the dorsum and venter than on the sides. At their adapical ends the costae are sharp and fine, separated by broad flat troughs. A similar relationship exists in the expanding adoral end of the rostrum. Between these terminal zones the costae are more rounded, and tend to be as wide as or wider than the intervening more or less U-shaped troughs. The costae are somewhat irregular. They bifurcate here and there in an adoral direction, and along the margins of the sulci geminati bifurcation takes place with striking frequency. On bifurcation both resultant costae are generally finer than the parent, and continue close together for a short distance before a point is reached at which they separate and reach normal size. Occasionally they "change their mind" at this point and reunite, or one of the branches may pinch out. In that portion of the rostrum which tapers orad, costae become finer and pinch out here and there, as if to prevent excessive crowding. Insertion is rare, and costae so formed are thin and discontinuous. Table 2 shows the costal relationships found on the holotype.

Table 2.

Distance from apical end	diameter	no. of dorsal costae	no. of ventral costae	ratio
10 mm	2.0 mm	15 ±	44	1:2·9
30 mm	3.6 mm	24	75	1:3·1
45 mm	3.0 mm	23	71	1:3·1

The sulci geminati first appear as a simple flattened area on each side of the apical tip. Orad each grades into a gentle trough; in a region about half way between the tip and the central, thickest portion of the rostrum the dorsal side of this trough assumes a vertical position and the ventral side a horizontal one, so that the trough becomes angular in cross section, delimited from the adjacent surface of the rostrum by sharply rounded shoulders. About 5 to 10 mm from the apical end the ventral side of the trough begins to carry a well defined secondary shoulder or terrace, which forms a sharp groove along its outer margin. In the adorally tapering portion of the rostrum the trough and its subsidiary groove become deeper and more sharply defined as the rostrum assumes a subtriangular cross section. The groove, originally on the outer margin of the trough, moves inward. On approaching the adoral end of the rostrum the trough loses its angular cross section and becomes broader, but maintains very sharp shoulders; the groove within it remains well defined. Where the rostrum becomes reduced to a thin sheath over the phragmocone the trough is almost lost, but the groove remains, as the shoulders on its sides have changed into strong ribs (Plate 1, fig. 6).

The trough is ornamented in its gentle adapical portion with costae much like those on the adjacent rostral surface, though somewhat finer and more crowded, and parallel to the trough. Where the latter becomes angular, the ornamentation disappears on the dorsal or vertical side and becomes obscure on the ventral, horizontal side. Fine costae reappear in the trough where it reaches the adorally tapering region of the rostrum, and continue orad where they become parallel and similar to the other rostral costae.

Except in the most orad portions of the rostrum the ornamenting costae of the rostral surface near the dorsal margins of the sulci geminati do not parallel the latter; instead, one after another follows orad and downward to or into the trough, to disappear there (Plate 1, figs. 2 and 4). The ribs along the ventral edge of the trough are more nearly parallel to the latter, though a true parallelism is not attained because of frequent bifurcation.

None of the specimens at hand show any trace of the branching vascular grooves characteristic of numerous aulacoceroids.

Internal structure and ontogeny of the rostrum.—Thin sections show the ephebic and gerontic rostra to be composed of three concentric portions, which represent three distinct stages of ontogeny, here referred to as nepionic, neanic, and ephebic-gerontic (text-fig. 2; Plate 2, figs. 1—4, 6). Also, some of the rock specimens at hand contain assemblages of individuals killed and buried at different stages of development (text-fig. 1); thus one bedding plane of approximately 50 square centimeters shows fragments of 38 rostra, of which one is estimated as nepionic, 7 as neanic, 24 as ephebic, and 6 as gerontic.

The nepionic rostrum is a very delicate needle-shaped body, 0.10 to 0.25 mm thick (apparently tapering adapically), perhaps up to about 50 mm long, and circular in cross section. In thin sections it appears as a structureless, recrystallized body of yellowish calcite (Plate 2, figs. 1, 3, 4, 6). In longitudinal sections (text-fig. 3) of neanic and ephebic rostra the nepionic stage appears to be expanded at the apex into a fusiform body which forms the core of the apical tip. Close inspection shows this to be an illusion—the apical end of the nepionic rostrum actually lies

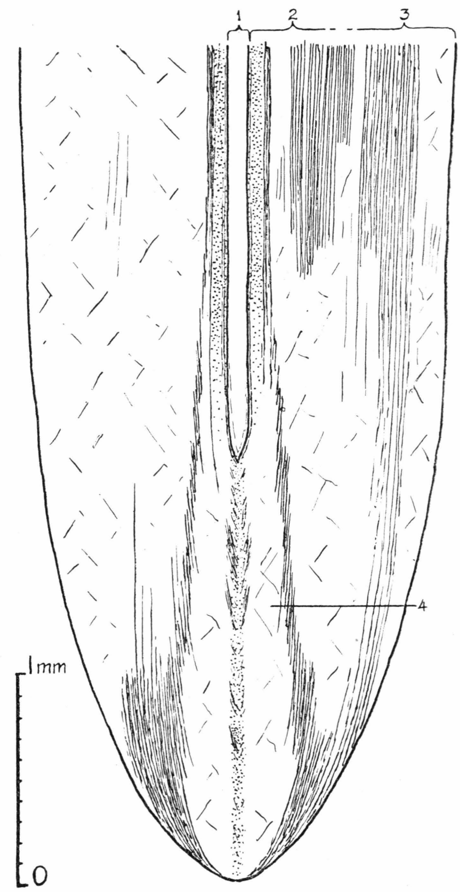

Fig. 3. Longitudinal dorso-ventral thin-section through apical end of rostrum of *Dictyoconites groenlandicus*. This specimen appears to be unusual in showing a heavily pigmented, non-laminated zone surrounding the nepionic rostrum. Loc. N. 77, Permian, R 14. 1, nepionic deposits; 2, neanic deposits; 3, ephebic deposits; 4, fusiform core of apical tip, probably neanic in origin.

somewhere near the adoral end of this fusiform structure, and the latter is a product of neanic growth.

The neanic stage is characterized by concentric growth of the rostrum with thin, smooth, and sharply differentiated laminae obscurae and pellucidae (Plate 2, figs. 1, 3, 4, 6). The rostrum is no longer circular in cross section, except at the extreme apical and adoral ends, but becomes elliptical, somewhat higher than wide, with flattened areas in the regions of the sulci geminati. It grows in thickness to a diameter of 1 to 1.4 mm and grows in length by the apical addition of the fusiform body mentioned above (text-fig. 3), which measures about 2.2 mm, and by orad overlap onto the phragmocone.

Ephebic-gerontic deposits generally account for half or a little over half of the thickness of large rostra. They are not sharply delimited from the neanic zone, from which they differ chiefly in their radial-lamellar

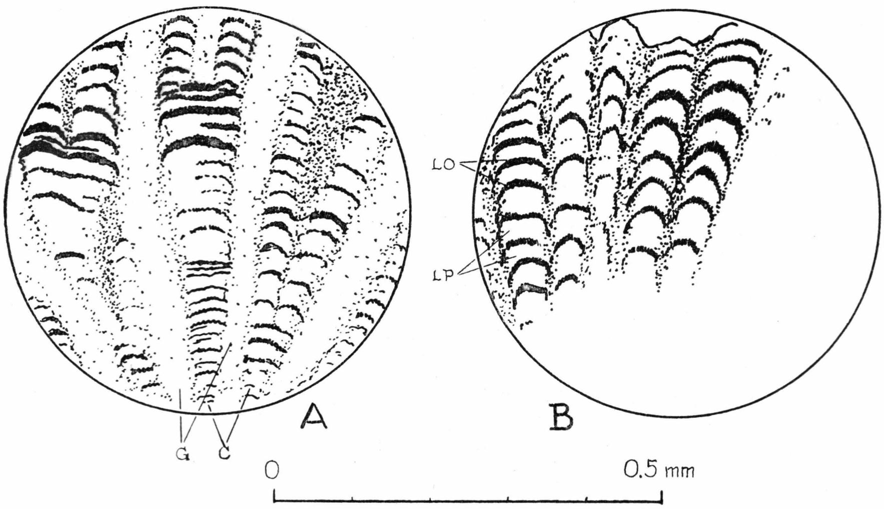

Fig. 4. Transverse thin-sections of ephebic rostral deposits of *Dictyoconites groenlandicus*, showing radial structure and growth laminations (laminae pellucidae, LP, and laminae obscurae, LO). Loc. N. 10, R 14—15, *Posidonomya* beds.

A — broad grooves, G, between costae, C; note costal bifurcations,
B — costae closely spaced.

structure, caused by the costate ornamentation, and in the development of the sulci geminati (Plate 2, figs. 1—7). The ephebic deposits pinch out near the apex (text-fig. 3) so that ephebic addition to the length of the rostrum is limited to progressive adoral overlap over the phragmocone. Ephebic growth in thickness is not uniform, but is greatest in the central region of the rostrum, and thus produces the characteristic clavate shape of the latter. At the very adoral edge of each growth stage the ephebic rostral deposits do not show the characteristic ornamentation and corresponding radial structure, as here the rostrum forms a thin, smooth sheath over the phragmocone.

Like the rostral deposits of the neanic stage, the costal traces of the ephebic stage are composed of alternating well defined laminae pellucidae and laminae obscurae (text-fig. 4). The traces of the intervening grooves show little or no differentiation, and tend to be unpigmented troughout.

Separating the groove and rib traces are narrow zones which show little differentiation but are pigmented. Where costae lie close together the clear groove traces are not developed, and the pigmented border bands of two adjacent costae merge to form a single, narrow, dark groove trace.

Bifurcation of costae may be seen in cross-section (text-fig. 4; Plate 2, figs. 3, 7) as well as on the surface, and is particularly frequent near the sulci geminati.

In transverse sections of the adapical portion of the rostrum, the zones of the sulci geminati show rather irregular, thin costal traces (Plate 2, fig. 3). In the central portion, where the rostrum reaches its greatest thickness, the sulci geminati are sharply incised and not ornamented, and their trace appears in thin-section as structureless (Plate 2, fig. 6) or marked by smooth laminae pellucidae and obscurae. Orad these laminae become finely crenulate, corresponding to the appearance of fine costae on the surface (Plate 2, fig. 5).

As is to be expected, the concentric layering of laminae pellucidae and obscurae is coarsest in the thick central portion of the rostrum, and finest at the ends, particularly at the adoral end, where very delicate laminae are formed, all of them somewhat pigmented but nevertheless very distinct (Plate 2, fig. 5).

The gerontic stage is in basic structure no different from the ephebic; it is marked by continued rostral thickening, which is particularly noticeable in the posterior half, so that the rostrum no longer gracefully tapers apicad from near the mid-point, but remains thick, to taper abruptly and convexly to the smooth apical tip (Plate 1, fig. 2).

The number of costae and the corresponding radial lamellae varies widely with position in the rostrum and age of the individual. Table 3 shows the development of costae seen in a thin section through the adapical region of a gerontic rostrum (Plate 2, fig. 1). The relationships given on p. 12 for the holotype are fairly typical for the larger ephebic rostra.

Table 3.

	Early ephebic (1:2·9)	Gerontic (1:2·2)
Dorsal	14	34
Ventral	41	75

The smallest total number of costae measured in any one specimen was 55 (early ephebic, adapical), the greatest 115 (ephebic, just apicad of alveole). The ratio of dorsal to ventral costae varies from 1:2.2 (gerontic, adapical, Plate 2, fig. 1) to 1:3.6 (ephebic, near tip of alveole).

The phragmocone.—Among the material studied there are many small fragments of phragmocones, but very few usable specimens. Even most of the rostra have been crushed at the alveolar end, and the unprotected portions of the delicate phragmocones have been almost completely demolished. A few specimens from the block labelled L. K. 38 show the alveolar portion of the rostrum with the enclosed parts of the phragmocone, and in association with these was found a shell fragment which appears to be part of a proostracum (text-fig. 5).

The phragmocone (Plate 1, fig. 7) is very delicate, with circular cross section (Plate 2, fig. 7). Its apical angle measures between 7°

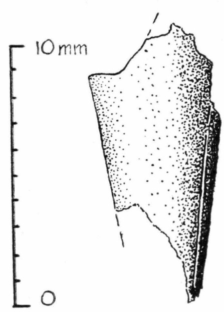

Fig. 5. Fragment of a proostracum? of *Dictyoconites groenlandicus*, from loc. L. K. 38.

and 8°. In one of the paratypes (Plate 1, fig. 6) the phragmocone measures 3.5 mm in diameter at the margin of the alveole, hence the length of the latter must have amounted to 25 to 30 mm.

The apical end of the phragmocone has not been observed. The septa are delicate and are strongly arched with the concave side orad. The length-width ratio of the chambers varies from approximately 1:1 in the adapical portions (at a diameter of about 0.3 mm) to 1:3 in the adoral portions of the alveole (at a diameter of about 2.3 mm). Plate 1 fig. 7 shows a paratype with the length-width ratios of 10 successive chambers indicated.

The siphuncle appears as a thin-shelled, clear, cylindrical, marginal tube (Plate 1, fig. 7); each septum meets it at a sharp angle. No septal collars appear to be developed; instead, the dark septal tissue is recurved, and, covering the septal tube described above, it follows the siphuncle apicad, getting thinner and thinner, until it has almost disappeared where the next septum is encountered. This picture may be misleading because of the poor preservation of the specimen sectioned. The only better specimens at hand (from loc. L. K. 38) are indispensable because of their surface features. A thorough study of even the alveolar portions of the phragmocone is therefore not possible at this time.

Fragments of crushed internal molds of phragmocones from loc. L. K. 38 indicate that chambers reached a length of 1.6 mm at a width of perhaps 4.5 mm, a ratio of about 1:2.8. Orad of each suture lies a dull bluish band, 0.6 mm wide, which may represent the impression of a cameral deposit; the structure much resembles that depicted by FLOWER (1945) in his Fig. 1 A for *Eobelemnites caneyense*. It is not certain that these fragments belong to *Dictyoconites groenlandicus* though the association suggests it. These same fragments show a faint wavy or zig-zagged transverse striation, which seems to carry through a thin

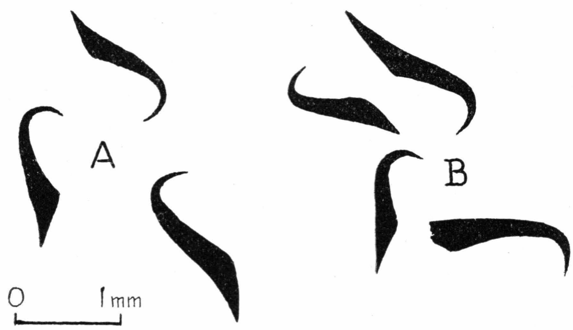

Fig. 6. Arm hooks (onychites) of *Dictyoconites groenlandicus*. A: loc. 17, Hird's Fox Farm, Clavering Island, KOCH and NOE-NYGAARD, July 17th, 1930. B: loc. L. K. 38.

layer of shell matter. Thin shell layers outside of this show a straight longitudinal striation.

Sections through the alveolar portion show a smooth conotheca. Among the fragments of loc. L. K. 38 there was found nothing resembling the costate conotheca generally ascribed to *Dictyoconites*. An interesting conothecal(?) fragment from this locality, possibly part of a proostracum, is illustrated in text-fig. 5. It is not known whether or not the form here described possessed the two proostraca with which the aulacoceroids are generally credited.

Arm hooks.—Many dibranchiates carry chitinous arm hooks. These are developed out of the more usual sucker discs, and represent a specialization for grasping and holding soft-bodied prey (NAEF, 1922). Such arm hooks (onychites) have been described for a number of Mesozoic belemnoids, but their discovery in the Greenland material (ROSENKRANTZ, 1930) appears to be their first in association with true aulacoceroids. The hooks involved are of two types. A streak of brown argillaceous matter (possibly a large coprolite) associated with rostra in the limestone block from loc. L. K. 38 was found to contain a considerable number of small hooks from 1.2 to 1.8 mm long (text-fig. 6). A block from the *Posidonomya* beds at Hird's Fox Farm (Clavering Island) shows a group of similar hooks, and among them a much larger one, 8.5 mm long, hollow, and of different shape (Plate 1, fig. 8). It is suggested that the small hooks belonged to *Dictyoconites groenlandicus*. The large interloper may represent an onychite of some other cephalopod.

DISCUSSION

Classification. With the exception of the Eocene *Vasseuria*, all belemnites with costate rostra have been referred to the genera *Aulacoceras* von Hauer (1860) and *Dictyoconites* von Mojsisovics (1902), which form the nucleus of the family Aulacoceratidae (Bernhard). To date these genera have been described from the Triassic only. Their rostra are straight and costate, and carry strongly developed sulci geminati. The phragmocones are straight, slender, circular in cross section, and pauciseptate, with marginal siphuncles. They are generally held to be costate, but the adoral portions of phragmocones have been described for only a few species, and the intra-alveolar portions of a number of species referred to *Dictyoconites* show no traces of costation, if one may judge from the illustrations in the literature (Hauer, 1892; von Bülow, 1915). Naef (1922) considers these costae to be periostracal deposits, rather than part of the conotheca, i. e. extensions of rostral matter which overlie the latter, but in the absence of thin-section studies this question remains unsettled. On the evidence of conothecal growth lines (questioned by Naef, 1922) *Aulacoceras* and *Dictyoconites* are generally thought to have had a small ventral and a larger dorsal proostracum. It is to be kept in mind that while numerous species have been assigned to these two genera, most of these are based on very incomplete and in many cases poorly preserved fragments. Only two species, *Aulacoceras sulcatum* Hauer and *A. timorense* Wanner, have been studied in detail, and even in these many features, such as the microstructure of the phragmocone, its length, and the nature of its adoral portions, remain obscure.

The differences between the two genera seem to lie mainly in rostral features; the phragmocones, once thought distinctive, appear to be fairly similar in surface features (Diener 1917, 1919). *Aulacoceras* is retrosiphonate with slight septal collars. Von Mojsisovics considered *Dictyoconites* to be prosiphonate, but von Bülow (1915) shed doubt on this determination. *Aulacoceras* is characterized by massive rostra with coarse costation. Its sulci geminati consist of 1) a pair of troughs which grade into the ventral part of the rostrum and are sharply overhung by the dorsal portion, and 2) a pair of sharp grooves which more or less parallel the trough on the dorsal side. The dorsal part of the rostrum is equal to or larger than the ventral. The phragmacone is deeply embedded in the rostrum. The forms referred to *Dictyoconites* possess slender, clavate, finely costate rostra, sharply divided by well-defined sulci geminati into a narrower dorsal and a broader ventral portion. In most species the sulci geminati consist of two pairs of depressions which are subject to much variation and provide striking specific differences. In contrast to *Aulacoceras* the *Dictyoconites* rostrum extends apicad far beyond the apical tip of the phragmocone.

In shape and rostral ornamentation the Greenland form is clearly allied with the species referred to *Dictyoconites*. Its sulci geminati are quite distinct from any previously described, but in view of the wide differences in this feature between the various species of the genus it was deemed inadvisable to erect a new genus on this basis. The internal structures of the phragmocone and rostrum are poorly understood in the various species referred to *Dictyoconites*, and can therefore not be used at this time for comparison or differentiation.

Biologic interpretation.—According to Abel (1916) and Naef (1922) *Dictyoconites* was probably a slender squid-like animal. The lack of information regarding the phragmocone and proostracum of *D. groenlandicus* prevents a reconstruction of this species, but the rostrum permits certain generalizations. The protoconch is generally considered as the first part of the cephalopod skeleton to be precipitated. Unfortunately the material at hand has not permitted the study of the apical tip of the phragmocone, so that the earliest chambers and their relationship to the nepionic rostrum remain obscure. It seems likely that the nepionic rostrum was not precipitated until the protoconch and perhaps additional chambers of the embryonic phragmocone had become vacated by the animal and filled with gas[1]). The nepionic animal then possessed a protoconch and probably one or more additional chambers, and a needle-shaped rostrum (text-fig. 2) perhaps 35 to 40 mm long; nothing is known regarding the existence and length of a living chamber or proostracum. To judge from the rostrum, the animal must have been

[1]) As Dunbar (1924) and Flower (1939) have brought out, the rostrum of belemnoids is one of several ways cephalopods have adopted to bring together the center of gravity and the center of buoyancy. The rostrum acts as a counterweight to the adorally concentrated visceral and muscular mass of the animal, with the buoyant phragmocone in between. This arrangement permits the animal to assume a horizontal position in the water, a position necessary for an active nektonic life, and affords maneuverability.

very slender and delicate, probably more or less planctonic in mode of life.

The neanic rostrum shows much growth in thickness, with some apical growth, and a considerable extension orad by overlap onto the phragmocone. The faint indications of sulci geminati may indicate the development of dorso-lateral fins. The growth of the rostrum in this and succeeding stages is no doubt in proportion to the addition of air chambers to the phragmocone, and to the increase of the visceral and muscular mass of the animal, so as to keep the organism in gravitational balance.

The ephebic-gerontic stages are characterized by the development of costation and the sulci geminati. The purpose of the costae is not clear. Obviously they increase the surface area of the rostrum, and it seems likely that they anchored the tissues somewhat more tightly to the skeleton. In the absence of any evidence for proterogenesis, ontogeny suggests that phylogeny has proceeded from smooth to costate rostra. Until thin-section studies of well preserved rostra of *Aulacoceras* are made it would seem wise to treat VON BÜLOW's statements on the microstructure of the rostrum of *Aulacoceras timorense* WANNER and his suggestions concerning the ontogeny and phylogeny of this form with caution.

According to ABEL (1917) the sulci geminati of belemnoids served to attach fin-muscles, and forms in which these grooves or troughs are well developed may be interpreted as active swimmers. This would certainly apply to the species at hand, and corroborates similar evidence afforded by the arm hooks, which in modern squids appear mainly among very active oceanic forms.

The scarcity of the costate aulacoceroids in terrigenous sediments suggests that they lived mainly in the open sea. The *Posidonomya* shales of East Greenland appear to have accumulated in more or less stagnant troughs or lagoons on the eastern margin of a continental mass, and the presence of the belemnoids in these sediments may be explained by the occasional influx of marine waters, which carried with them radiolarians, belemnoids, and fish. It seems probable that the environment of the stagnant basin, low in oxygen and high in hydrogen sulphide, killed the newcomers, and thus large groups of belemnoids, including juveniles as well as adults, were buried together (text-fig. 1).

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PLATES

Plate 1.

Fig. 1. Dorsal view of an ephebic rostrum (the holotype), ×3. Loc. L. K. 38.

Fig. 2. Side view of a gerontic rostrum (a paratype), ×3. Loc. L. K. 38.

Fig. 3. Ventral view of a slightly gerontic rostrum, ×3. Loc. L. K. 38.

Fig. 4. Anterior end of specimen illustrated in fig. 2. Oblique view into left sulcus, × 5. Loc. L. K. 38.

Fig. 5. Adoral "neck" of a rostrum, dorsal view, × 3. Loc. L. K. 38.

Fig. 6. Fragments of alveolar portion of a rostrum (a paratype), × 3. Upper and lower fragments expose the left, middle fragments the right side. On the uppermost fragment the rostrum is represented by a thin brown film on the conotheca; the latter is exposed in the light area in the upper middle portion. Loc. L. K. 38.

Fig. 7. Longitudinal dorso-ventral thin-section of alveole and included phragmocone, ×16, a paratype. The phragmocone is partly silicified. Light colored deposits on walls and septa appear to be secondary. The siphuncle (Si) may be seen in the five chambers at the right. The length-width ratio of the chambers shown is, from left to right: 1:1.3, 1:1.5, 1:1.5, 1:1.5, 1:1.6, 1:2.1, 1:2.1, 1:2.1, 1:2.0, 1:2.3. Loc. L. K. 38.

Fig. 8. Small arm hooks referred to *Dictyoconites groenlandicus*, and a large hook of uncertain affinities. × 4.5, retouched. Loc. Nr. 17, Clavering Island, Hird's Fox Farm, leg. Koch and Noe-Nygaard, August 17th, 1930.

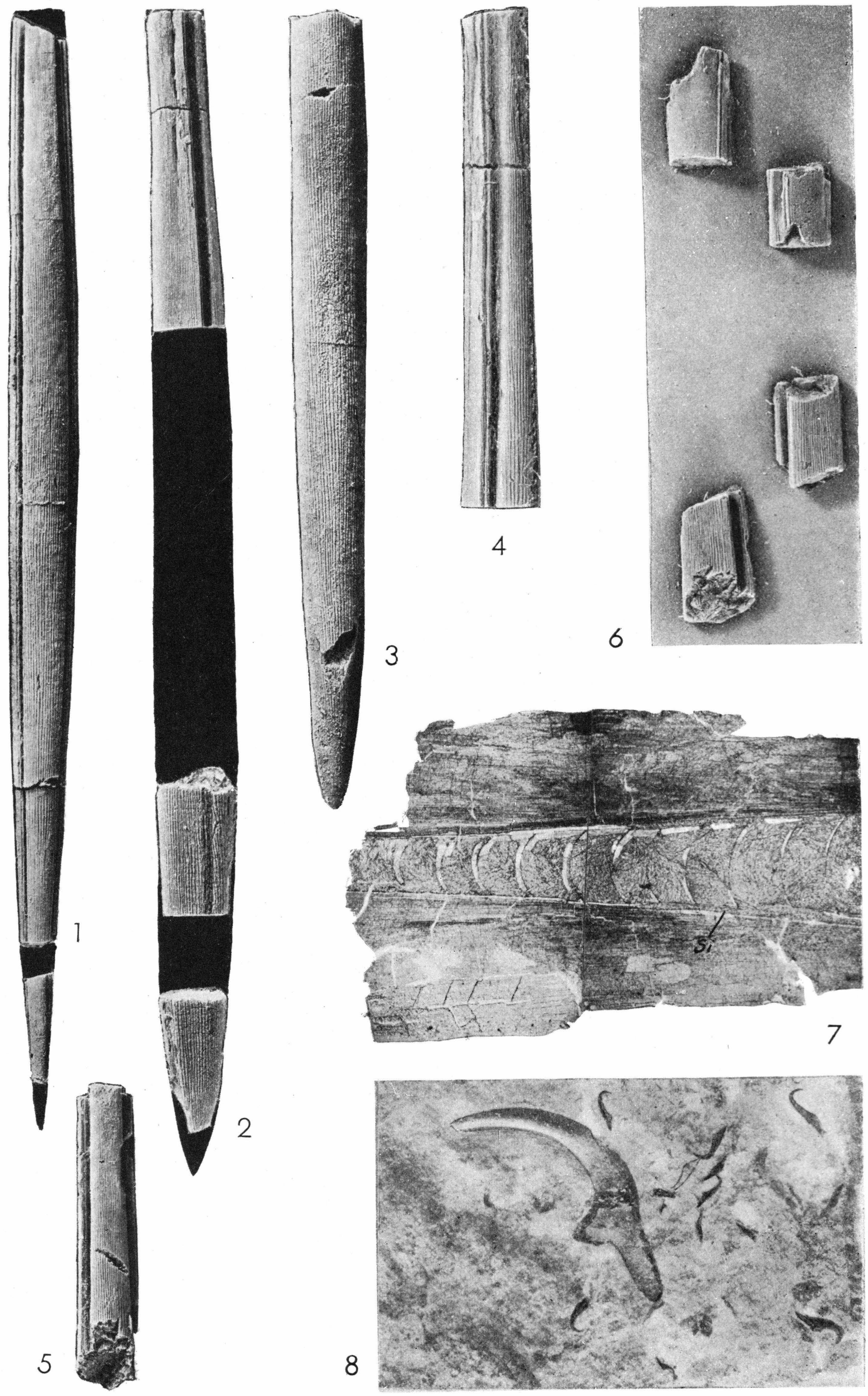
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Plate 2.

Thin sections of *Dictyonites groenlandicus* from the *Posidonomya* zone, Sta. N. 10, R. 14—15, 7—21—1937.

Fig. 1. Cross section of median region of a gerontic rostrum. Note that the neanic stages are "lying on their side", oriented at approximately 90° to the later deposits. This may be the result of an injury sustained at the end of neanic life. ×13.

Fig. 2. Cross section of median portion of a young ephebic rostrum. Note cross sections of the pelecypod *Posidonia* sp. in the surrounding matrix. ×13.

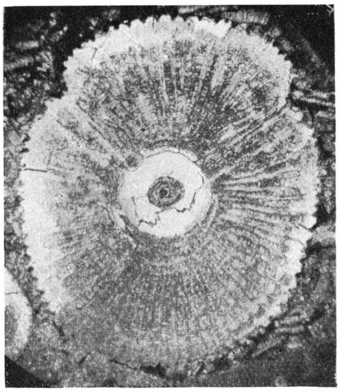
Fig. 3. Cross section of adapical portion of an ephebic rostrum, partially silicified. ×13.

Fig. 4. Cross section of adapical region of a gerontic rostrum. Note bifurcation of costae in the regions of the sulci geminati. ×13.

Fig. 5. Cross section of alveolar portion of an ephebic or gerontic rostrum, somewhat compressed dorso-ventrally. ×24.

Fig. 6. Cross section of median portion of an ephebic rostrum. ×24.

Fig. 7. Cross section of alveolar portion of an ephebic rostrum, partially silicified. Note traces of conotheca and siphuncle. ×24.



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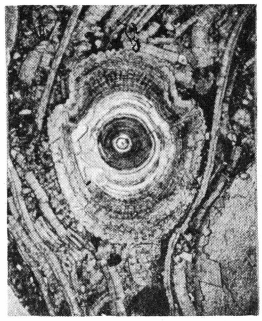

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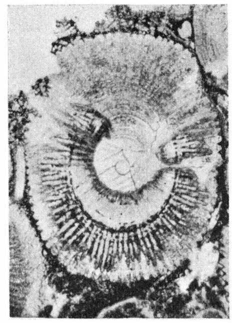

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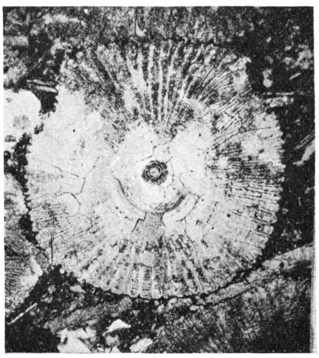

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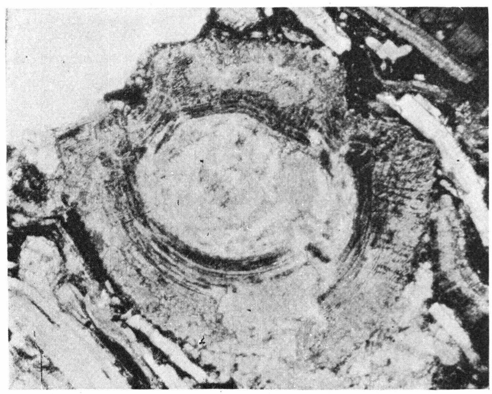

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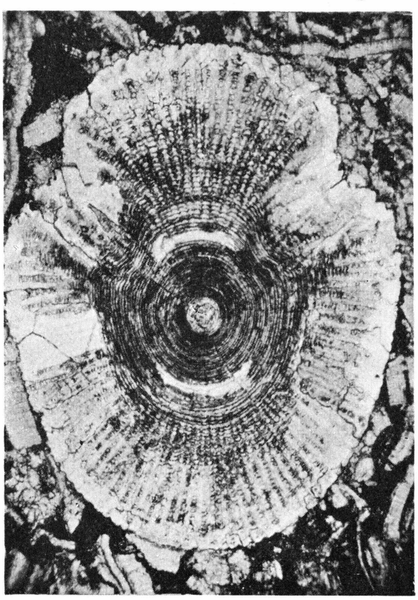

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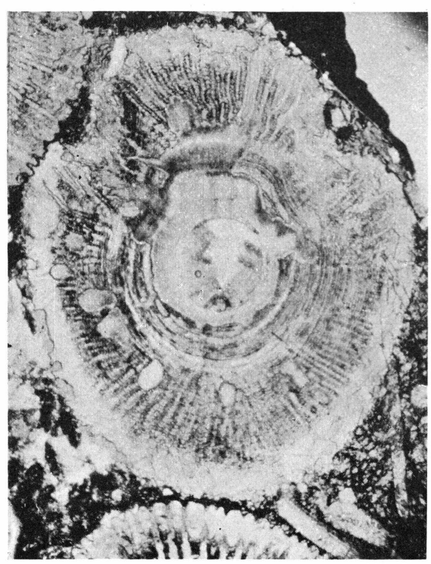

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