

Reconstruction and biostratinomy of Devonian cephalopods (Lamellorthoceratidae) with unique cameral deposits.

With 3 text figures and 10 plates.

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Abstract.

Study of many Devonian specimens of the Family Lamellorthoceratidae TEICHERT 1961, traditionally regarded as orthoconic nautiloid cephalopods, reveal details of their ontogeny, life habits, biostratinomy and diagenesis. Representatives from the Hunsrück Slate of West Germany now yield new insight into the origin of the unique radiating cameral lamellae-features that set these cephalopods apart from all other Paleozoic nautiloids. — The Hunsrück material is compared with additional new specimens from Nevada, which constitute the first report of this cephalopod family in the western Cordillera. These specimens, together with topotype material of *Esopoceras* STANLEY & TEICHERT 1976 from New York, *Coralloceras* ZHURAVLEVA 1962 from Morocco, and *Lamellorthoceras* TERMIER & TERMIER 1950 from France, show that many features of the internal and external conch are actually spurious morphologic by-products of diagenesis and biostratinomy. This leads to the conclusion that the four to five currently recognized genera have been unduly split and that perhaps only one genus actually exists. — The unique internal lamellae of the lamellorthoceratids were originally organic sheets, secreted by the cephalopod visceral mass during chamber formation. The complex arrangement of several sets of these sheets served to compartmentalize the camerae and to decouple cameral fluids from the siphuncle, as well as to hold bubbles of gas at a fixed place within each chamber. Analogous features in *Sepia*, ammonites, and *Nautilus*, collectively serve to explain the functional morphology of the lamellorthoceratids. In posterior chambers within the phragmocone, sheets formed templates for mineralization of calcitic intracameral crusts. The added weight, coupled with the growing body mass of the animal and the buoyancy of the gas-filled chambers, served to balance the swimming organism hydrodynamically.

Kurzfassung.

[Rekonstruktion und Biostratinomie devonischer Cephalopoden (Lamellorthoceratidae) mit einzigartigen Kammer-Ablagerungen.]

Untersuchungen an zahlreichen Individuen aus der Familie der Lamellorthoceratidae TEICHERT 1961 ergaben Einblicke in ihre Ontogenese und Lebensweise sowie zu ihrer

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Einbettungsgeschichte und Diagenese. Besonders Vertreter aus dem Hunsrück-Schiefer ermöglichen eine morphologische und funktionelle Interpretation der Kammer-Lamellen, die dieser den orthoconen Nautiloideen zugeordneten Gruppe einzigartig sind. Weiteres Material aus Nevada wird vorgestellt, das bisher zum ersten Mal aus den westlichen Kordillern der USA beschrieben ist. Zusätzlich konnte topotypisches Material von *Esopoceras* STANLEY & TEICHERT 1976 von New York, *Coralloceras* ZHURAVLEVA 1962 von Marokko und *Lamellorthis* TERMIER & TERMIER 1950 von Frankreich belegen, daß viele Merkmale der Fossilien während der Diagenese entstanden sind. Eine Rekonstruktion der Vorgänge im Sediment bis zur Fixierung als Fossil legt nahe, daß die Aufteilung der Gruppe in vier oder fünf Gattungen nicht berechtigt ist und daß möglicherweise nur eine einzige Gattung vorliegt. — Die einzigartigen Innenlamellen der Kammern der Lamellorthoceratiden bestanden aus organischen Häutchen, die vom Epithel des Eingeweidetasches des Cephalopoden ausgeschieden wurden, als er sich aus dem Raum einer neuen Kammer zurückzog. Die organischen Lamellen dienten dazu, die Kammer in kleine Räume aufzugliedern und damit der darin enthaltenen Kammerflüssigkeit den direkten Kontakt zum Siphonalrohr zu erschweren. Beim Leerpumpen der Kammern entstandene Gasblasen wurden zudem durch die Lamellen an fixierten Orten in der Kammer festgehalten. Die Funktion des Kammerapparates der Lamellorthoceratiden kann mit Hilfe der Gehäusemerkmale rezenter Cephalopoden wie *Sepia* und *Nautilus* gedeutet werden. Rückwärtige Kammern des Phragmokons wurden sekundär wieder geflutet und in ihnen bildeten sich Kalzitkrusten auf den organischen Lamellen. Das zusätzliche Gewicht des hinteren Gehäuseabschnittes sowie das Gewicht des Körpers, wie die dazwischen gelegene Zone mit geleerten Kammern, balanzierten das Tier in seinem Lebensbereich im Meer aus. Eine Rekonstruktion als ectocochleater wie auch als endocochleater Cephalopod ist möglich.

Introduction and past work.

Living cephalopods, like *Sepia*, *Spirula*, and *Nautilus* construct their hard parts in different ways, but buoyancy control is a prime concern in all cases. Two extremes in chamber construction are represented among these cephalopods. One, represented by the ectocochleate shells of *Nautilus*, exhibits large, open and cylindrical chambers, whereas the other, represented by the endocochleate cuttlebone of *Sepia*, displays narrow, flat chambers differentiated into numerous interconnected chamberlets separated from each other by mineral and organic sheets and walls (pl. 10 figs. 57-59). In both forms the liquid filling a chamber is withdrawn slowly and steadily, as soon as chamber formation is complete.

Cephalopods of the Family Lamellorthoceratidae TEICHERT 1961 are a group of presumed nautiloids distributed worldwide, but restricted to the Lower and Middle Devonian (TEICHERT 1961; TEICHERT & al. 1964; RUZHENTSEV 1962). They are represented by five genera known from the Urals, Germany, France, North Africa, Turkey, and North America. Although from the exterior they may resemble normal orthoconic nautiloids, the apical chambers contain unusual and complex sets of radially disposed cameral deposits (lamellae). These lamellae converge from the walls toward the siphuncle, filling the cameral space with densely packed, complexly oriented "deposits". In cross-section, lamellorthoceratid cephalopods show a resemblance to rugose corals (HOWELL 1942; LE MAÎTRE 1950). This similarity prompted BEYRICH (in CARNALL & EWALD & ROTH 1850) to describe the first known genus as *Arthrophyllum*, believing it to be a coral.

Internally, the lamellorthoceratid chambers are composed of lamellae, unlike other Paleozoic nautiloids which usually contain cameral deposits that line chamber walls or septal surfaces (TEICHERT & al. 1964). TEICHERT (1961) demonstrated that in lamellorthoceratids, the radial lamellae are closely packed and fill the apical chambers but become less voluminous in the chambers toward the aperture. Furthermore, they are absent from the living chamber and the first few chambers behind it.

There has been considerable discussion about the origin and function of cameral deposits in Paleozoic nautiloids. These discussions centered around the question of whether organized intracameral deposits could have been formed under direct tissue control (FLOWER 1955) in contact with tissue only (organic origin), or whether they formed indirectly by inorganic mineralization within chambers not occupied by living tissue connected to the siphuncle (inorganic origin). Both theories were discussed by FISCHER & TEICHERT (1969). CRICK (1982) more recently revived the issue with regard to the nautiloid Family Pseudorthoceratidae. BARRANDE (1859) first discussed the possibilities of an organic origin for cameral deposits, whereas MUTVEI (1956) used the lamellorthoceratids as evidence supporting inorganic precipitation. More recently, STANLEY & TEICHERT (1976) favored an organic origin based on the intricate, complex and repetitive nature of the lamellae in lamellorthoceratids from New York. Lamellar orientation within the chambers and clear bilateral symmetry suggested a function in stabilization and balancing of the conch.

Lamellorthoceratids are a small, relatively short-lived group of Devonian cephalopods that attained worldwide distribution. Because of their unusual morphology and lack of close living relatives, they are puzzling with regard to their origin and function of the lamellae as well as their relationships to other cephalopods. This is further complicated because conchs of different ontogenetic stages from different localities reveal different types of diagenesis. An understanding of these factors permits a reasonably accurate reconstruction of the diagenetic sequence of alteration.

Abundant lamellorthoceratid material from New York and Nevada, coupled with new discoveries from the Hunsrück Slate of West Germany and topotype material from France and Morocco, now provides the basis for review of the biology and functional morphology of this unusual group of cephalopods. Available data now suggest that lamellorthoceratids were radically different from their nautiloid counterparts and show previously unrealized similarities with coleoids, aulacoceratids, and ammonites.

Notes on the Hunsrück Slate.

The Lower Devonian Hunsrück Slate of the S. W. Rheinische Schiefergebirge is celebrated since long for its well preserved fossils, including occasional soft-part preservation. Specimens from the most famous slate mine, the Kaisergrube at Gemünden (Hunsrück) are from the collections of W. STÜRMER. In addition, collections from various universities, museums and private individuals in Germany, were used for this study.

Regarding the environment of deposition, stratigraphy and thickness of the Hunsrück Slate, many different interpretations have been presented and many features are still controversial (MITTMAYER 1980). Paleontologically, the Hunsrück has been an important source of information for the interpretation of ichnofauna (SEILACHER & HEMLEBEN 1966),

echinoderms (LEHMANN 1939), for the first development of the ammonites (ERBEN 1966) and for early coleoids (BANDEL & REITNER & STÜRMER 1983; STÜRMER 1985; BANDEL & BOLETZKY 1979, 1988).

Materials and methods.

The specimens that form the basis of this study come from five Devonian sites: (NY) New York State, Esopus Formation, Lower Devonian (Emsian; see STANLEY & TEICHERT 1976); (GI) Morocco, near Oued Dra, Lower Devonian (Upper Emsian; see LE MAÎTRE 1950); (CR) Nevada, Cortez Range, Wenban Peak (Lower Devonian); (LF) France, Lanvoy en Le Faou (Finistère), Middle Devonian (lower Couvinian); W. Germany, Hunsrück Slate (Lower Devonian), S. W. Rheinische Schiefergebirge, Kaisergrube quarry, Gemünden.

The Nevada locality yielded the first lamellorthoceratids known from the western Cordillera of North America. They occur in limestone of the McColley Canyon Formation (Lower Devonian) in the Cortez Range, central Nevada at Wenban Peak (DAVID J. CHRISTENSEN 1980, University of California, Riverside, M. S. thesis "Petrology and biostratigraphy of middle Lower Devonian strata, Cortez Mountains, Nevada").

Specimens from the NY and LF localities are housed in the U. S. National Museum of Natural History (USNM), Washington/D. C.; GI and CR, (SUI) in the Department of Geology, University of Iowa; WS, in the Department of Geology and Paleontology, University of Hamburg and in the private collection of the late WILHELM STÜRMER (Erlangen, W. Germany). In addition, a collection of duplicate radiographs of the Hunsrück specimens prepared by WILHELM STÜRMER are housed in the "Geologisches und Paläontologisches Institut und Museum" in Hamburg.

The methods employed in this study utilize standard thin sections and radiography of specimens preserved with iron sulfides such as pyrite (STÜRMER 1970; STÜRMER & BERGSTRÖM 1973). Scanning electron microscopy has provided details of modern *Sepia* and *Spirula*, and fossil ammonites, allowing comparisons with our fossil material.

Description of the conch.

In the following discussion, we will first describe exterior, and then the interior of the conch. Our comments are based upon approximately 60 well-preserved specimens of lamellorthoceratids from the various localities.

Conch morphology.

The conchs are characteristically straight, gradually expanding, cylindrical and circular in cross-section. An angle of expansion from 4-6 degrees could be measured on undeformed individuals from all localities except on one specimen of *Arthrophyllum* BEYRICH 1850 from France. Conchs of the smallest juveniles, probably just hatched from their egg-cases, occur in a fair number in radiographed slates from the Hunsrück Slate. They are abundant in some layers and can be found together with juvenile conchs of other nautiloids and coleoids (BANDEL & REITNER & STÜRMER 1983), as well as tentaculites. The initial chamber is spherical, measures about 0.6 mm in width and constricts at the first septum. The smallest complete conchs measure about 5.0 mm in length, showing about four chambers including a living chamber that is twice as long as the phragmocone.

Conch dimension and shape.

Lamellorthoceratid living chambers in contact with the chambered portion of the shell are commonly preserved in the Hunsrück material, with individuals from 5.0 mm to 50 cm long. In contrast, only one individual from New York shows a living chamber. Even though living chambers are not always preserved, it is expected that their size and shape are similar in all studied material.

Juvenile conchs from the Hunsrück Slate show that the living chamber was rapidly enlarged, whereas the phragmocone grew only slightly during the initial growth of the newly-hatched animal. At early stages, when the entire organism was only 5.0 to 6.0 mm long, the living chamber was about twice as long as the phragmocone. The living chamber continued to expand more rapidly until, at a length of 2 to 4 cm, it measured about 2 times the length of the phragmocone. At larger sizes, this tendency toward further growth was actually reversed. In an 8.0 cm-long conch, the living chambers and phragmocone are of about equal length, whereas a 24 cm-long conch displays a living chamber of 10 cm, and finally, a 50 cm-long conch has a living chamber 19 cm long (pl. 3 fig. 18, pl. 8 fig. 45a, pl. 9 fig. 52).

Conch sculpture.

All studied individuals had a smooth shell sculptured only by faint lines of growth. These are best-preserved in two individuals from New York (pl. 1 figs. 5, 7) and less well-preserved in several individuals from the Hunsrück. The growth lines are not straight but show a broad dorsal saddle and a wide ventral lobe. As a result, the aperture traces a shallow ventral sinus and a broad dorsal salient. Sutures display a low ventral saddle and are straight or slightly lobed on the dorsal side. Other sculptural elements on the surface of the conch developed during diagenesis (see below).

Shell composition.

The shell of lamellorthoceratids was secreted as aragonite in nacreous and prismatic structure, as in recent cephalopods with a chambered conch (BANDEL & BOLETZKY 1979) and in other fossil cephalopods showing preserved shell structure (MUTVEI 1984; ERBEN & FLAJS & SIEHL 1969; BANDEL 1981, 1982; BANDEL & ENGESER & REITNER 1984). The shell walls have either converted to calcite, been replaced by other minerals (calcite, pyrite, or limonite) or totally or partially dissolved. In a few individuals from New York, the aragonite has been replaced by very fine-grained calcite. The recrystallized shell shows a composition of fine, longitudinally arranged rods about 0.02-0.03 mm wide (pl. 1 figs. 1, 4). These rods are parallel to each other and parallel to the long axis of the shell, except within the ventral portion of the conch where the rods are inclined toward each other, forming a small angle pointing toward the apex of the conch. Rods are the result of the transformation of nacre stack-rows into calcite needles (DULLO & BANDEL 1988), representing the most gentle transformation known of nacreous aragonite into calcite in fossil molluscs.

A similar orientation of rods can also be noted where the original aragonitic shell had been demineralized during diagenesis, but organic shell material still remained.

In this case, fine, longitudinal costules developed (pl. 1 figs. 2, 6). Because they belong to the outer shell wall, these costules cross the suture line uninterrupted. About 6 costules are present in each millimeter of shell surface. The costules are parallel on the dorsal and lateral sides (STANLEY & TEICHERT 1976: pl. 2 figs. 2, 6) forming a small angle with each other along the ventral line. In contrast to the longitudinal rods that formed by the transformation of nacre into calcite, the angle here points towards the aperture (pl. 1 fig. 2). Such costules were also noted on the flattened living chambers and conchs of some individuals from the Hunsrück. The shell must have been demineralized before it was flattened and compacted into the bedding plane because signs of fracturing are absent. The costules serve as evidence that similar features preserved on the undeformed or only slightly deformed New York material also originated after dissolution of the mineralized shell. Demineralization brings out the pattern of the organic shell hidden within the mineral matrix. In other Paleozoic cephalopods, such as the Bacritoidea, comparable lines are regarded, reasonably, as having taxonomic importance.

Internal shell surface — ventral side.

Some undeformed lamellorthoceratid conchs from New York show a conchal furrow on the internal mold of the phragmocone along the ventral portion of the steinkern. The furrow is usually expressed as a narrow, deep depression in the aragonitic shell of the living chamber (pl. 1 fig. 10) and never occurs on the outer shell surface where only the shallow sinus growth lines are developed. A common feature in cephalopod conchs (FLOWER 1964), the furrow was noticed by BABIN (1964: pl. 15 fig. 3) in *Lamellorthoceras vermiculare* TERMIER & TERMIER 1950 from France.

Dorsal side of conch.

Of the numerous specimens from New York, only two conchs clearly display the interior surface of the dorsal inner shell wall. In these specimens, a longitudinal scar composed of parallel furrows is continuous across the sutures (pl. 1 fig. 9). In a 1 cm-wide conch, this feature measures 3.0 mm in width. The general shape and nature of this scar suggest the presence of a well-attached muscle mantle inside the shell, similar to that found today in *Spirula* (pl. 1 fig. 11) (BANDEL & BOLETZKY 1979; BANDEL 1982). Similar scars are known from *Pseudorthoceras* (RISTEDT 1971: pl. 33), and also from belemnites and aulacoceratids (BANDEL & ENGESER & REITNER 1984; BANDEL 1985; BANDEL & KULICKI 1988).

Siphuncle.

The siphuncular tube penetrates all chambers at approximately the same position just ventral of center (pl. 4 fig. 22, pl. 5 fig. 28c). The diameter of the siphuncle increases more slowly than that of the conch. In the earliest-formed chambers the siphuncular tube measures about one-third of the chamber width (pl. 5 fig. 28). In juvenile to mid-sized individuals, it is about one-sixth of the chamber width (pl. 5 fig. 29), and in full-grown conchs (4-5 cm diameter), its width is about one-eighth of chamber diameter (pl. 4 fig. 22). The position of the siphuncle relative to the

ventral line, which is the dorsal tissue attachment scar, produces a surface deflection formed by costules of the wrinkle layer and lobes and sinuses of the growth lines, clearly differentiating the dorsal from the ventral side. In the nearly cylindrical, circular diameter conch, individuals without compactional deformation show exactly the same course of the siphuncle, just ventral to a median plane in the conch (pl. 4 figs. 22, 24, pl. 5 figs. 29, 31). Siphuncle construction is similar to that of Mesozoic ammonites, and its material consisted of an elastic organic substance (WEITSCHAT & BANDEL 1989).

Septa.

Lamellorthoceratid septa are retrochoanitic where the siphuncle penetrates the septum (pl. 2 fig. 13b, pl. 5 fig. 27a). Because this portion of the siphuncle is shifted slightly towards the ventral side of the conch, the contact of the septum with the inner surface of the shell wall (suture) developed a shallow lobe ventrally. The mural area is narrow and disrupts both the ventral furrow and dorsal tissue attachment scars (pl. 1 figs. 9-10).

At the point of transition into the siphuncular tube, the septum becomes depressed backwards (retrochoanitic) into the septal neck (pl. 2 fig. 12, pl. 6 figs. 37-38). Septal necks are suborthochoanitic and extend one-fifth of the distance of each tube segment, producing the septal foramen (pl. 6 figs. 34, 35, 37). The length and construction of the septal neck is identical in individuals from all localities. Only in the material from the Hunsrück the actual organic siphuncular tube is still preserved, as revealed in radiographs (pl. 8 figs. 45a, 47-48) and in thin section (pl. 7 fig. 44).

The space between the siphuncular tube walls, septa and inner surfaces of the outer walls is the chamber from which liquid could be pumped during buoyancy control. In general, the shape of the siphuncular tube is similar to that of the living *Nautilus*, but in construction, it resembled that of belemnites and ammonites, being porous except in the mineralized necks (BANDEL & KULICKI 1988). During ontogeny, chambers increased more rapidly in width than in height. In a 5.0 mm-wide conch, the chamber is about 3.0 mm high (pl. 9 figs. 51-52), whereas in a 16.0 mm-wide conch, it is 4.0 mm high, and finally, in a 20.0 mm-wide conch, it is approximately 6.0 mm high. The height of neighboring chambers is also variable. Therefore, the chamber width-height ratio appears to be dependent on the conch size.

Chamber lumina and cameral deposits.

When initially formed, the chambers contained not only liquid, but also organic sheets that were suspended between chamber walls. The traces of such organic sheets are actually preserved in some conchs from the Hunsrück (pl. 7 fig. 42) and their original configuration can be reconstructed by the thin calcite crusts that precipitated around them (pl. 9 figs. 54-56). This is best observed in the area of internal deposits (see below), which provides data for the following interpretations.

A solid triangular organic sheet was most likely suspended between the apical portion of the organic siphuncle and the ventral inner shell wall. This sheet formed an attachment membrane for the siphuncle, somewhat similar to that found in other

chambered cephalopods, as in the ammonite *Quenstedtoceras* (pl. 10 fig. 61) (BANDEL 1981). Other thin sheets, suspended from this sheet and from the siphuncular tube, radiated toward the outer walls of the conch and separated the chamber into liquid-filled compartments. The distance between these radial sheets is kept relatively constant at about 0.1 to 0.2 mm in successive chambers by branching of the sheets toward the outside (pl. 5 figs. 27a-b). In widely expanding chambers, more branching can be observed than in narrower chambers (pl. 6 fig. 33a). One complication of this simple radiating system lies in the ventral area where the organic attachment membrane and the organic sheets of the siphuncle interfere with the lamellae. Another complication arises from the presence of one, and in larger chambers, several additional inclined organic sheets.

A single inclined sheet is present in smaller chambers, including almost all New York and Hunsrück specimens with up to 1 cm chamber diameter. This sheet is rooted on the ventral side near the apical base at the surface of the septum, exactly where the attachment membrane of the siphuncle is anchored (pl. 5 figs. 27-28). From there the organic sheet crosses the chamber in an inclined position on the left and right sides of the conch until it reaches the edge of the septum closing the chamber in a dorsal position (pl. 10 fig. 63). This inclined sheet becomes fused with the radial sheets, and thus the lumen of the chamber is split into two separate regions. Both of these regions are differentiated into narrow radial rooms. The suspended, inclined sheet or sheets, especially in smaller chambers, interfere with and affect the regular course of the radial sheets, especially on the left and right sides of each chamber where both sheets fuse and the radial sheets branch. This interference results in the sinuous or wavy — rather than straight — lamellae in this region (pl. 4 fig. 21, pl. 5 fig. 27b).

The sheets themselves, as a rule, are no longer present but their pyritized casts are preserved as traces in several Hunsrück specimens (pl. 6 fig. 38). Their original courses and general outline can be reconstructed because of internal calcite crusts that were later precipitated on the organic sheets, and from the intervening void space. In both New York and Hunsrück fossils, void space frequently filled with pyrite (pl. 5 figs. 27-28, pl. 7 fig. 43, pl. 9 fig. 53).

Internal rostrum.

Cameral deposits of lamellorthoceratids were produced inside a posterior portion of the shell, and can be considered as an "internal rostrum", where some of its functions were analogous to the external rostrum of belemnites. Cameral deposits are present only in those conchs that show more than about 20 to 25 chambers (pl. 2 fig. 12a, pl. 3 fig. 14, pl. 9 fig. 50a), and they seem to have formed only within those chambers measuring 1.0 mm and greater in diameter. Because the cameral deposits of the internal rostrum are composed of calcite, in contrast to the aragonite of the conch proper, they commonly survived diagenesis better than other elements of the conch. A number of complete conchs were measured from Hunsrück Slate. In a 5.0 cm-long conch, a rostrum almost 1.0 cm long had formed, having an average thickness of about 1.0 mm. In a 5.5 cm-long conch, a rostrum about 1 cm long is followed by a chambered, unfilled phragmocone of about 2.0 cm-long and a 2.5 cm-long living chamber. That portion of the conch containing the rostrum is preserved in the original cylindrical shape, but the remainder has become flattened. From 15

to 23 chambers are present between the chambers containing considerable amounts of internal calcite growth and the living chamber (pl. 2 fig. 12a). These occur without any or with only faint traces of cameral deposits (pl. 2 figs. 12-13, pl. 6 fig. 37).

In the New York material, one individual shows 16 adoral chambers completely unfilled before the "internal rostrum" makes its first appearance. The succeeding seven chambers are partly filled and at least ten more consist of filled chambers. In the material from Morocco and Nevada only a few unfilled chambers were present (four observed), but in these specimens the living chamber is not preserved. One incomplete Nevada specimen shows seven empty chambers, seven partially filled, and eight filled chambers.

Judging from our specimens and from published material, it seems likely that observations regarding conch preservation in the Hunsrück Slate can be applied to all lamellorthoceratids. In material from the Hunsrück, many conchs of different sizes are preserved with the whole shell and all of its component parts included. Only atypically, from the fifteenth to twenty-third chamber (counting backward from the living chamber), do calcitic deposits occur. The amount of mineralized lamellae increases within 4-7 chambers until further posterior lamellae remain constant (pl. 8 fig. 45). Within the actual internal rostrum, all chamber fillings are similar and can only be seen in chambers larger than 1 mm diameter. Increasing growth of cameral lamellae within the anterior chambers of the rostrum were found in material from New York, Morocco and Nevada (pl. 2 fig. 13, pl. 3 figs. 15-18, pl. 4 figs. 19, 23-26, pl. 6 fig. 36, pl. 8 figs. 45-46, pl. 9 fig. 53).

The mineral deposits of the internal rostrum define the internal shape of each chamber, as well as the disposition of the various organic sheets suspended within them. When apical chambers were reflooded, only a dorsal gas bubble remained in each chamber.

Our specimens indicate that calcite growth started simultaneously at all internal walls (pl. 9 figs. 54-56, pl. 10 fig. 62). During the mineralization process, the organic sheets acted merely as templates. The lamellae were continuously thickened by the calcite cement (pl. 6 fig. 36). No growth of calcitic crusts occurred within the remaining gas-filled void which was flooded after death. During later diagenesis these voids may have become filled with calcitic cement (pl. 4 figs. 19-26, pl. 6 figs. 32, 34, 38). When the organic siphuncular tube was dissolved during early diagenesis or, more likely, from the activity of fungi or bacteria even before this time, sediment could enter the chamber and fill the dorsal gas void. The anterior-most 4-7 chambers of the internal rostrum and the dorsal portion of the posterior rostrum were deformed by sediment compaction when voids were not filled by sediment or mineral deposits (pl. 6 figs. 33b, 38, pl. 9 fig. 55).

Some nearly complete conchs from the Hunsrück show a 3.5 cm-long internal rostrum in an 18 cm long conch, and a 4.5 cm long rostrum in a 37 cm-long conch. Within these and other less complete specimens, the chambered portion is about twice as long as the internal rostrum. Based on 100 measured internal rostra from the Hunsrück, the following diagnostic features can be established: (1) internal rostra vary in length between 2 and 14 cm and are commonly between 3 and 8 cm long; (2) those rostra between 6 and 9 cm long are about 1 cm wide at their apertural end; and (3) the smallest rostra are only 0.5 mm wide and their apical width lies in the 0.2-0.5 mm range.

Depositional environment and taphonomy.

Conchs of the various lamellorthoceratids studied have obviously undergone very different modes of diagenesis. Because more complete individuals were preserved in the Early Devonian Hunsrück Slate, a detailed study of the taphonomy and diagenetic history of these specimens was carried out. In the following discussions, Hunsrück specimens are described in detail and other fossils are compared to them.

The burial and other taphonomic changes of lamellorthoceratid conchs were reconstructed from their orientation in rocks of the Hunsrück Slate quarry Kaisergrube at Gemünden, W. Germany. Of the numerous individuals of various sizes studied in the field by the first author, some were found complete, including living chambers, whereas others are mostly reworked fragments, consisting mainly of the internal rostrum. Several complete specimens were preserved after death, more or less in the position in which they reached the sediment-water interface. These conchs show clear indications that the apical part became lodged in the sediment first and remained inclined until covered by sediment. Many individuals now lie in the slate matrix with their apex visibly deeper in fine slate laminae than their apertural portion. For many, deposition of the sediment was sufficiently rapid to completely bury the conch in strongly inclined positions, or in a few instances, almost vertical positions. In other cases, the conch slowly reached an almost parallel orientation relative to the bedding plane before burial.

Shells must have been buoyant to some degree and were floating before coming to rest on the sediment surface. Initial changes affected the shell shortly after death, when the conch was partly lifted from the bottom by the buoyancy of its anterior part, or when it was floating in the sea. Anterior segments of the organic siphuncle were destroyed, probably due to the activity of scavenging or detritus-feeding organisms and decomposing fungi. Water then entered the chambers and gas was released until buoyancy had been lowered so much that the conch sank to the substrate. It can be established from the Hunsrück material that about 5-6 chambers were flooded in this way before the conch remained fixed to the substrate. Aside from this, each individual conch is preserved with a different number of sediment-filled chambers showing that chamber flooding was variable and connected to the shell decay.

Once the specimen was on the substrate, sediment could enter those chambers where the siphuncular tube had been destroyed, whereas chambers with complete tubes remained filled with liquid and gas. At this stage, the conch, now buried in the sediment, consisted of four different portions, each of which reacted differently to the subsequent effects of solution, bioturbation, mineralization and compaction. These parts are: (1) the living chamber, which was open to the surrounding sediment (pl. 3 fig. 18, pl. 8 fig. 45a, pl. 9 figs. 51-52); (2) the chambers that were filled by fine-grained, pelletoidal sediment (pl. 7 fig. 41); (3) the sealed off chambers that were filled with liquid and gas only, (except for the interior of the siphuncular tube); and (4) the internal rostrum with its calcitic lamellar structure, where gas filled the dorsal portion and liquid filled the voids between lamellae.

As revealed in radiographs, small worm-like organisms entered the living chamber and the sediment-filled anterior chambers, constructed feeding burrows, and filled some of these burrows with pellets (pl. 6 figs. 36-37, pl. 7 figs. 41-42).

They also disrupted any organic sheets that were preserved in some of the chambers (pl. 7 fig. 41a, pl. 8 figs. 45, 47). These organisms usually entered the conch through the aperture and into the chambers through septal neck openings (pl. 6 fig. 37), but some came through the porous outer walls (pl. 8 figs. 45a, 47). Mineral deposition started in liquid-filled spaces during their probing activities and after they had disappeared.

In many internal rostra the spaces between calcitic lamellae became closed by growth of calcitic cement (pl. 9 figs. 55-56). In other rostra, these voids were filled by pyritic cement. In some specimens voids were at first partly filled by pyrite cement, and later closed by the precipitation of calcite (pl. 7 fig. 43). Chambers without calcitic lamellae may have become partly encrusted by pyrite or filled with it. Concomitant with pyritization, the aragonitic shell began to demineralize. This process probably did not happen under deep sediment cover, but occurred fairly close to the surface, since partly-dissolved shells were released by erosion and the calcitic internal rostra redeposited nearby. Most internal rostra, in fact, have been redeposited after destruction of the aragonitic outer shell and the nacreous septa. The open anterior portion of each rostrum could then be filled, like the open alveole of belemnites (BANDEL & SPAETH 1988). Sometimes large living chambers were also redeposited as steinkerns, separate from the detached phragmocone.

In the Hunsrück material, as in the New York material, erosion and redeposition is common, but in some instances complete conchs have also been preserved. The entirely calcareous specimens from Morocco consist primarily of steinkerns that lack the outer shell. Sediment filling the internal features of the conch lithified before the surrounding sediment, so that upon synsedimentary erosion, the steinkerns were washed out of the enclosing sediment and occasionally colonized by epifaunal organisms. Some specimens retained the original outer shell, through recrystallization into calcite. Before burial, the organic siphuncle, as well as the organic internal sheets, had been destroyed, and all cameral space became sediment-filled, with the exception of that between calcite laminae. Conchs were fractured before they became lithified in the sediment; later diagenesis consisted only of recrystallization.

In the Hunsrück material, chambers with pelletoidal sediment were subsequently compacted less (approximately 50%) than either the sediment surrounding them or that in the living chamber. During diagenesis of the slate, these chambers provided the only areas where certain original sediment features were preserved; elsewhere, pellets, as well as most calcium carbonate, disappeared during compaction and diagenesis. The living chamber of the conch became compressed much more strongly than chambers with pelletoidal sediment.

A difference in compaction of the lamellorthoceratid conchs is noted regarding the size of living chambers. As a rule, on those conchs in which the living chamber measures less than about 15.0 mm in diameter, the walls had been demineralized before compaction and the conch was flattened and substantially widened (pl. 9 fig. 52). Where the living chamber measures above 15.0 mm in diameter, the conch retains its original shape, but the shell is broken into many irregular fragments. In the larger conchs the base and top of the conch shell almost touch and a thin lamina of compacted shale separates it. This difference in compaction can be related to original shell thicknesses. In smaller conchs, the whole shell became demineralized when compaction began, but in larger conchs, the thick shell walls were at least

partially retained. In most specimens from New York, the shell also was demineralized, but compaction was minute. Compaction may also change the original circular conch into an oval shape and deform the septa not by fracturing, but by folding and wrinkling (pl. 1 fig. 8).

Those chambers that had only been filled with liquid and gas were completely demineralized; during compaction they totally collapsed (pl. 8 figs. 45, 48-49). The organic sheets representing the demineralized outer wall and septa were then wrapped around, adhering to the sediment-filled, siphuncular tube. This is easily seen in many radiographs of complete conchs, for the organic remnants of the shell became slightly pyritized (pl. 9 figs. 50b-c). In thin section the collapsed chambers are visibly flattened into one lamina of the slate, whereas filled chambers and the internal rostrum are preserved in three dimensions (pl. 7 figs. 39-40).

Often, these organic sheets are twisted where they expand to connect with anterior edges of the internal rostrum of the conch (pl. 3 figs. 17-18, pl. 8 fig. 49). This twisting was due to the different behavior of the organic and flexible sheets on one side, relative to the solid rostrum on the other, during compaction and sediment flow.

When the internal rostrum was subjected to the stress of the compacting sediment, the liquid-filled space between the lamellae often had already been filled either by growth of pyrite crusts or by calcite. If not filled totally, as observed in many specimens, the rostrum collapsed and the lamellae were fractured into angular patterns (pl. 7 fig. 43). In the material from the Hunsrück, both of these conditions occur. In all individuals studied from New York, liquid-filled spaces were completely filled by pyrite (pl. 5 figs. 27-28, 30). Here only the dorsal, originally gas-filled room remained open, and was either preserved intact or suffered collapse during compaction. The result of this compaction is a dorsal flattening of the shell, which is the rule in the material from France (pl. 6 fig. 33b) and is also noted on many individuals from the Hunsrück. In the Morocco and Nevada material, the gas space had been filled with sediment prior to deformation (pl. 5 fig. 31, pl. 6 fig. 34). The organic siphuncles were dissolved before sediment was indurated. Compaction probably had been slight anyway due to the more rapid lithification of carbonate sediment into limestone, compared to lithification of clays.

Decalcification of the portion of the conch containing the internal rostrum results in features not seen on the complete shell. On the outer shell wall, the disappearance of aragonite brings out the structure and composition of the organic components of the shell. The outline of the organic components are preserved especially well on the undeformed internal rostra from New York, where a very well-developed ridge and groove pattern is apparent. Complications insue, however, as two sets of patterns may develop. One small-sized pattern developed when the aragonitic shell was remineralized into calcite (see DULLO & BANDEL 1988 for more detail on the transformation of nacre into calcite). Another large pattern came into existence when the mineral components of the shell broke down. Differences in diagenesis control the dimension of the large patterns and the directions of the ventrally developed angle. In the Hunsrück material, some conchs show this second type of structure. Where the original shell recrystallized into a coarsely crystalline mosaic, as in the Morocco and Nevada material, such features are not apparent. After induration of the surrounding sediment, the conch dissolved totally before a new calcite cement closed the cavity left by the actual shell.

The material from New York, Morocco and Nevada was not further changed after diagenesis, but that from the Hunsrück was later metamorphosed into slate. Schistosity in the Kaisergrube quarry is almost parallel to bedding, but it still retains metamorphic features, including shearing of pyritic structures, flow of calcitic features, and smearing of the fossils (pl. 7 fig. 40). Often pyritized portions of fossils were affected to a lesser degree than calcified parts, which were greatly deformed by mineral flow (pl. 9 figs. 50b-c).

Diagenesis has had a strong impact on the conchs of lamellorthoceratids, changing them into the various forms studied here. Variation in the conchs was further accentuated by weathering, which in the case of the New York material, left only the pyritic portions unaffected, dissolving all other minerals. As a result, the lamellae observed in the New York material are actually filled cavities. Only the unusual preservation found in the Hunsrück fossils resulted in the preservation of the primarily organic portions of the conch, including finely detailed remnants of the thin organic sheets filling the cameral lumina. In the calcareous material from Nevada and Morocco these organic features are not preserved, but the original calcite lamellae of the internal rostrum do occur with unparalleled preservation. Where calcite crusts developed between laminae, later recrystallization and coarsening of the grains modified original structures, but never completely destroyed them (pl. 6 figs. 32-33). The internal rostrum of the conch was most resistant to erosion and diagenesis because it was composed of calcite, and therefore, like the calcitic rostrum of belemnites, it was preferentially selected for preservation, whereas the remainder of the shell disappeared. The relics of lamellae showing the double-layered, calcite crusts on top of a dark-colored central sheet have become preserved as inclusions within larger calcite crystals (pl. 9 figs. 54-56). A similar feature was observed by BANDEL & WEITSCHAT (1984) where original color patterns and growth increments of calcitic gastropod shell also became preserved as inclusions within larger crystals. In this way they survived all changes brought about by later diagenesis.

Eoteuthis elfriedae, an eight centimeter-long cephalopod from the Hunsrück Slate of Kaisergrube described by STÜRMEER (1985), may well represent a juvenile *Arthrophyllum* BEYRICH 1850 with its arms partly preserved. From the Lower Jurassic Posidonia Shale, we know of *Belemnoteuthis* and belemnites with arms and other soft parts present but with only decalcified phragmocones. From the Upper Jurassic Solnhofen Limestone, the belemnite *Acanthoteuthis* is also preserved in this way and the phragmocone may even have become twisted after decalcification. In both of these occurrences that had similar depositional environments as the Hunsrück Slate, the endocochlear conchs have little or no trace of their original cover of muscular mantle. The fossil described by STÜRMEER does not show a muscular mantle. What has been interpreted as a fin on *Arthrophyllum* (STÜRMEER 1985: text fig. 4) actually is a stretched decalcified shell (pl. 9 fig. 50b). Whereas nothing can be said regarding the presence or absence of a muscular mantle from this fossil, the remains of arms (STÜRMEER 1985: text figs. 1-2) confirm the interpretation of MEHL (1984) who suggested that some orthoceratid cephalopods in the Silurian-Devonian transition had ten arms, similar to that of Recent squid and fossil ammonites. STÜRMEER (1985) interpreted the Hunsrück fossil *Eoteuthis* without taking into consideration diagenetic changes, especially effects of compaction. Without careful attention to the diagenetic history, a comparison between the radiographs of Recent

squid and the fossil cephalopods may be misleading. Compaction and diagenesis must also be taken into consideration when the "more than 100 gladii and cuttlebones of other teuthid coleoids" mentioned by STÜRMER (1985) are evaluated (BANDEL & REITNER & STÜRMER 1983; BANDEL & BOLETZKY 1988).

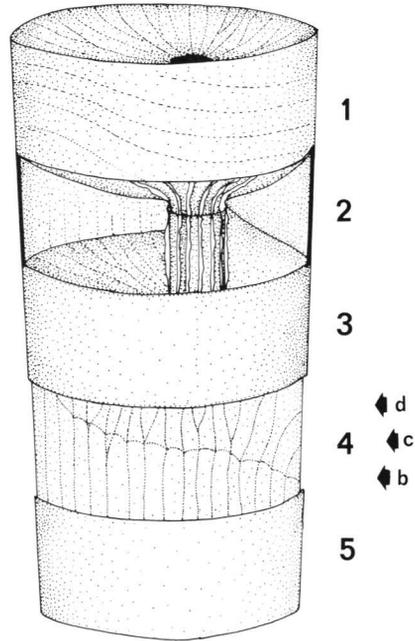
Reconstruction of the ontogeny and growth.

Some generalizations can be made from the detailed study of the ontogeny and growth of our specimens. The young lamellorthoceratids, after they hatched from eggs, were probably about 5 mm long and almost adult-like in shape and body organization. The conch, about 4 mm long, consisted of a spherical first chamber and perhaps one or two more chambers. The phragmocone at the moment of hatching could be used as an aid in buoyancy control, since some of the cameral liquid was pumped from it by the activity of the siphuncular tissue situated in the siphuncular tube. From the second septum onward, the siphuncular tube penetrates the chambers just ventral of the conch center. Contact between chamber lumina and siphuncular tissue was established through the organic portion of the siphuncular tube. Porosity probably was along the whole tube, as in ammonites and belemnites (BANDEL & KULICKI 1988) and not along specialized sections of the tube as in *Nautilus*, *Spirula* and some aulacoceratids (BANDEL 1982, 1985; BANDEL & SPAETH 1984). Chambers were crossed by a siphuncle that in its ventral, apical course was attached to the septum and the wall by a more or less solid sheet.

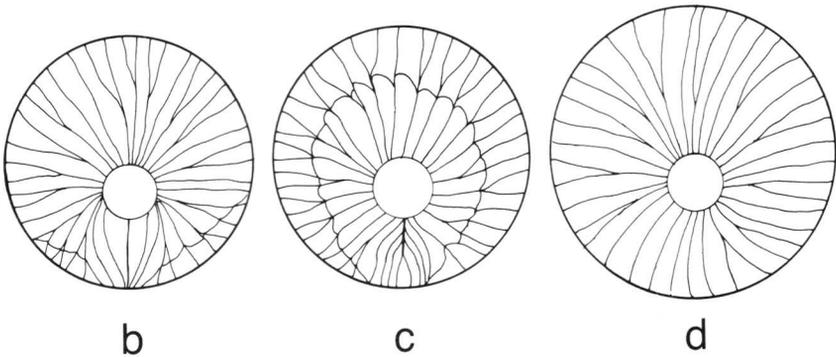
Aside from this single solid sheet, chambers were differentiated into compartments by thin organic sheets suspended within the lumen. These sheets are arranged radially around the organic siphuncle and its attachment sheet, and they show an almost constant distance from each other. As the visceral mass withdrew from the space apical to the living chamber, it must have secreted the organic sheets of the siphuncular tube, as well as those of the chamber. This type of chamber formation also occurs in the living *Sepia*, where organic sheets are produced mainly parallel to the chamber bottom and to a lesser degree vertically to it (pl. 10 figs. 57-59). WEITSCHAT & BANDEL (1989) observed similar organic sheets in the chamber of Triassic ammonites from Spitsbergen and Siberia.

In lamellorthoceratids, the vertical sheets are more common, usually with not only one, but with several inclined sheets in larger chambers. The inclined sheet solidly adhered to the base of the attachment sheet of the siphuncular tube and terminated on the organic sheet that represents the template on which the calcareous septum was deposited. Wherever the inclined sheet came in contact with the radial sheets, it interfered with their orientation and produced a somewhat irregular curving course of internal cavities on the dorsal side (text fig. 1 and STANLEY & TEICHERT 1976: pl. 1). In larger chambers, the number of all sheets increased so that the frequency of branching or bifurcating sheets was respectively greater. This partitioning kept the interior of the chamber filled with about equally-spaced compartments of liquid and effectively slowed down contact of chamber liquid with that of the siphuncular tube. Immediately after formation of a new chamber, the tissue of the siphuncle must have started to pump liquid from the chamber in the same manner as it is accomplished in *Sepia* or *Nautilus*.

Text fig. 1. *Arthrophyllum* BEYRICH 1850. — World-wide; Lower and Middle Devonian. — a) Reconstructed section of the conch. At top, the first chamber shows lines of growth on the shell surface. The second chamber is opened and the thin sheets are removed to show the siphuncular tube with its ventral attachment membrane. The third chamber is drawn with the outer wall, which omits the fourth chamber. Note that the attachment of the cameral sheets to the wall is present. The fifth chamber is toward the apical end of conch. — b-d) Transverse views of sections through a chamber just below the apertural end of the septum: b) in central position; c) just apertural-ward of the previous septum; d) two dimensional view of the course of vertical sheets and the inclined sheet intersecting them.



1 a



b

c

d

The construction of the chamber in these Devonian lamellorthoceratids combined principles of siphuncle morphology found in ammonites (pl. 10 fig. 61) with an anterior chamber anatomy like that of *Sepia* (pl. 10 fig. 59). This amounted to decoupling of the chamber liquid from the tissue of the siphuncle to such a degree that some portions of the chamber could be pumped dry later than others. Obviously within a given chamber, those compartments that ended close to the

porous siphuncular tube could be pumped more rapidly than those isolated by sheets. Even when pumped empty, the walls of the chamber and each sheet segment probably did not dry out; they probably were covered by a layer of mucus, as in Recent *Nautilus* (BANDEL & SPAETH 1984). Gas could diffuse into these compartments, driven under low pressure by chamber and body fluid — fluids produced by the liquid-pumping tissue. An asymmetrical cone of gas formed around the siphuncle, thinnest and shortest at the ventral side and thickest and highest on the dorsal side. During life, the orientation of this gas cone was related to hydrodynamic stability, resulting in a proportionally differentiated lifting force, capable of affecting the dorsal side of the conch more strongly than the ventral side. Text figs. 2-3 show reconstructions of the lamellorthoceratid *Arthrophyllum* which comprise most of our material.

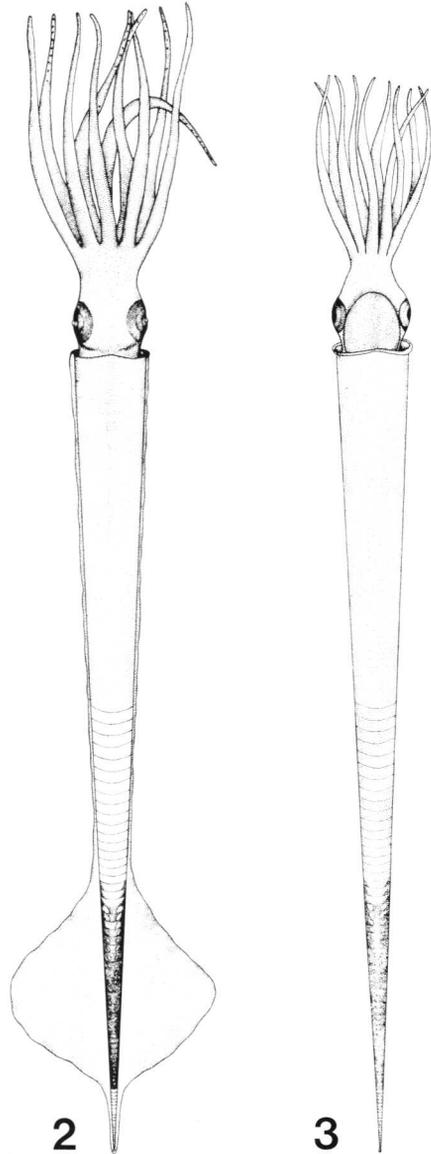
Our material indicates that approximately 14-23 chambers were utilized by the lamellorthoceratids for buoyancy control. These chambers counterbalanced the weight of the growing tissue mass of the body, assuring neutral buoyancy. In this respect, lamellorthoceratids functioned like living *Nautilus* and *Sepia* (DENTON & GILPIN-BROWN 1961). When more than 20 chambers had been constructed in the enlarging phragmocone, the opposite process began, during which the apical chambers became heavier. At this time, a rostrum, similar to that of fossil belemnites and aulacoceratids, started to form. Unlike those cephalopods, however, the rostrum of the lamellorthoceratids did not form on the outside of the conch, but within it.

The formation of the rostrum was probably triggered by the siphuncular tissue, providing extrapallial liquid which seeped slowly into the chambers, in a manner opposite to which liquid had earlier been extracted. In order to do this, the salt pump of the living siphuncle had to be turned off. Living cephalopods with a phragmocone can do so; for example, an outgrown *Sepia* floods early chambers. After the pump was turned off, liquid slowly seeped into the chamber and triggered the deposition of calcite crusts on the various organic sheets. Growth of calcite crusts started on all surfaces within the chamber interior, indicating that extrapallial liquid had been enriched with calcium carbonate. As a result, lamellae, composed of laminar layers of calcite, were precipitated, mineralizing all of the organic sheets suspended in the chamber and still surrounded by the liquid. Mineralization could not occur within gas-filled spaces on the dorsal side of each chamber after reflooding of the chamber and after return of normal gas pressure. The same holds true for the siphuncular tube, where spherulitic growth of calcite proceeded to develop only on the sides and in ventral portions. Mineral growth occurred only in 4 to 7 chambers of the anterior portion of the internal rostrum; apically, it stopped altogether because normal gas pressure and salinity of chamber liquid prevented any more liquid from entering the chambers.

Although a chamber became filled with calcite growth, it still retained the liquid-filled lumina between the mineralized sheets, along with a sealed-in gas bubble. Thus, ventral portions of each chamber became heavy, whereas dorsal portions remained light. During this process, the internal rostrum, as a whole, had become heavier relative to seawater and the apical portion of the shell was balanced, assuring proper shell orientation.

The functional morphology and chamber construction of lamellorthoceratids can thus be explained as a mixture of processes and features present in living

Nautilus and *Sepia*, as well as in some fossil coleoids, like the extinct belemnites. The morphology of the attachment scar between shell and tissue in lamellorhynchoceratids is reminiscent of *Spirula*, a chambered cephalopod alive today. Long, broad, and longitudinally striped, the scar is also very much like that of aulacoceratids (BANDEL 1985), belemnites (BANDEL & ENGESER & REITNER 1984),



Text figs. 2-3. *Arthrophyllum* BEYRICH 1850. Reconstructions. The internal cameral deposits and septa are shown. — 2: Represented as a squid-like endocoelate decapod with fins. — 3: Represented as a conventional nautiloid with hood.

and belemnoteuthids (BANDEL & KULICKI 1988). Such an attachment between dorsal tissue and conch, indicates that lamellorthoceratids possibly could have been a type of extinct endocochleate cephalopod, quite different from any of those living in our seas today (text fig. 2). Unfortunately, we do not know how far the scar-tissue attachment extended towards the aperture of the living chamber.

The lamellorthoceratid animal probably lived in a manner similar to living *Sepia*, spending much time resting on the bottom in expectation of prey. Approaching the prey probably occurred by a sudden jump forward, with the funnel of the hyponome pointing toward the apex of the conch. In contrast to *Sepia*, the lamellorthoceratid animal, if ectocochlear (text fig. 3), could not swim backward in a stabilized way, without fins that could guide the slender conch. Therefore, it probably remained straight within the water, with apex pointing in the direction of movement, as in slender squids today. If the animal wanted to change its location, it would swim forward, with a backward directed hyponome, and water would have squirted out, toward the apex of the conch. Unfortunately, there is no living creature to be studied that could tell us what kind of shell-muscle-tissue attachment functions in such a movement. The only extant ectocochleate, *Nautilus*, has a coiled shell and a very short living chamber, and, accordingly, functions very differently. Although the question of endocochlear versus ectocochlear in the reconstruction of lamellorthoceratids cannot be proven, our findings suggest the viability of the endocochleate idea. There is a good possibility that "*Eoteuthis*" of STÜRMER (1985) represents a juvenile *Arthrophyllum*. If so, we can assume that it had ten arms.

Implications for the systematic standing of the group.

STANLEY & TEICHERT (1976) gave a comprehensive review and comparison of the Devonian Lamellorthoceratidae. TERMIER & TERMIER (1951) discussed their new genus *Lamellorthoceras*. TEICHERT (1961) erected the Family Lamellorthoceratidae, recognizing two genera, *Arthrophyllum* BEYRICH 1850 and *Lamellorthoceras* TERMIER & TERMIER 1950, whereas ZHURAVLEVA (1961) established an additional genus *Gorgonoceras*. The "Treatise" (TEICHERT & al. 1964) recognized the validity of all three genera. BABIN (1964), however, preferred unification of all lamellorthoceratids into only two genera, *Arthrophyllum* and *Gorgonoceras*. The latter is distinguished from other genera by longitudinal furrows and a terminal bifid lamella, located in the ventral position. In describing an additional new genus, *Esopoceras*, from New York, STANLEY & TEICHERT (1976) remarked on the close similarity with *Gorgonoceras*. In addition these authors considered an older genus, *Coralloceras* ZHURAVLEVA 1961, previously put in synonymy with *Lamellorthoceras* (TEICHERT & al. 1964: K234), to be valid. As a result, five genera were included in the family (STANLEY & TEICHERT 1976: tab. 1).

In our study of toptype material and newly discovered specimens from Nevada, we compared representatives of all genera, except *Gorgonoceras*. Because these specimens are from a variety of geologic and depositional settings, they afford contrasting views of the various diagenetic processes which have taken place. Previously, much taxonomic weight has been placed on the disposition and arrangement of the unique internal cameral deposits (lamellae) of the various genera. Our

findings on the origin of these structures, coupled with the reconstructions of the diagenetic histories and ontogeny, suggest that splitting of genera and species may be unduly artificial.

Previous workers recognized similarities between some genera and species of lamellorthoceratids. TEICHERT (1961) pointed out similarities between *Arthrophyllum* and *Lamellorthoceras*. BABIN (1964) found great similarities between *Arthrophyllum vermiculare* (TERMIER & TERMIER 1950) and *A. kahlebergense* (DAHMER 1939) and *A. cf. planiseptatum* (G. SANDBERGER & F. SANDBERGER 1852). Although his individuals from the Armorican area of France are larger than those studied by us, they are of Couvinian and upper Siegenian age and close to the age of the Hunsrück Slate.

Regarding representatives of the lamellorthoceratids as a whole, we may summarize major points of their morphology as follows:

Ornament: The surface features of various genera, such as transverse crenulations and annulations, can vary due to the type of original shell layer preservation and subsequent diagenetic changes. We know from study of *Esopoceras* from New York and *Arthrophyllum* from the Hunsrück, that features such as longitudinal ridges form during diagenesis because of early demineralization of the outer shell. So-called variations in transverse crenulation can only be attributed to growth lines.

Apical angles: We know from ontogenetic studies of various individuals that apical angles change during the ontogeny of the cephalopod. Measurements of fossil material may be misleading because extensive deformation (i.e., flattening) has taken place, exaggerating the angles. STANLEY & TEICHERT (1976: tab. 1) listed angles varying from 4 to 24 degrees but did not consider flattening.

Chamber height and length-width ratios: Differences in chamber height and height-width ratios can be demonstrated to be artificial. Changes occur during ontogeny so that only fossils of exactly the same dimensions can be compared validly with each other. To some degree compression and deformation have affected all specimens and this must be considered when dealing with laterally compressed versus circular conchs.

Curvature of conch: TEICHERT & al. (1964) noted that the Family Lamellorthoceratidae was characterized by straight to slightly endogastric, longiconic cyrtocones. We have observed only straight, orthoconic conchs. Any apparent endogastric conditions can be attributed to either diagenetic alteration or to mechanical deformation.

Position of the siphuncle: The siphuncle in lamellorthoceratids from New York is said to vary from central to subcentral and slightly eccentric (STANLEY & TEICHERT 1976). Other genera appear to have central or subcentral siphuncles (TEICHERT 1961). Our study shows by means of radiographs, that the position of the siphuncle is variable but distinctly subcentral, and always ventral of the medial plane. Septal necks are bent slightly outward.

Cameral deposits and radial lamellae: The disposition and arrangement of the internal "lamellae" within each chamber are said to vary and have high taxonomic significance (TEICHERT & al. 1964; STANLEY & TEICHERT 1976). In *Esopoceras* as in *Gorgonoceras*, there is a bilateral symmetry along the longitudinal axis but in *Esopoceras* the lamellae are more complex, being curved or sinuous around the ventral region. Both *Arthrophyllum* and *Coralloceras* have apparently straight, radially-disposed cameral lamellae but SCHMIDT (1956: 54) noted that

Arthrophyllum has strongly folded lamellae. The "Treatise" (TEICHERT & al. 1964) uses the terms episepal and hyposepal to describe the radial arrangement of the internal lamellae within the chambers of the conch.

Our study has shown that the "lamellae" reflect the pattern of fine organic sheets suspended in the chamber. With respect to the siphuncle, the sheets were secreted in complex arrangements. That remnants of these sheets are preserved at all, is due to precipitation of calcite in the micro-environment of the chambers. The organic sheets acted merely as templates. Only in exceptional Hunsrück specimens, as seen in radiographs, are the original traces of the organic sheets still present. Even though the pattern of calcified sheets formed during the lifetime of the cephalopod, later diagenesis of the conch must have dramatically changed this original structure. Organic sheets disappeared, voids filled with substances such as pyrite, mud or calcite, and the remaining voids were compressed during compaction. The use of terms like episepal and hyposepal deposits must be abandoned because these terms apply to entirely different kinds of cameral deposits (FISCHER & TEICHERT 1969). We prefer using the term "organic sheets" for the original biologically secreted structures and "lamellae" for the calcified remnants of these sheets, keeping in mind that the resulting diagenetic features may not bear close correspondence to the original organic features. Therefore, the term "radial lamellae" as used in the "Treatise" (TEICHERT & al. 1964) for a special kind of calcified cameral deposit, is incorrect because these structures are actually a mineralized system of internal organic sheets. A radial pattern relative to the siphuncle was ascribed by various workers to lamellorthoceratid lamellae. This is not supported by our research. The lamellae were originally sheets attached to a central siphuncle. The apical sheet of each siphuncle segment and the inclined sheet in each dorsal chamber have a very complex configuration, and, as shown in text fig. 1, are anything but radial!

The posterior part of a conch may be filled by lamellae but it is never completely filled, contrary to descriptions given by other workers. The original conch was open between lamellae. On the dorsal center, open void space existed and again, diagenesis acted to alter the appearance of various taxa.

Systematic description of *Arthrophyllum*.

Class Cephalopoda CUVIER 1798.

Subclass uncertain.

Order uncertain.

Family **Lamellorthoceratidae** TEICHERT 1961.*Arthrophyllum* BEYRICH in CARNALL & EWALD & ROTH 1850.* 1850 *Arthrophyllum* BEYRICH in CARNALL & EWALD & ROTH, Protokoll dt. geol. Ges.: 8-10, pl. 1 figs. 1-10.Type species: *Orthoceratites crassus* A. ROEMER 1843.Synonyms: *Lamellorthoceras* TERMIER & TERMIER 1950, *Lamelloceras* MUTVEI 1956, *Gorgonoceras* ZHURAVLEVA 1961, *Esopoceras* STANLEY & TEICHERT 1976.

Diagnosis: Small, straight to slightly endogastric longiconic cyrtocones. Slowly to moderately expanding conchs with circular to slightly compressed cross section. Apical angle varies from 4 to 12 degrees. Surface ornament variable, usually with annulations and longitudinal striations (costules). Siphuncle varies from central to subcentral and is slightly eccentric. Septal necks retrochoanitic. Camerae characterized by irregularly arranged straight to sinuous cameral lamellae inclined longitudinally, which fill most adapical chambers and converge toward to siphuncle.

Discussion of "genera".

TERMIER & TERMIER (1950) distinguished *Arthrophyllum* from *Lamellorthoceras* by their laminae. The former possesses wavy lamellae whereas the latter is said to contain bifurcating laminae. Our material from Morocco reveals that the laminae from both genera are actually the same — wavy if cut across one section of the chamber, branching if cut across another.

With *Arthrophyllum*, BEYRICH (in CARNALL & EWALD & ROTH 1850) called the conch endogastric and cyrtoconic, but these features can be demonstrated to be the result of weathering. In *Gorgonoceras*, ZHURAVLEVA (1961) deduced faint longitudinal ribs or costules. We have not studied the type material of *Gorgonoceras*, but our study of other specimens indicated that such features are simply the result of remineralizing processes. The thicker, distally bifid lamella of *Gorgonoceras* is in a ventral position and feature may be, in fact, the attachment sheet of the apical siphuncle. At its connection to the siphuncle, the lamella has become mineralized in the ventral area, whereas the dorsal portion has not. This Russian specimen should be reinvestigated to test our interpretation.

Our study leads us to the inescapable conclusion that all four or five genera are synonymous and that variations between them are due to preservation. The only major difference in our material is size, but size alone may not be the critical factor for generic level separation. The specimens from the Armorican region of France are about two to three times the size of the New York material, and the conchs expand much more rapidly. When the chambers are filled by only fine-grained sediment, without extensive mineralization of the lamellae, *Lamellorthoceras* is created. When

chambers are only partially filled with sediment, diagenetic alterations produce specimens characteristic of *Gorgonoceras*, whereas pyrite replacement produces *Esopoceras*.

The time range of all lamellorthoceratid specimens, Late Siegenian to Eifelian, encompasses about 13 million years (HARLAND & al. 1982). During this time there was a rapid evolution of nautiloid groups, as well as the emergence and differentiation of new groups like goniatites and coleoid-like forms. Certainly, we do not deny that this time span was long enough to allow some speciation within the short-lived lamellorthoceratid group. Small variations that we see in our material could be related to different species-level taxa, but on the basis of diagnostic and taphonomic criteria, we argue that many of the larger-scale, generic-level differences are not biologic and hence have no validity in systematics. Our initial findings thus reduce the generic diversity of the Lamellorthoceratidae from four or five genera to a single genus. *Arthrophyllum* is a lamellorthoceratid that was first erroneously described by BEYRICH (in CARNALL & EWALD & ROTH 1850) as a coral. Since *Arthrophyllum* is the oldest described genus, priority dictates it as the valid generic name for all of these cephalopod taxa.

Conclusions.

Because our studied material represents such a large number of lamellorthoceratid specimens illustrating different preservational styles, we may confidently make a number of conclusions regarding the ontogeny, biostratinomy, and diagenetic history of these unusual cephalopods. Upon hatching from eggs, the juveniles possessed a conch about 4 mm long. At first the living chamber was enlarged faster than the phragmocone, but shortly thereafter, growth proceeded equally in both sections of the conch. Ventral and dorsal sides are easily differentiated, both internally and externally, by characteristic features of the shell. Growth lines, the only external sculpture, show that at the ventral side of the aperture, the conch was shorter than at the dorsal side. Where the hyponome was situated, therefore, the conch produced a low lobe. Above the head of the cephalopod, the conch was a little longer. On the inner side of the shell, the ventral side shows a narrow groove, and the dorsal side shows the impression of tissue attachment. In the interior of the phragmocone, chambers are connected to each other by a siphuncular tube located just ventral of a median plane. Each section of the tube was originally attached apically by a supporting organic sheet located on the ventral side.

Until the shell was about 5 cm long, all chambers of the phragmocone had been pumped dry or were being pumped empty. When the animal had a conch over 5 cm long and a phragmocone containing over 15 chambers, deposition of calcitic material started within the apical-most chambers because they had been reflooded. New chambers were quickly filled with organic sheets that had been produced by the cephalopod as the apical end of the visceral mass withdrew. At this time the organic sheets became templates for calcite crystal growth. Mineralization of these deposits started when the tissue pump of the siphuncle was turned off. A pressure and salinity gradient forced extrapallial liquid, enriched in calcium carbonate, into the chamber through the porous siphuncular tube. With the exception of a dorsal space occupied by a gas bubble, the chamber could become flooded and all organic

sheets suspended within it became mineralized until the calcification process eventually ceased. The function of organic sheets suspended within each chamber was to decouple chamber liquid from that liquid in contact with the siphuncle, therefore minimizing energy consumption of the siphuncle pump. When a chamber was emptied, as occurred within the anterior 15-25 chambers, a gas-filled cone was produced.

The animal lived on the bottom near the substrate, weighted down in the front by its soft tissue, lifted up in the center by its pumped-empty chambers, and weighed down at the end of the conch by partly-flooded and mineralized chambers. Some evidence suggests that it could have been an endocochlear cephalopod (text figs. 2-3), but it remains unclear whether it was an animal with an external shell or had an internal conch like the aulacoceratids. In the latter case, it would have been capable of more rapid movements with the aid of fins. When the animal died, the soft tissue disappeared and the frontal part of the shell was uplifted. In this orientation, complete conchs could become embedded in the sediment in vertical or inclined positions with the apex down, as suggested by orientations of our fossil material in the Hunsrück Slate.

Diagenesis changed the structure and morphology of the conch in several ways and varied depending on the nature of the surrounding matrix. Internally, mineralogical differences between the aragonitic conch and the calcitic chamber deposits controlled later diagenetic changes. The diagenetic history of the "internal calcite rostrum" and the conch varied as we know it did in belemnites. Partial to total demineralization of the aragonitic conch and recrystallization into calcite, brought out new sculptural elements not previously present. These elements include fin striae, larger external costules and folds, and flattening and stretching of the remaining organic shell.

We judge that the lamellorthoceratids have been unduly split into genera, without regard to diagenetic effects. Our study suggests that only one or at best, two genera should be recognized. Because *Arthrophyllum* is the oldest valid name, it should take priority over *Lamellorthoceras* as the generic name. Minor variations do occur in our material, but these probably reflect differences at the species level.

Lamellorthoceratids are unique, as evidenced by the unusual lamellae which fill their chambers. We know of no other orthoconic cephalopod with this characteristic. The abundance and apparent world-wide distribution of lamellorthoceratids suggest that they were a fairly successful group, but not a diverse one. The complex arrangement of the organic sheets secreted within the chambers must have functioned to compartmentalize and decouple cameral liquid, but this method is clearly quite different from that employed by living *Nautilus* and extinct ammonites (WARD 1979). The mineralization of the organic sheets served a hydrostatic function, to insure balance and improve hydrodynamic stability of the conch.

The question of whether lamellorthoceratids were endo- or ectocochlear is indeed an intriguing issue. The long muscle scars found on the surface of some steinkerns are possible indicators of internal shells. Acceptance of these cephalopods as endocochlear dictates some revisions of their reconstruction and life habits (text figs. 2-3).

The Early Devonian was an important time in the evolution of cephalopods because it was during this interval of adaptive radiation that some major groups such as coleoids and ammonoids arose (ERBEN 1966; BANDEL & REITNER & STÜRMER

1983; BANDEL & BOLETZKY 1988). Externally, lamellorthoceratids are superficially like orthoconic nautiloids, but internally they are clearly quite different, probably at a high taxonomic level. If endocochlear, they would have been fundamentally different cephalopods and therefore must be removed from Nautiloidea and reclassified. Rather than constituting a main evolutionary line, we prefer to think of the lamellorthoceratids as side branch of a rapidly radiating group, which gave rise to all modern cephalopods except *Nautilus*. The remains of the short-lived lamellorthoceratids now occur nearly world-wide in Devonian rocks of Siegenian to Eifelian age.

Acknowledgements.

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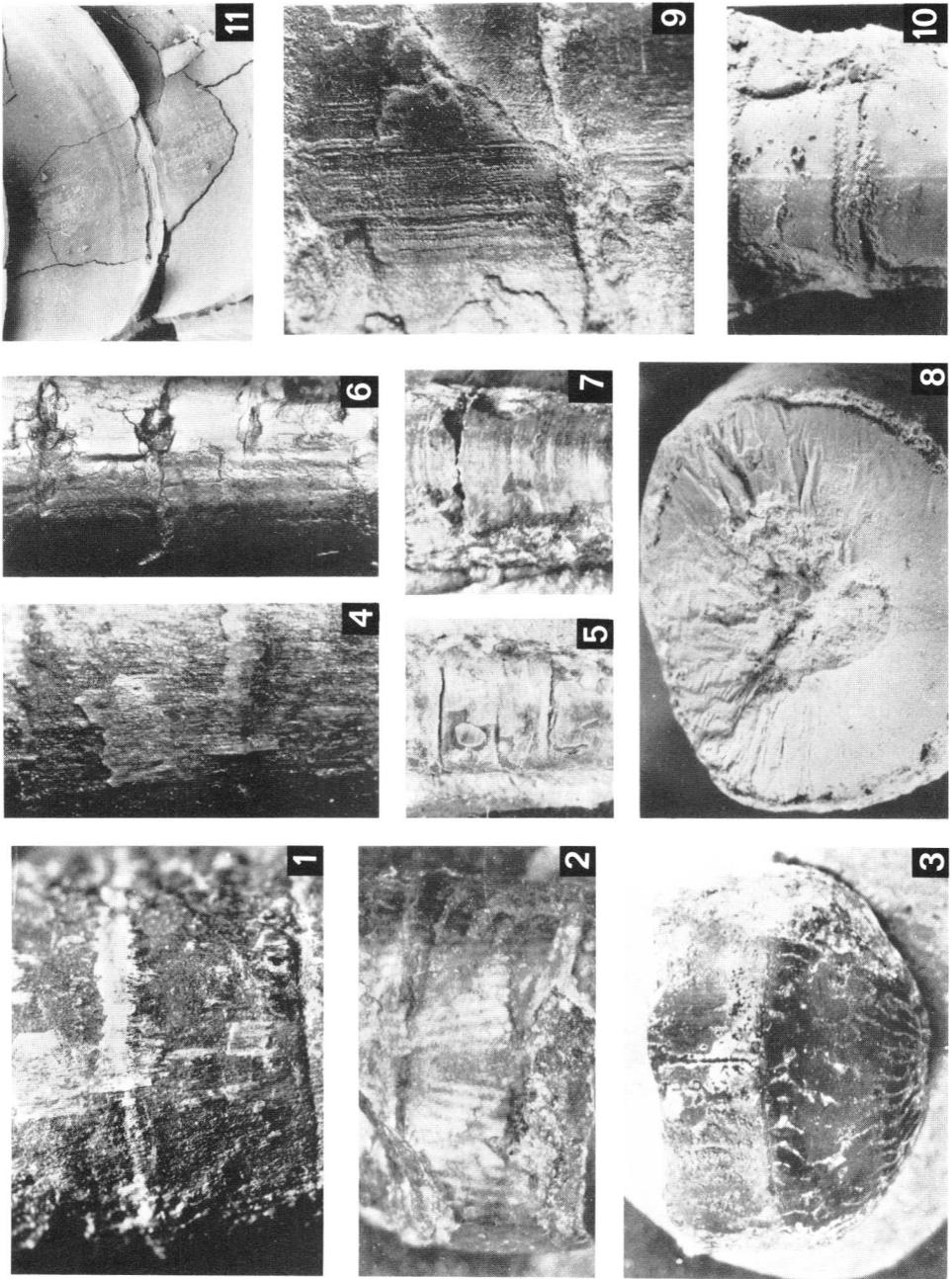
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Plate 1.

Figs. 1-10. Lamellorthoceratid fossils. — New York, N. Y.; Esopus Formation, Lower Devonian.

1. Specimen USNM 403709. — Details of specimen showing fine rods, slightly inclined toward the ventral furrow. These developed secondarily when the originally aragonitic shell recrystallized into calcite. Chamber height 0.2 mm.
2. Specimen USNM 403712. — Ventral side of conch. Here longitudinal lines are slightly inclined, forming an angle which points towards the aperture. Chamber height 0.5 mm.
3. Specimen USNM 403715. — Internal mold of a single chamber showing faint demineralization ridges on the side and impressions of the original organic sheet on the septal surface. Chamber width 7.0 mm.
4. Specimen USNM 403710. — Longitudinal rods developed within the outer conch-wall. Note that they cross sutures uninterrupted. Chamber height 0.2 mm.
5. Specimen USNM 403713. — Growth lines from a shallow saddle laterally. Conch width 4.0 mm.
6. Specimen USNM 403711. — Dorsal side of conch. Longitudinal lines slightly inclined, forming an angle which points towards the aperture. When the conch became demineralized the remaining organic shell formed round longitudinal ridges which have straight paths on the dorsal side; note how they cross chamber sutures uninterrupted. Chamber height 0.9 mm.
7. Specimen USNM 403708. — Growth lines form a low lobe ventrally. Conch width 4.0 mm.
8. Specimen USNM 403716. — View of a septal surface. Before compaction the septa had become demineralized so that they formed wrinkles but did not fracture. Chamber width 3.0 mm.
9. Specimen USNM 403714. — Impressions of the tissue-attachment scar on the internal fill of the fossil; compare with fig. 11. Chamber height 4.0 mm.
10. Specimen USNM 403717. — Ventral furrow preserved as mold on the steinkern. Chamber width 5.0 mm.

Fig. 11. *Spirula spirula* (LINNAEUS 1758). — Atlantic Ocean, near Canary Islands; Recent. — SEM photograph showing the conch broken open to show furrows on its internal surface of the dorsal side. Furrows formed where tissue attached to the shell. Chamber width 3.5 mm.

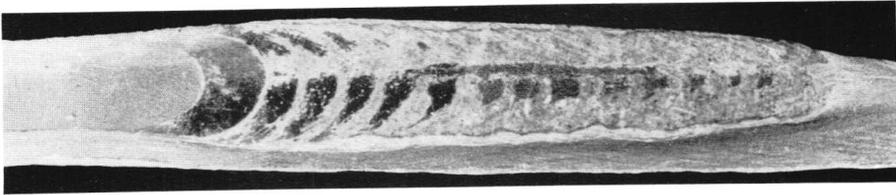


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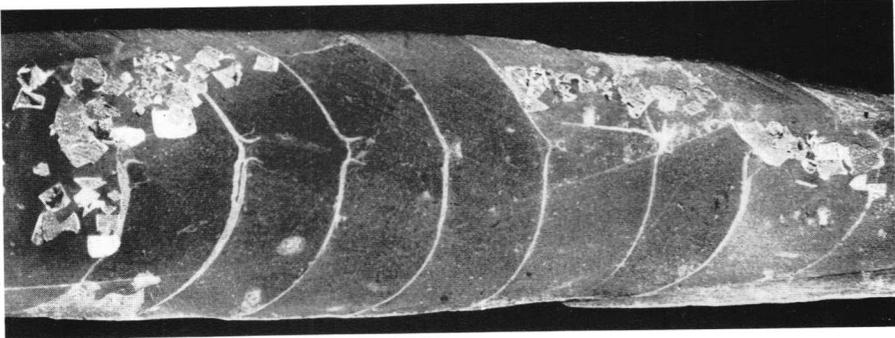
Plate 2.

Figs. 12-13. Lamellorthoceratid fossils. — Polished sections. — Kaisergrube quarry near Gemünden, Hunsrück, Rhenish Slate Mountains, W. Germany; Hunsrück Slate, Lower Devonian.

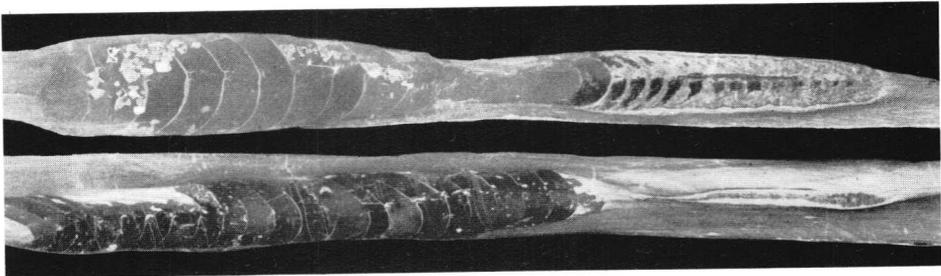
12. Specimen with 21 unfilled chambers, almost all preserved. — a) General view. The filled "internal rostrum" is attached, but slightly twisted out of the bedding plane because of compaction. Length of figure 7.0 cm. — b) Detail of upper portion. Sediment-filled chambers are well-preserved and still show the septal necks.
13. Specimen with only the anterior chambers well-preserved and the central ones mostly destroyed by compaction. — a) General view. The posterior "internal rostrum" is again undeformed. Length of figure 7.0 cm. — b) Enlarged detail showing the sediment-filled, anterior chambers and the well-preserved septal necks which are twisted backward and slightly outward. — c) Enlarged detail showing only the internal rostrum with progressively-filled, calcite lamellae. The anterior-most chambers of the conch have collapsed.



13c

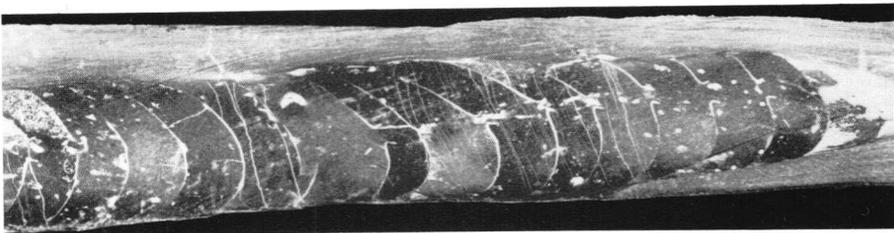


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13a

12a



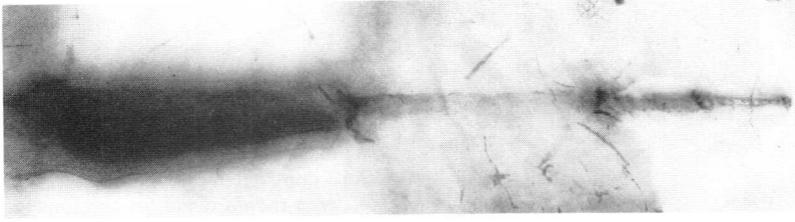
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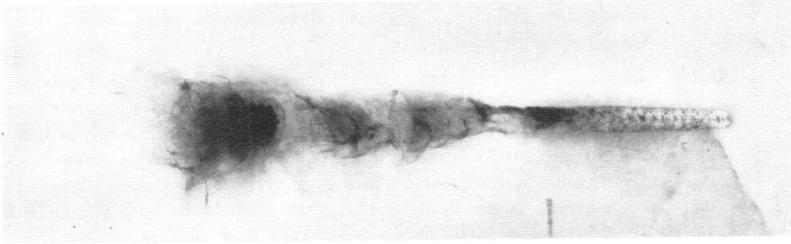
Plate 3.

Figs. 14-18. Lamellorthoceratid fossils. — Radiographs by WILHELM STÜRMER †. — Kaisergrube quarry near Gemünden, Hunsrück, W. Germany; Hunsrück Slate, Lower Devonian.

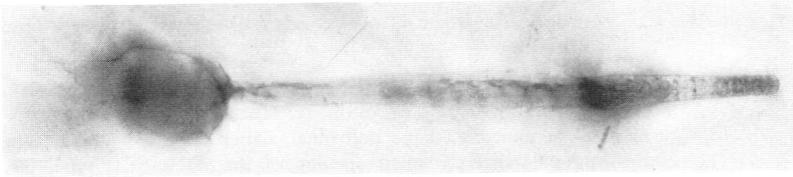
14. Conch with chambers of the anterior phragmocone well preserved, and a part of the living chamber preserved but much more compacted. The posterior "internal rostrum" is basically uncompacted and has almost retained its original shape, but was secondarily encrusted by pyrite crystals. Length of conch 18 cm.
15. Individual with some chambers totally collapsed. The sediment-filled chambers broadened by compaction, unlike the basically unaffected "internal rostrum". Length of conch 7.0 mm.
16. Conch in which all chambers have collapsed except the living chamber and posterior-most chambers. Length of conch 8.0 cm.
17. Well-preserved "internal rostrum", with collapsed and fractured phragmocone anterior to it. Length of fig. 9.0 cm.
18. Complete conch having a preserved living chamber, followed by collapsed chambers of the central phragmocone. Those posterior to the central phragmocone are somewhat diagenetically altered and sheared within the "internal rostrum". On this and other radiographs, note the dark "halos" surrounding parts of the conchs. Length of conch 20 cm.



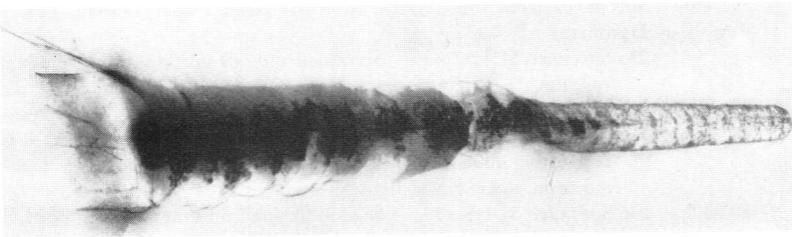
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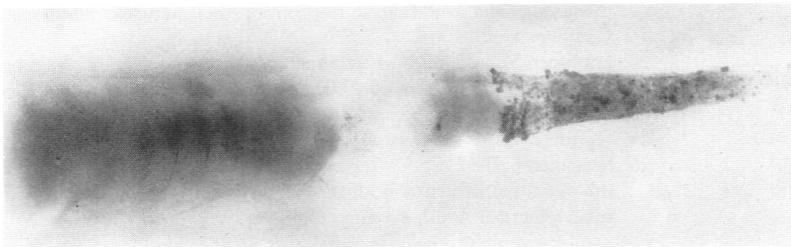
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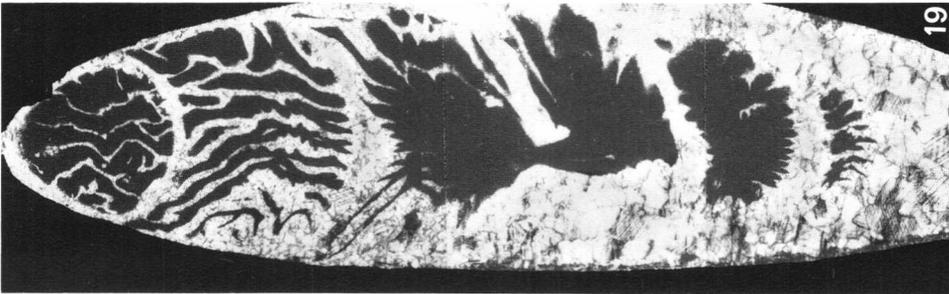
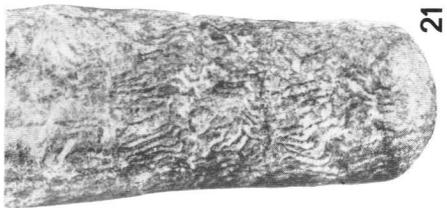
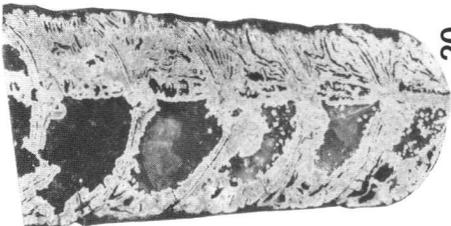
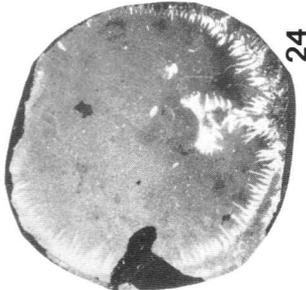
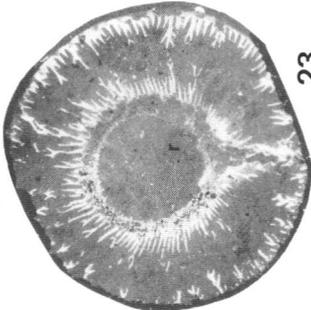
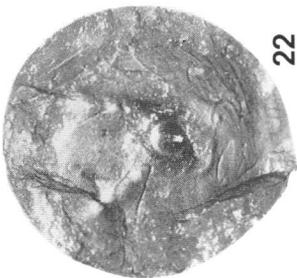
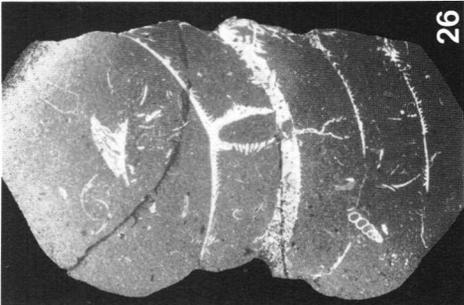
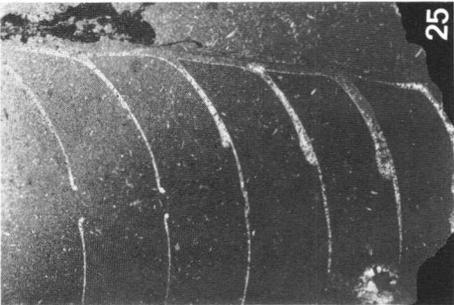
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Plate 4.

Figs. 19-26. Lamellorthoceratid fossils.

19. Specimen from Cortez Range, Nevada (CR); Lower Devonian. Specimen SUI-52147. — Tangential thin section through six successive chambers. A central chamber between the third and fourth chambers shows a siphuncular tube. Sediment must have entered intralamellar spaces (upper chambers) and could fill only those open to areas neighboring the siphuncle, whereas others became filled with calcite. Chamber width 9.0 mm.
- 20-21. Specimens from New York (NY); Esopus Formation, Lower Devonian.
 20. Specimen USNM 403718. — Cut and polished pyrite-replaced individual. The dorsal side is to the left and the ventral side of the chambers is to the right. The narrow lumina between mineralized organic sheets became filled with pyrite early during diagenesis, whereas larger void spaces were filled with calcitic material. Chamber width 10 mm.
 21. Specimen USNM 403719. — Outer, wavy lamellar surface of an individual, showing the sheet and intrasheet fillings of the "internal rostrum". The original, outer conch wall is totally eroded. Apical width 7 mm.
22. Specimen from the Kaisergrube quarry near Gemünden, Hunsrück, Rhenish Slate Mountains, W. Germany; Hunsrück Slate, Lower Devonian. — Septum of a large individual, flattened on a bedding plane showing the relatively small opening of the siphuncular tube. Fig. diameter 3.7 mm.
- 23-26. Specimens from Oued Draa, Morocco (GI); Upper Emsian, Lower Devonian.
 23. Specimen SUI-52148. — Sectioned anterior portion of the "internal rostrum" parallel to septum. Calcified sheets radiate from the septum (inner circle) and the conch wall (outer circle). The siphuncle was apically attached to the septum and ventrally secured by a supporting mineralized membrane, with mineralized sheets branching from it. Length of figure 18 mm.
 24. Specimen SUI-52149. — Section through the anterior-most portion of the "internal rostrum", showing the concentrically arranged mineralized sheets as well as the mineralized siphuncle supporting membrane and the ventral portion of the encrusted siphuncle. Chamber width 2 cm.
 25. Specimen SUI-52150. — Section almost along the siphuncular tube in the transition from non-filled to filled chambers of a phragmocone. The initial calcite deposits are visible on the surface of the septum and they thicken apically. Chamber height 2.7 mm.
 26. Specimen SUI-52151. — Transverse section of a steinkern showing the initial calcite crusts both on the sheets and on the siphuncular tube. Chamber width 4.5 mm.

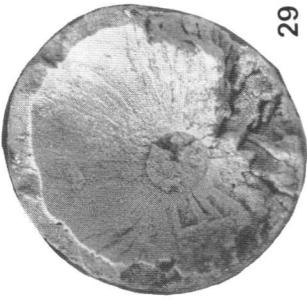


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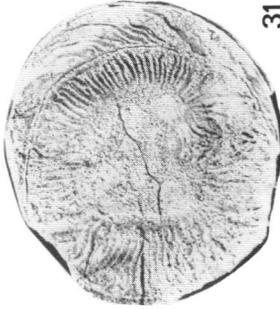
Plate 5.

Figs. 27-31. Lamellorthoceratid fossils.

- 27-30. Specimens from New York, N. Y.; Esopus Formation, Lower Devonian.
27. Specimen USNM 403720. — Chamber height 3.0 mm. — a) Longitudinal section through the "internal rostrum", parallel to the median plane and following the siphuncular tube. Pyrite filled the cavities such as siphuncular tubes and gas-remnants of each chamber as well as the spaces between mineralized sheets. To the left (ventral) side, the small gas space, originally occupied by a bubble, can be seen in one chamber. — b) Longitudinal section parallel to fig. a), but in more marginal position away from the siphuncle. The transverse dorsal sheet coming from the base of each siphuncle and going to the edge of the septum is well-traced by the pyrite-filled cavities between the sheets.
28. Specimen USNM 403721. — Transverse sections through various positions within the "internal rostrum" of a specimen similar to that of fig. 27 demonstrating the configuration of the mineralized sheets within different regions of the chamber. Diameter of specimen 10 mm. — a) Cut through the anterior-most portion of the chamber, showing the mineralized septal neck. The course of the primary set of sheets and spaces between them are affected by another inclined set of sheets in the dorsal portion of the chamber. — b) Cut near the central part of the chamber and c) a little below centre. The dorsal set of sheets is still close to the siphuncle, but does not interfere with it. The ventral siphuncle attachment sheet does interfere with and complicate the course of ventral sheets. Due to the strong septal concavity, fig. c) shows a bit of the next chamber behind. The ventral siphuncle attachment sheets are clearly visible.
29. Specimen USNM 403722. — View onto the cast of a convex septum and the septal neck, showing radial arrangement of sheets in the apertural portion of the chamber, as well as the position and size of the siphuncular tube. Chamber width 9.0 mm.
30. Specimen USNM 403723. — Naturally weathered surface, revealing the space originally taken by the last vestiges of the cameral gas filling within the "internal rostrum" and the mineralized sheets. Chamber width 8.0 mm.
31. Specimen from Cortez Range, Nevada (CR); Lower Devonian. — SUI-52152. — Naturally weathered transverse surface, whitened by Mg-ribbon. Calcite fillings of inter-sheet and intracameral cavities have become eroded and the actual lamellae are visible, but the resulting morphology more closely resembles that of pyritized specimens like those in fig. 28b-c). Chamber width 2.3 cm.



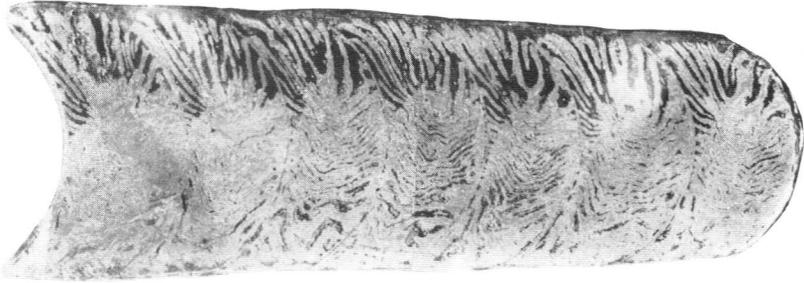
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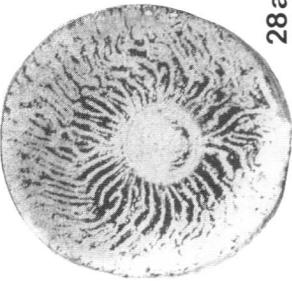
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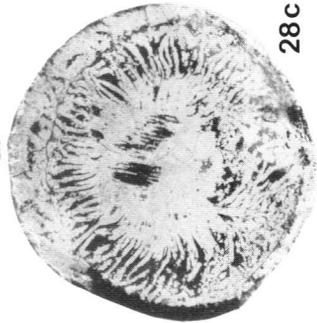
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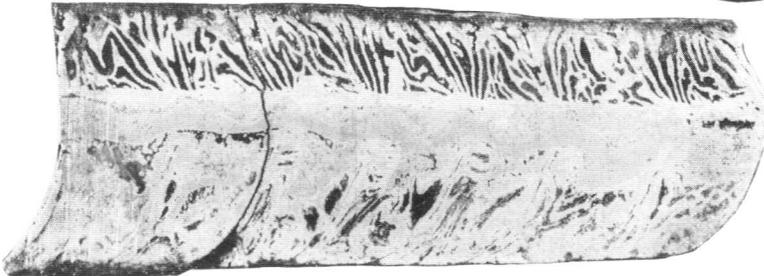
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28b



28c



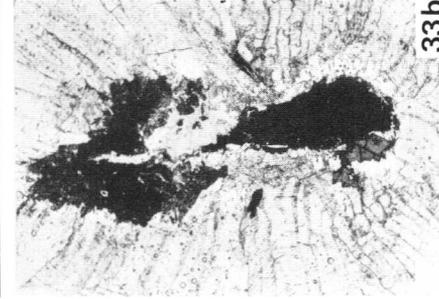
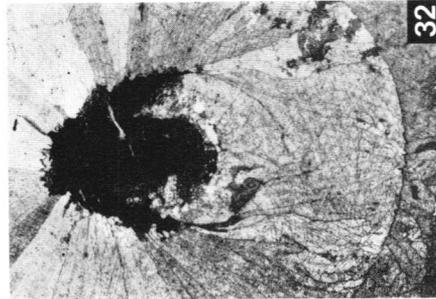
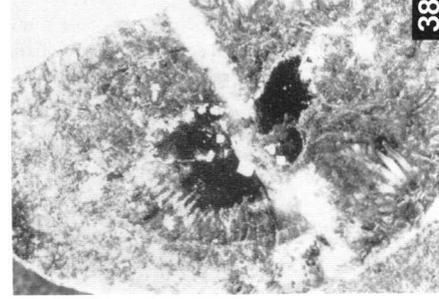
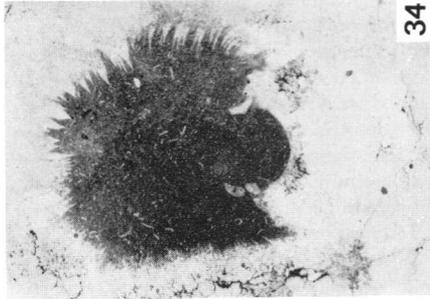
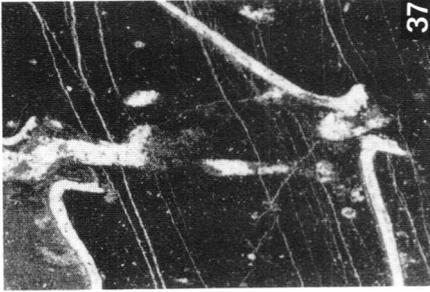
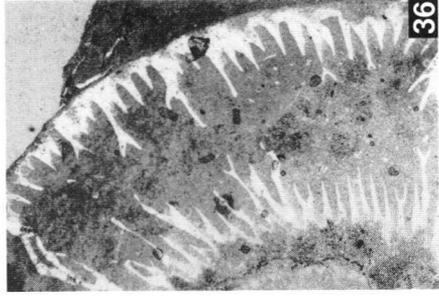
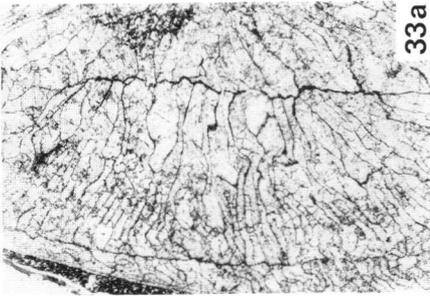
27a

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Plate 6.

Figs. 32-38. Lamellorthoceratid fossils.

- 32-33. Specimens from Lanvoy en Le Faou, France (LF); Middle Devonian.
32. Specimen USNM 403724. — Transverse thin section. Dorsal cavity and filled siphuncular tube in this "internal rostrum" have remained basically unchanged after infilling with sediment. The organic sheets and cavities between them have become transformed into coarsely crystalline calcite, but still show traces of the original structure. Distance between base of siphuncular tube and septum 4.0 mm.
33. Specimen USNM 403725. — a) Transverse thin section showing collapsed internal cavities of "internal rostra". Compression formed an oval, rather than round section. Greatest length of sediment-filled cavity 5.0 mm. — b) Transverse thin section marginal to fig. a). Same scale.
- 34-36. Specimens from Oued Draa, Morocco (GI); Upper Emsian, Lower Devonian.
34. Specimen SUI-52153. — Transverse section of "internal rostrum", having similar recrystallized preservation as specimen of fig. 32. The ends of mineralized sheets are well-preserved and sediment did not enter intersheet spaces because inclined sheet closed them to sediment, but not to pyrite (see pl. 5). The calcitic growth surrounding the siphuncle is spherulitic. Cavity width 8.0 mm.
35. Specimen SUI-52154. — Septal necks of unfilled chambers display their backward and slight outward twist in this specimen. Siphuncle width 2.0 mm.
36. Specimen SUI-52155. — Incompletely mineralized chamber. The mineralization of sheets started at the same time from the septum surface (left) and the chamber wall. Branching of sheets near the chamber wall indicates the influence of the dorsally inclined sheet in addition to the radially arranged sheets. Width between septum and outer wall 5.0 mm.
- 37-38. Specimens from Kaisergrube quarry near Gemünden, Hunsrück, Rhenish Slate Mountains, W. Germany; Hunsrück Slate, Lower Devonian. Coll. W. STÜRMER †.
37. Longitudinal section showing siphuncular necks the upper of which provided an avenue into the chamber interior for burrowing organisms, which left traces of their activity. Neck width 1.0 mm.
38. Slightly deformed "internal rostrum" with internal cavity partly filled by pyrite. Interlamellar cavities were filled with calcite and thin pyrite crusts. Some original calcite lamellae are preserved in this calcite (lower left). Cavity width 3.5 mm.

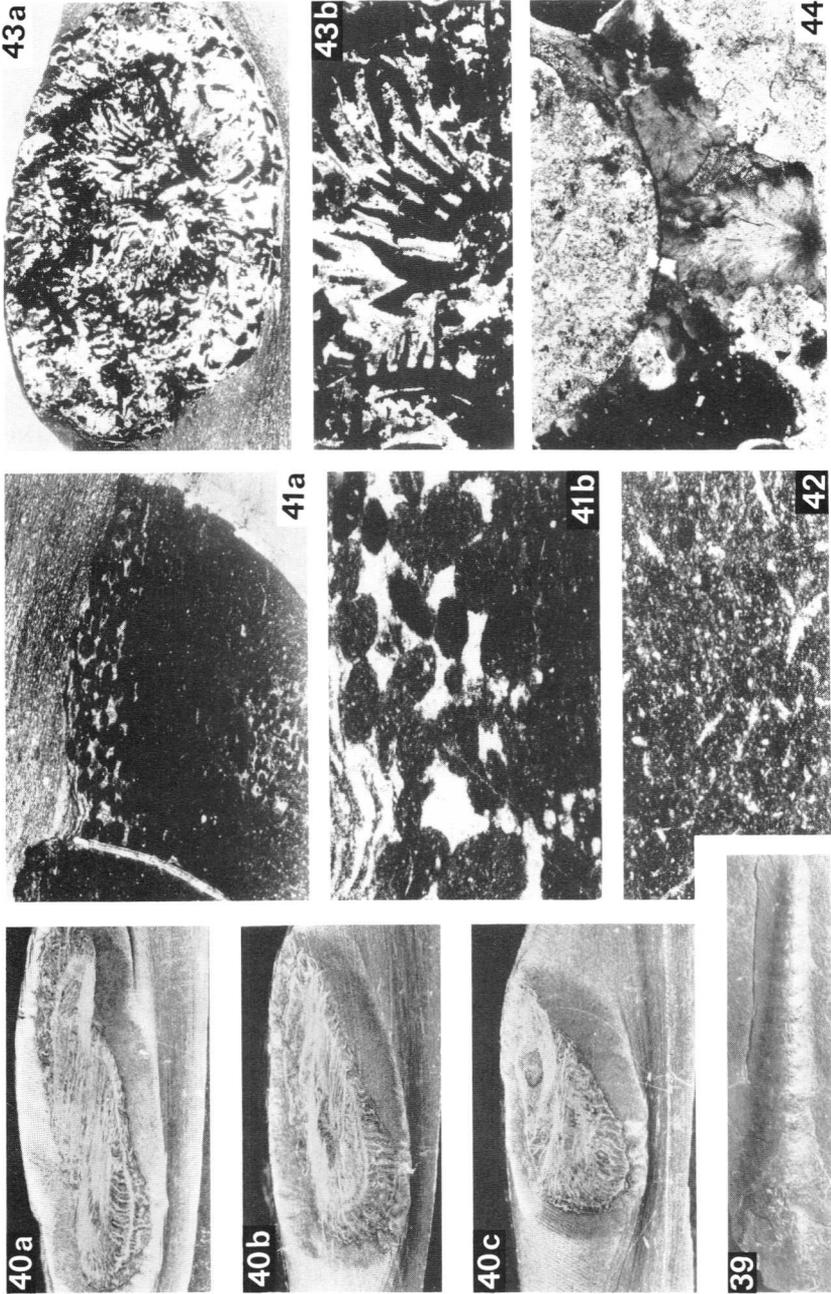


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Plate 7.

Figs. 39-45. Lamellorthoceratid fossils. — Kaisergrube quarry near Gemünden, Hunsrück, Rhenish Slate Mountains, W. Germany; Hunsrück Slate, Lower Devonian. Coll. W. STÜRMER †.

39. Photograph of a typical "internal rostrum". Length 10 cm.
40. Sections through a typical "internal rostrum", as is shown in fig. 39. In the Hunsrück Slate, compaction and tectonic deformation has complicated the already-complex diagenetic changes of the conch. The dark organic material forms a halo around the rostrum. — Thickness of the sections a) to c) about 5.0 mm.
41. Thin section of details within partly filled chambers. — a) General view. The original composition of the sediment is preserved, whereas outside the deformed regions its original structure was totally destroyed. Height of figure 0.5 cm. — b) Detail showing the originally pelletoidal mud which has become a micaceous slate.
42. In some chambers, disrupted fragments of the original organic sheets are preserved. Width of thin section 3.0 mm.
43. Transverse thin section of an "internal rostrum" containing pyrite space fillings like those normally found in the material from New York. Calcite fillings and relicts of the original lamellae are also preserved. — a) General view. Width of "rostrum" 14 mm. — b) Detail showing opaque fillings of pyrite between mineralized sheets. Even traces of the organic sheet material are preserved between calcite crusts.
44. Spherulitic calcite crystallization around the siphuncle and its attachment sheet. Width of thin section 4.0 mm.

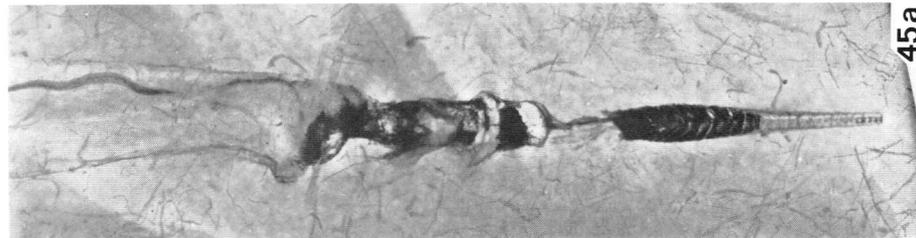
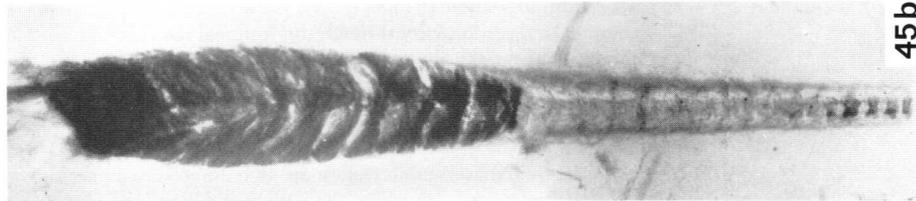
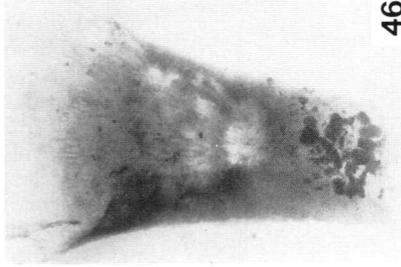
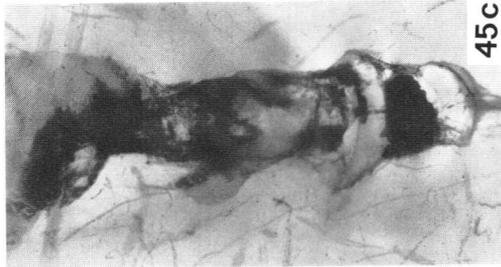
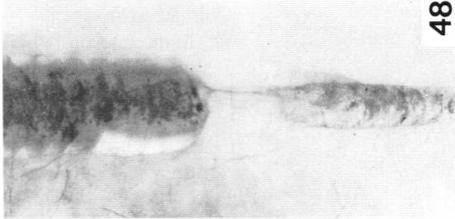
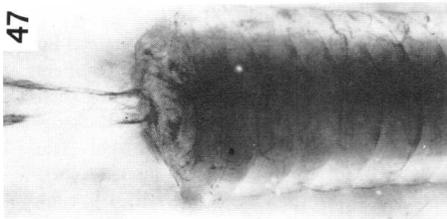


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Plate 8.

Figs. 45-49. Lamellorthoceratid fossils. — Kaisergrube quarry near Gemünden, Hunsrück, Rhenish Slate Mountains, W. Germany; Hunsrück Slate, Lower Devonian. Coll. W. STÜRMER †.

45. Complete conch showing a well-preserved living-chamber with partly to totally collapsed anterior phragmocone and well-preserved "internal rostrum" — a) General view. Length of specimen 20 cm. — b) Detail, showing the "internal rostrum" having anterior chambers partially filled by mineralized lamellae and the remaining chambers completely filled by lamellae. Sediment entered the "rostrum" from an apical fracture and filled remaining gas bubble voids. — c) Detail showing demineralized shell with the collapsed anterior chambers of the phragmocone. The degree of collapse depended on the amount of sediment that had entered a chamber prior to deformation.
46. The apical portion of an "internal rostrum" showing calcite crusts on organic sheets which were preserved by a thin film of pyrite on all surfaces. Anterior width 1.2 cm.
47. The anterior phragmocone collapsed in this conch. Scavenging organisms had entered the demineralized posterior portion of the conch, allowing it to be filled with sediment and the chambers to remain undamaged. Chamber width 4.7 mm.
48. A conch of which the chambers in the anterior phragmocone had become sediment-filled whereas those between these and the "internal rostrum" remained unfilled and subsequently collapsed during compaction. Width of anterior chambers 2.7 cm.
49. Demineralized specimen of which the 24 chambers between the living chamber and the "internal rostrum" were partly or totally destroyed when the liquid within them was squeezed out through the ruptured conch walls during compaction. Width of living chamber 2.7.

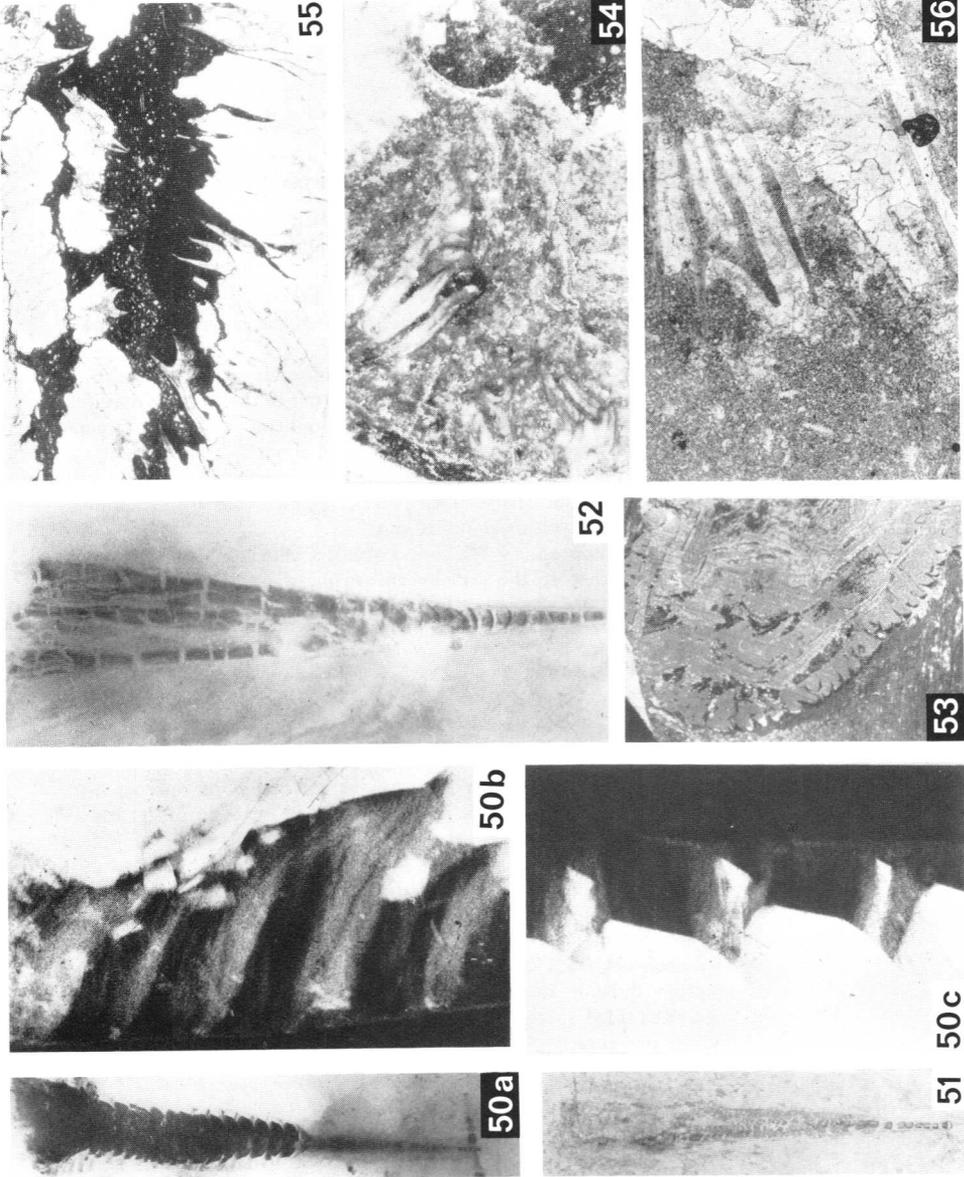


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Plate 9.

Figs. 50-56. Lamellorthoceratid fossils.

- 50-54. Specimens from Kaisergrube quarry near Gemünden, Hunsrück, Rhenish Slate Mountains, W. Germany; Hunsrück Slate, Lower Devonian. Coll. W. STÜRMER †.
50. Radiographs of a young individual with anterior chambers filled by massive pyrite. — a) General view. Compaction in the chambers free of calcite deposits is quite different from those containing such deposits. Length of conch 9 cm. — b) Detail of pyrite-filled chambers which show up as a bright reflection field to the right. The organic, demineralized conch wall and septa to the left stretched during compaction and strongly deformed. — c) Detail of pyrite-filled chambers (bright field at the left) and the demineralized conch wall stretched off it to the right. During compaction, the extreme corners of the pyrite-filling were broken off and dislocated, as indicated by the fragments.
51. Surface photograph of a juvenile individual which developed about 10 chambers that are almost as wide as high. Length of figure 3.5 cm.
52. Radiograph of a young individual with about 12 chambers. During this stage the phragmocone was shorter than the living chamber, which became flattened during compaction. Length of figure 3 cm.
53. The pyrite filled anterior portion of the internal phragmocone viewed in transverse section. Void spaces between calcitic lamellae were filled, in a similar way as the mineralized specimens from New York. Width of section 10 mm.
54. Transverse thin section view through the "internal rostrum" having a siphuncular tube at right with calcite fill. A few lamellae with their double calcite crust on the central organic sheet can be discerned. Distance from outer wall to siphuncle 5.0 mm.
55. Specimen from Lanvoy en Le Faou, France (LF); Middle Devonian. — USNM 403726. — Transverse thin section through the collapsed interior of an "internal rostrum", showing the sediment-filling, the calcite deposits between lamellae, and a few branching lamellae in their original shape and configuration. Width of section 5.0 mm.
56. Specimen from Oued Draa, Morocco (GI); Upper Emsian, Lower Devonian. — USNM 403727. — Thin section showing contact between filling and lamellae. A few lamellae are preserved in their original morphology with a central remnant of the organic sheet. Note darker original calcite layer. Between such layers is the secondary calcite growth. Their juncture is a dark seam. Photograph width 7.0 mm.



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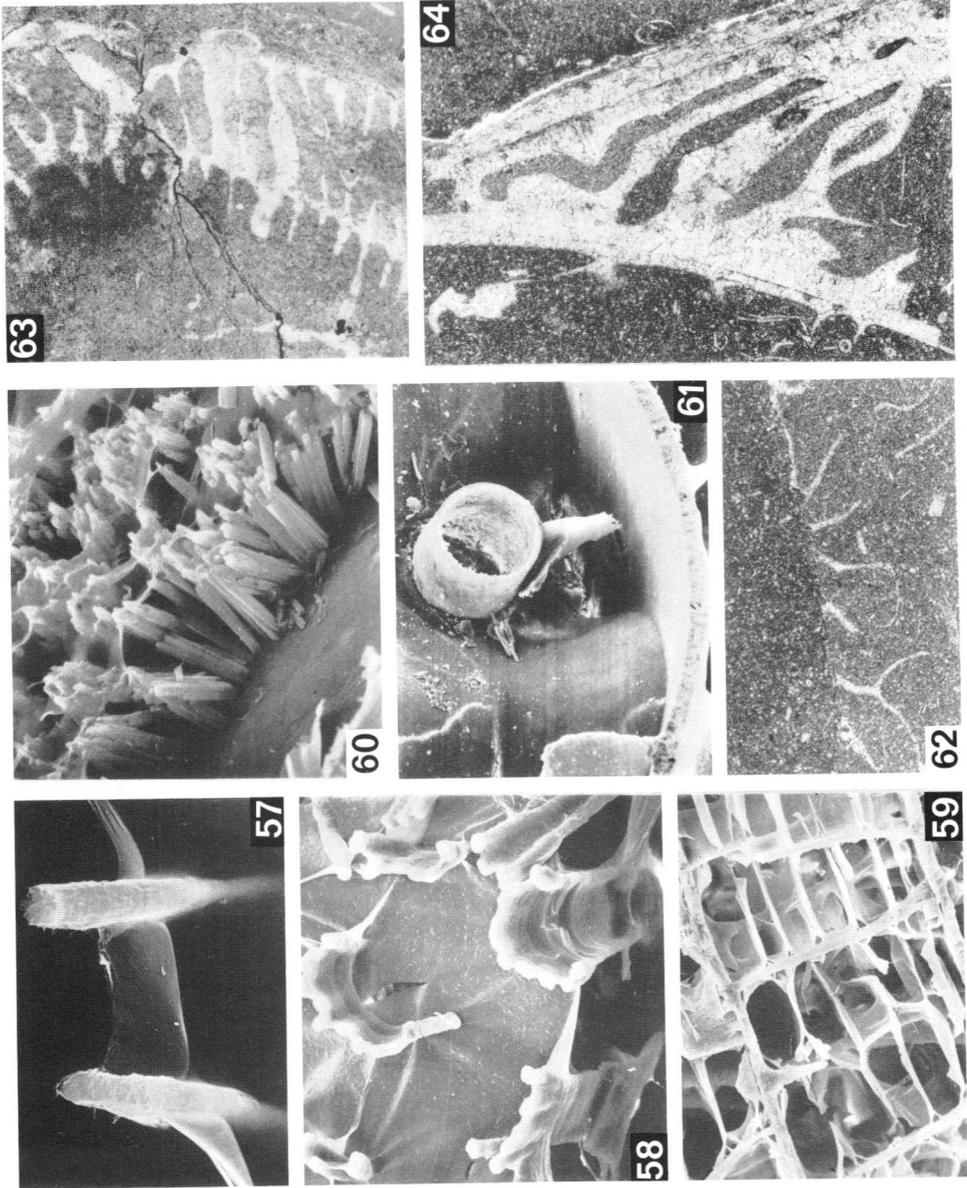
Plate 10.

Figs. 57-61. Scanning electron microphotographs of comparative material.

57. *Sepia pharaonis* EHRENBERG 1831. — Red Sea; Recent. — Organic sheet suspended between aragonitic pillars within the chamber. Pillars about 1 μm wide.
58. *Sepia officinalis* LINNAEUS 1758. — Mediterranean Sea; Recent. — Vertical and horizontal organic sheets constructed within the chamber. Pillars about 10 μm wide.
59. *Sepia orbigniana* FERUSSAC 1826. — Mediterranean Sea; Recent. — Chamberlets broken in longitudinal direction to demonstrate chamber bottom and chamber roof, supported by mineral pillars with organic sheets suspended between. Chamber width about 100 μm .
60. *Nautilus pompilius* LINNAEUS 1758. — Indo-Pacific Ocean; Recent. — Between aragonitic prisms of the pillars, organic sheets are also present. Width of single prisms about 0.2 μm .
61. *Quenstedtoceras* sp. — Luckow, Poland; Callovian, Jurassic. — The tube is attached to the wall by an organic sheet comparable to that present on the ventral side of lamellorthoceratids. Tube diameter 150 μm .

Figs. 62-64. Lamellorthoceratid fossils. — Oued Draa, Morocco (GI); Upper Emsian, Lower Devonian. — Thin section photographs.

62. Specimen SUI-521456. — Section through a septum and first mineralized sheets. The originally aragonitic septum has disappeared during diagenesis and its course can be traced by the differences in chamber filling (upper more densely filled than lower chamber) and by the upgrowth of calcite lamellae which are preserved. Width of section 2.0 mm.
63. Specimen SUI-521457. — Section through radial sheets and a transversal sheet that were mineralized by original chamber deposits. Width of figure 6.0 mm.
64. Specimen SUI-521458. — Section similar as fig. 63, but parallel to septum showing the end of the transversal dorsal sheet (right) and sediment-filled spaces between radial sheets below the septum (left). Width of figure 1.5 mm.



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