

Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends

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Chapter 8

Cephalopod Shell Structure and General Mechanisms of Shell Formation

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I. Introduction

Cephalopod shells are constructed of the calcium carbonate polymorphs aragonite and calcite in close association with organic material. Like all molluscs, cephalopods use their mantle to secrete their shell. However, various other hardparts, such as the jaws, radula, statoliths, operculum (aptychi) and brood chambers, are secreted by tissues other than the mantle. Three different mantle portions, the muscular mantle, the periostracal gland zone and the shell mantle, are responsible for the secretion of different parts of the shell. Shell deposition begins at the mantle edge with the formation of the periostracum, a layer consisting of organic

sheets and fibers (Grégoire, 1987) produced by specialized cells within the periostracal groove. The shape of these deposits is determined by the muscular mantle adjacent to the groove. Mineralized shell consisting of nacre and various prismatic structures is added to the periostracum by the shell mantle, which lies behind the periostracum gland zone. Many cephalopods with an internalized shell also add mineralized shell material of a variety of structures exterior to the periostracum using the muscular mantle.

Cephalopod shells consist of the primary shell, which is mineralized inside the protection of the egg-capsule, and the secondary shell, which is mineralized after the primary shell has formed. The secondary shell is secreted largely after the animal hatches from the egg. The primary shell is initially attached to the mantle and it becomes mineralized only after the mantle margin detaches from the shell margin (Bandel 1982). The secondary shell, in contrast, is secreted without attachment between the mantle and shell margins.

During evolution some cephalopods abandoned the ancestral mineralized chambered shell for a non-mineralized shell, as in modern squids. Other cephalopods, like Jurassic *Trachyteuthis* (vampyromorph octopod) (Figure 1; Bandel and Leich, 1986) and Tertiary and extant sepiids continued to mineralize only the exterior portion of their shell. The Lower Devonian palaeoteuthomorph genera *Boletzkya* and *Naefiteuthis* (Figure 2) possibly represent intermediate forms, secreting mineralized shells when young but later secreting organic shells only (Bandel *et al.* 1983).

According to Bandel and Hemleben (1975) secretion by the shell mantle results in 'true' biomineralizates such as nacre in which the structural arrangement is very closely controlled by the organism. Prismatic structures, usually with basic elements 0.2 microns in width, are also produced by the shell mantle (Bandel, 1979). In contrast, biomineralizates produced by the muscular mantle appear to be less subject to biological control, and they resemble patterns of inorganic mineral growth. Similar poorly organized shell structures are sometimes also formed by non-mantle epithelia, such as the arm folds in the case of the *Argonauta* shell, and the lips in the case of the *Nautilus* beak.

II. Preservation in the Fossil Record

Because of their generally aragonitic composition, fossil cephalopods are commonly altered by a variety of diagenetic

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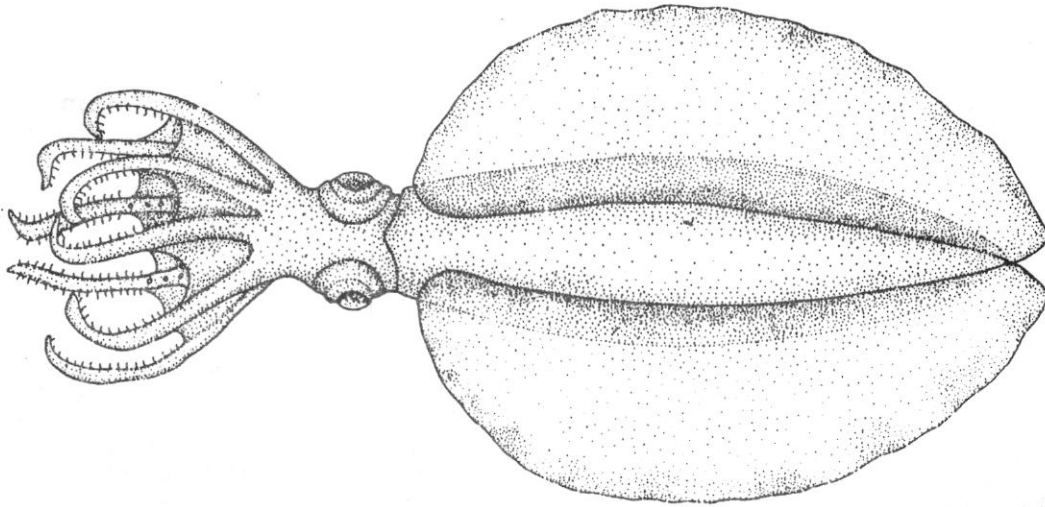


Fig. 1. Reconstructed *Trachyteuthis hastiformis* seen from above. The vampyromorph squid was up to 53 cm long and lived near the lagoons of the Solnhofen area (southern Germany) in the shallow northern margin of the Tethys Ocean during Upper Jurassic times. From Bandel and Leich (1986, Fig. 20).

processes. Even before burial, their shells are subject to organic decay, micritization, boring, and cementation in primary and secondary cavities. After burial, aragonitic nacreous, prismatic and spherulitic prismatic structures are commonly transformed into diagenetic low-Mg calcitic structures such as 'pseudostacks', 'pseudo-crossed lamellae', and prismatic and blocky structures. Alternatively, they may retain their primary pattern by allochemical replacement with quartz, phosphate, pyrite and gypsum (Dullo and Bandel, 1988, Bandel *et al.*, 1986). Calcitic shell structures are rare among cephalopods, but they have better potential for preserving their original structural pattern and crystal orientation. Here sometimes only crystal enlargement occurs during diagenesis.

The diagenetic pathways leading from the original shell to the fossil are sometimes very difficult to trace, but must be taken into consideration when analyzing fossil cephalopods. Many diagenetic structures can be mistaken for primary ones, and *vice versa*. For example, marine aragonitic cements, which are usually needle-like and commonly grow syntaxially with the same orientation as crystallites in the prismatic layer, are commonly difficult to distinguish from intracamerar deposits such as those in pseudorthoceratids (Ristedt, 1971). One might well call these pseudorthoceratid intracamerar deposits a cement which formed while the animal was living. During shell repair, similar prismatic cements are known to have been deposited by *Belemniteuthis* (Bandel and Kulicki, 1988) (Figure 3, arrows). In contrast, calcite cements were deposited during life on organic sheets in the chambers of Devonian lamellorthoceratids, as described by Bandel and Stanley (1988). In some shells, calcitic cement growth continued under marine conditions after the animal's death.

A number of diagenetic structures can replace nacre. The columnar (stacks of coin) nacre in *Pseudorthoceras* from the Triassic Cassian Formation is sometimes transformed into low-Mg calcite 'pseudostacks' (Dullo and Bandel, 1988);

The 'pseudostack' structure in Devonian lamellorthoceratids can form a very regular diagenetic pattern of calcitic rods which represents a totally different structural type. This is formed only under certain diagenetic conditions. Nacre can also be transformed into calcite rods and needles which resemble common crossed lamellar structure in thin section (Bandel and Dullo, 1988, Text-fig. 9).

The patterns of diagenesis of aragonitic prismatic structures depend on the size and arrangement of the crystallites. During diagenesis, finer prismatic structures consisting of basic elements of 0.2 microns wide behave like nacre and are destroyed. Coarser prismatic structures altered to calcite may retain much of the original orientation of their needle-like crystallites, as observed in the intracamerar deposits of a Triassic pseudorthoceratid and in the rostra of the aulacoceratids (Bandel, 1985; Dullo and Bandel, 1988). Growth lines are commonly retained in shells with this kind of preservation.

When the original aragonitic shell material is demineralized during diagenesis, fine, longitudinal costules may

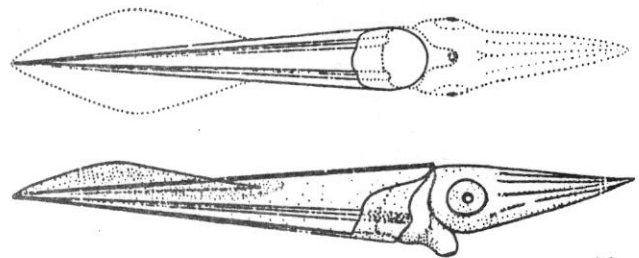


Fig. 2. Reconstruction of the shell of *Naefiteuthis*, with a conceivable soft body surrounding it. The shell measures up to 20 cm in length, and animals were living during Lower Devonian times in the seas covering what is now the southern Rheinische Schiefergebirge near Bundenbach, Germany. From Bandel and Boletzky (1988, Fig. 1).

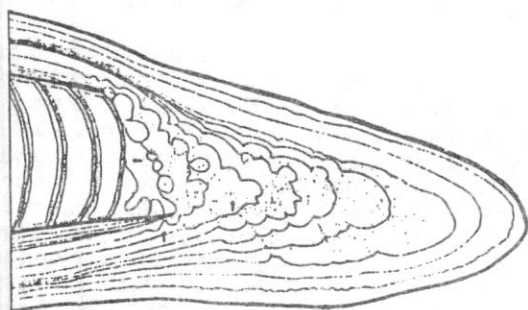


Fig. 3. Sketch of the cut and polished end of the phragmocone and rostrum of *Belemnoteuthis polonica* (Middle Jurassic, Poland). The phragmocone was fractured during life but then healed. Portions of the healed rostrum show spherulithic structure (arrows). Chambers close to the repair are partly filled by secondary deposits. From Bandel and Kulicki (1988, Fig. 9).

develop which reflect the ultrastructural pattern of the organic shell contained in the mineral matrix (Bandel and Stanley, 1988). About six costules are present in each millimeter of *Arthrophyllum* shell with this kind of diagenesis, and these features can be used for taxonomic purposes, with good reason, when their origin is taken into account. It has to be understood that the fine costules were formed by dissolution of the mineral parts of the shell, so they represent nothing that would be visible on a fresh shell, neither lines of growth, ornament, nor microstructural morphology.

III. Structure of the Embryonic Shell.

A. Mineralization of the Organic Primary Shell.

As in many other molluscs the structure and morphology of the embryonic cephalopod shell are related to the amount of yolk involved in embryogenesis. Among modern cephalopods, only *Spirula* has eggs so small that shell gland differentiation and formation of the first shell coincide with the time of yolk rearrangement and morphological lifting of the embryo. During this process the disc-like embryo lifts from the yolk egg or actively deforms it and acquires its characteristic shape, which is now more like that of the hatching young. Boletzky (1974) noted that in cephalopods with eggs smaller than 2 mm (*Spirula* eggs measure 1.7 mm in maximum diameter) the longitudinal axis of the animal is predetermined by the longitudinal axis of the egg. Here the embryo covers about half of the yolk when the outer and inner yolk mass are separated from each other. The mantle secretes an organic shell whose shape reflects the round, inner yolk mass. It becomes functional and free from its secretory epithelium (the periostracum-secreting cells) before it is mineralized.

Mineralization of the organic primary shell occurs in two phases (Bandel and Boletzky, 1979). During the first phase, aragonitic crystallites penetrate and partly replace the organic primary shell. During second phase, the primary shell is covered by inner prismatic deposits. Mineralization of the embryonic shell in *Spirula* resembles the mode of mineralization of the ammonitella (the ammonite embryonic shell) in

all well-preserved Triassic, Jurassic and Cretaceous ammonites so far studied (Birkelund, 1967; Birkelund and Hansen, 1968; Drushchits and Khiami, 1969; Erben *et al.*, 1968; Kulicki, 1979; Bandel *et al.*, 1982; Bandel, 1982; Khiami, 1986). A similar pattern is found in the embryonic shell of belemnites and aulacoceratids (Bandel, 1985; Bandel *et al.*, 1984; Bandel and Kulicki, 1988), and this probably also occurs in bacritids and orthoceratids, which have embryonic shells like belemnites in general.

As in *Spirula*, the first chamber within the ammonite ammonitella is spherical, ovoid or lenticular (spindle-shaped) and it probably surrounds the embryonic inner yolk sac. Secretion of the entire ammonitella was completed in contact with the mantle epithelium prior to mineralization, because the ammonitellae are devoid of growth lines, and the first mineralization affects only their outer walls (Figures 4 and 5; 5A: first mineralization, 5B: mineralization of inner walls, 5C: shell before construction of teleoconch). This first mineralization appears as needle-shaped crystallites arranged in slightly spherulitic orientations growing from the inside outwards. When a sculpture of tubercles is present, the crystallites show their spherulitic orientation best within these tubercles.

Interestingly, archaegastropods initially mineralize their organic embryonic shell in a manner similar to ammonites and such cephalopods that have an embryonic shell similar in size to ammonitellae. The Cambrian ancestors of cephalopods and gastropods alike may have developed this mode of shell mineralization in response to a change from free swimming, non-feeding larvae requiring a light shell to benthic juveniles in need of protection through mineralization. The very rapid growth of needles 0.2 microns in diameter into the organic shell may represent a primordial mode of initial mineralization in conchiferan molluscs.

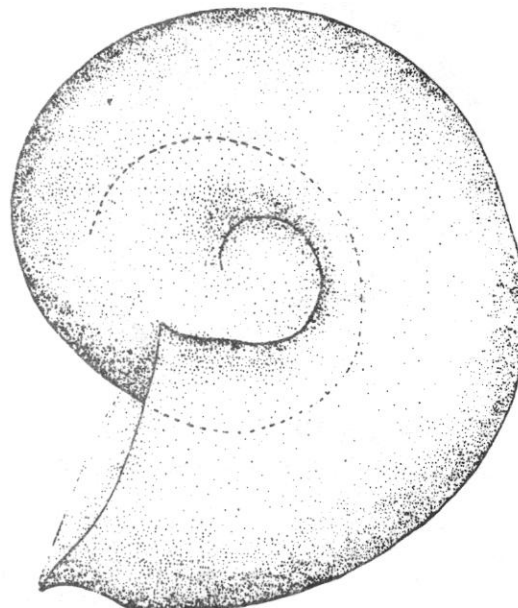


Fig. 4. The outer shell of the ammonitella, already detached from the gland cells of the mantle edge, but before mineralization has covered much of its initial shell cup (indicated by the stippled line). The ammonitella was initially unmineralized. From Bandel (1982, Fig. 40).

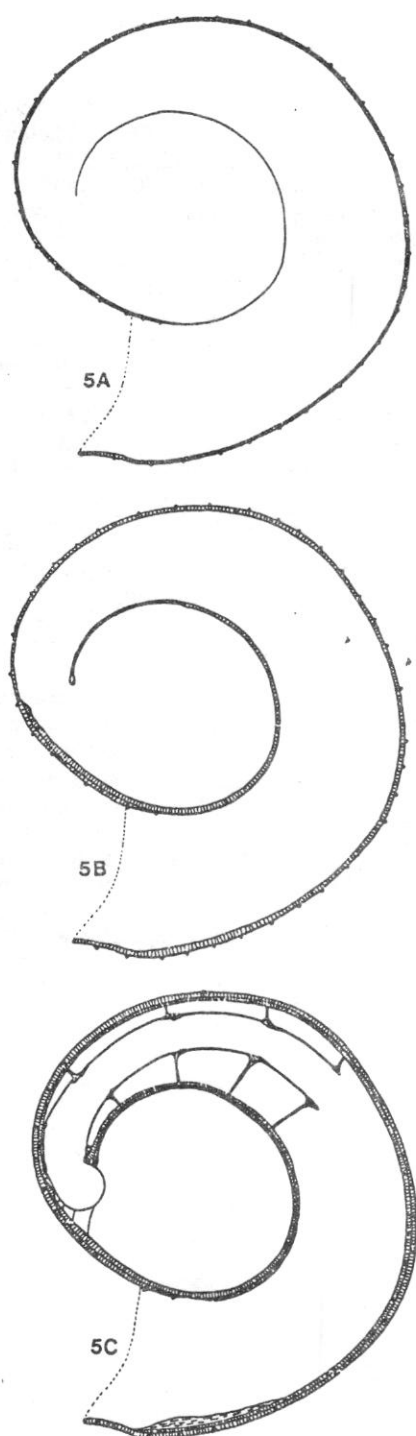


Fig. 5. Stages in the mineralization and construction of the first chambers in the ammonitella of *Quenstedtoceras* from the Middle Jurassic of Poland. A: Median section through an ammonitella after mineralization of the outer shell walls. B: Ammonitella after deposition of the first inner prismatic layer. C: Young ammonite ready for adding teleconch with six chambers of nacreous nepionic constriction. A and B from Bandel (1982, Figs. 46 and 47).

B. Biomineralizates Covering the Primary Shell.

In *Nautilus* and *Sepia* the eggs are yolk-rich and much larger than 2 microns in maximum diameter. Here the shell gland develops on a disc-like cell plate resting on the yolk mass.

In *Sepia officinalis* the primary shell detaches from the mantle at a length of about 0.9 mm. During reorganization of the yolk, the conch is deformed and pulled inward along a central line of shell-tissue attachment (Figure 6). Further shell growth occurs with the formation of clear growth increments. At about 2 mm shell length, the first mineralization occurs both outside and inside the shell (Figure 7). Both exterior and interior deposits are organized in the same manner as normal adult shell, being accreted onto an organic periostracal layer. There are no early shell structures comparable to those seen in shell-bearing cephalopods with eggs smaller than 2 mm.

Nautilus develops on a very yolk rich egg within a large egg capsule measuring up to 20 x 14 mm (Arnold *et al.*, 1987). Here as in *Sepia* the primary organic shell becomes strongly deformed before initial mineralization fixes its shape. The primary organic shell is larger than 2 mm and it sits cap-like on the top of the embryo (Arnold, 1987; Arnold *et al.*, 1987, Fig. 1C). The initiation of mineralization and continued growth of the large embryonic conch are clearly visible in its exterior morphology. The wrinkled, unmineralized primary shell, formed by the still connected mantle and shell, changes abruptly and quite visibly to the regularly sculptured, well formed secondary embryonic shell. The primary shell is stretched and becomes wrinkled around a central fold before it becomes mineralized and fixed in shape (Erben and Flajs, 1975). The initial mineralized deposits consist of aragonite crystallites in the shape of single needles, crystal aggregates and wheat-grain-like aggregates dispersed in simple black organic material (Blind, 1967; Arnold *et al.*, 1987). This initial deposition is then underlain by nacre which is not unlike that formed by adults. As in *Sepia*, the embryonic shell does not differ in style of mineralization from the adult shell with the exception of the small portion of primary shell. This primary shell became deformed before it was mineralized, in the case of *Sepia* initially from the outside, in the case of *Nautilus* initially from the inside. Observations of well preserved Miocene *Aturia* indicate that its organic primary shell was also deformed before it became mineralized from within. Here irregular prismatic deposits are concentrated in the narrow zone of the cicatrix (initial cap of organic primary shell), and a normal nacreous layer covers most of the embryonic shell. The secondary shell was being deposited within the egg capsule, but after detachment of the mantle margin from the margin of the growing shell.

C. Mineralization of the First Septum.

The first septum of *Nautilus* and *Sepia* is constructed in the same way as their later septa. However, in cephalopods such as ammonites and belemnites with a spherical first chamber, the first septum differs considerably in structure and morphology from later septa. The proseptum, or first septum, of the ammonite ammonitella always develops at the transition from the cup-like first chamber (protoconch) to the planispiral first whorl. This proseptum closes off the spherical to elliptical first chamber, but it leaves a large circular medial opening, the diameter of which equals the

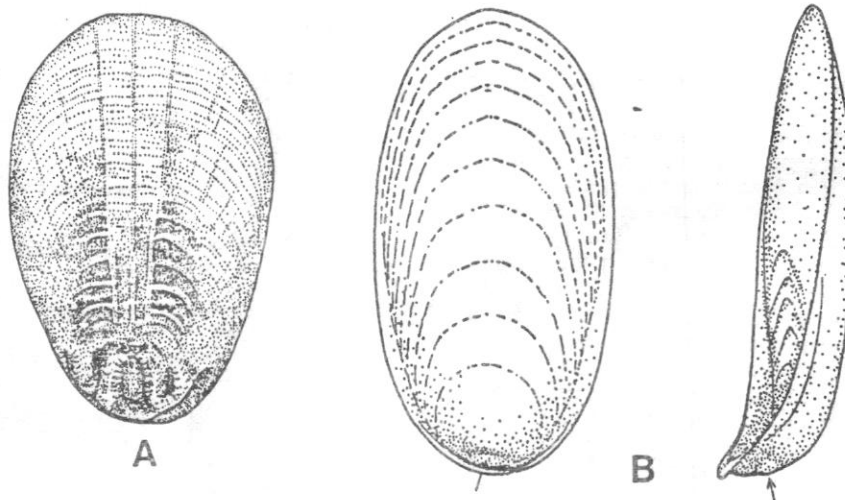


Fig. 6. Cuttlebone of young *Sepia*. A: *Sepia officinalis* cuttlebone before secretion of the first mineral layer on the inside shows the scar on the primary shell (cicatrix) and growth increments on the secondary shell. These are later covered by outer mineral deposits. From Bandel (1982, Fig. 55). B: The cuttlebone of freshly hatched *Sepia orbignyana* with rudiment of the spine (arrow) visible on the rounded posterior part. From Bandel and Boletzky (1979, Fig. 13).

whorl height. The prosepium is prismatic whereas the second septum is nacreous (Kulicki, 1979; Bandel, 1982; Landman and Bandel, 1985). The microstructure of the prosepium and the following septa is known from Triassic, Jurassic, and Cretaceous ammonites (Birkelund and Hansen, 1974; Kulicki, 1979; Bandel, 1982; Landman and Bandel, 1985; Bandel, personal observations). An organic precursor of the prosepium is firmly attached to the walls of the protoconch in a prismatic ridge, as shown in *Baculites*, *Scaphites*, *Quenstedtoceras*, and *Kosmoceras* (Landman and Bandel, 1985). This organic precursor is later mineralized, wrinkles and all, to form the prismatic prosepium.

This type of prismatic prosepium, which closes the first chamber to form the siphuncular system, was apparently inherited by the ammonites from Upper Silurian orthoceratid cephalopods. The latter are also believed to have evolved into the first coleoids (Bandel *et al.*, 1983; Bandel and Boletzky, 1988). Belemnoids in the broad sense (including aulacoceratids and belemnites) have a similar prismatic septum which differs in shape from the later nacreous septa. But belemnites also have an organic septum that is not penetrated by a siphuncle (the closing membrane of Jeletzky 1966; Bandel *et al.*, 1984; Bandel and Kulicki, 1988). This suggests that belemnites were able to hatch and utilize their first chamber before their visceral mass had differentiated a siphuncle. The belemnite tissues therefore pumped liquid from their first chamber in a manner comparable to modern *Sepia*. However, whereas *Sepia* uses this pumping epithelium on the dorsal visceral mass throughout its life, belemnites used it only during their embryonic development.

The first mineralized septum in belemnites (the second septum following the first purely organic one) is concave and has a marginal aperture with forward-bent septal necks. This differs from the later septa, which have backward-bent septal necks. Crystallites within the first mineralized septum are arranged perpendicular to the septal surface except in the

central portion, where needles are oriented horizontally. This indicates that the septum was initiated by a mucus-covered organic sheet with mineralization beginning in the central sheet, followed by needle-like crystal growth on both sides of the sheet. The first mineral septum is attached to the outer walls by a mineral ridge that lies partly on top of the mineral-attachment ridge, with which the first organic septum is anchored to the outer walls of the phragmocone.

In *Spirula* the aperture of the spherical first chamber becomes constricted by a prismatic ridge before the siphuncular tube is secreted (Bandel and Boletzky, 1979) (Figure 9, A: opened first chamber, B: sectioned first septum and siphuncle, C: shell of *Spirula* adult). The first septum has thus been reduced to a prismatic ridge. Transitional forms between this condition in *Spirula* and more ancient

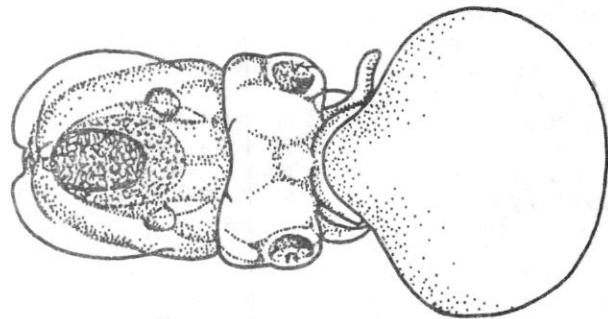


Fig. 7. Embryo of *Sepia officinalis* some time before hatching, with large outer yolk sac which will be absorbed by the time of hatching. At that time, the animal will have doubled in size. The shell has two complete chambers, and the third is being formed. The first-formed chamber has been emptied of liquid. From Bandel and Boletzky (1979, Fig. 17).

conditions are yet unknown with the possible exception of the Upper Cretaceous *Groenlandibelus* (Jeletzky, 1966). In addition, the Eocene *Vasseuria* is transitional between the *Groenlandibelus-Spirula* organization and the more simplified condition of *Sepia*. In *Vasseuria* the spherical first chamber has been altered due to an increase in the content of yolk of the egg, which influences later calcification of the primary shell. The siphuncular tube opens in the manner hypothetically postulated by Bandel and Boletzky (1979). They found that in *Spirula* and belemnite aulococeratids a wide zone of the siphuncular tube is occupied by the pillars. This pillar zone is distinct from the actual chamber. In *Sepia*, however, the actual chamber is lost and the pillar zone opens up into a broad blade. The organic sheets, confined to the anterior part of the pillar zone in *Spirula*, now extend throughout the chamber of the cuttlebone. During this process the characteristic biomineralizates of the embryonic conch and its first septum are lost and replaced by adult-like biomineralizates.

IV. Microstructure of the Adult Shell.

A. Nacreous and Associated Structures.

Well-preserved ammonoids, belemnoids and nautiloids have microstructurally similar shell walls. Their periostracum is underlain and sometimes even infiltrated by aragonite needles in spherulitic arrangements, grading inward into a spherulitic prismatic layer and then a nacreous layer. Nacre comprises the bulk of the shell material and is usually covered by a thin prismatic layer on the inside of the conch (Appellöf, 1893; Boggild, 1930; Mutvei, 1964, 1970, 1972a, 1972b; Meenakshi *et al.*, 1974; Grégoire, 1962; Erben *et al.*, 1969). Meenakshi *et al.* (1974) demonstrated that *Nautilus* secretes wheat grain-shaped aggregates of aragonite needles just posterior to newly formed periostracum. These grow into a spherulitic prismatic layer (Mutvei, 1964) which becomes well ordered farther back from the shell rim. This layer is usually abruptly overlain by nacre. But in the septal necks and where the shell is repaired, a gradual transition from the spherulitic prismatic layer to nacreous structure can be observed (Bandel, 1977).

In the belemnoid phragmocone the periostracum is underlain by an extremely thin, aragonitic granular layer. The aragonite granules measure about 0.2 to 0.3 microns in diameter and they form a layer with a maximum thickness of 1 micron. The granules are rounded to angular and they show no specific structural pattern. They form a densely packed, tight mosaic when viewed parallel to the growth surface. Below this exterior layer, the basic granular elements form rows and become arranged into needle-shaped units which are straight or branched. The needles are initially randomly arranged and irregularly intergrown in a thicket-like manner, similar to the dendritic structure of gastropods (Bandel, 1979, 1989). Here the basic structural elements comprising the needles are irregularly shaped.

Toward the inner part of the dendritic layer, the needles assume a mutually parallel orientation which is inclined at a low angle to the shell surface. Here the basic structural elements change from irregular granules to regular rhombohedra which are oriented in rows not only within each needle but also inclined to each needle, extending from needle to needle. Each basic element is thus engaged in the composition of two needles which dissect each other at an angle of

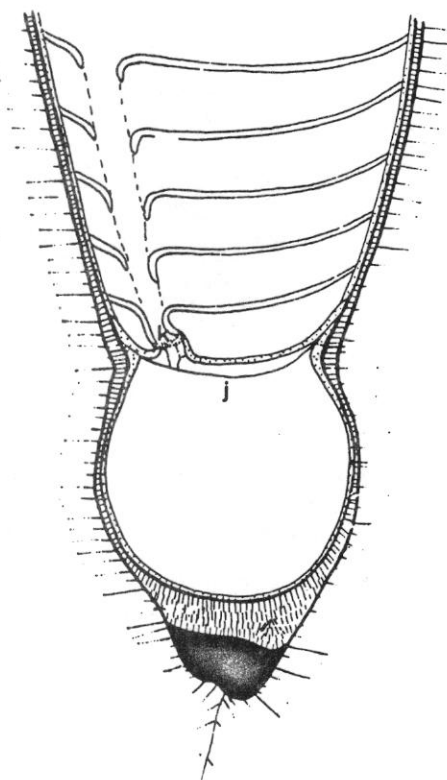


Fig. 8. Schematic drawing of the conch of *Hibolites* as contained within the calcitic rostrum. The first septum (j) is organic, while the following second septum is prismatic and the third and later ones are nacreous and mineralized. The primordial rostrum is in part aragonitic, prismatic and organic (indicated in black). From Bandel, Engeser and Reitner (1984, Fig. 22).

about 45 degrees. This crossed prismatic structure ("dissected crossed prismatic" of Carter and Clark, 1985) is characterized by two needle directions, with the needles oriented within a plane that is vertical to the apertural edge and to the growth surface. A similar structure exists in gastropods, where it does not grade into nacreous structure but into crossed lamellar structure. Crossed prismatic structure may also grade rapidly into spherulite sectors wherein the marginal needles dissect each other, *e.g.*, in archaeogastropods like *Guildfordia* (Bandel, 1977) (Figure 10).

In nautiloids, ammonoids and belemnoids from the onset of the adult shell to the embryonic shell, the nacreous layer is interleaved between an outer crossed prismatic or spherulitic prismatic layer and an inner blocky prismatic or acicular prismatic layer. With continued growth of the conch, nacre usually comprises a progressively larger portion of the total thickness of the shell walls. The nacre tablets are arranged in layers separated from each other by organic sheets. Within each tablet the basic structural elements are fused to form an apparently monocrystalline or polycrystalline aggregate. The nacre tablets are usually deposited in discrete stacks on the depositional surface. These stacks expand laterally as they

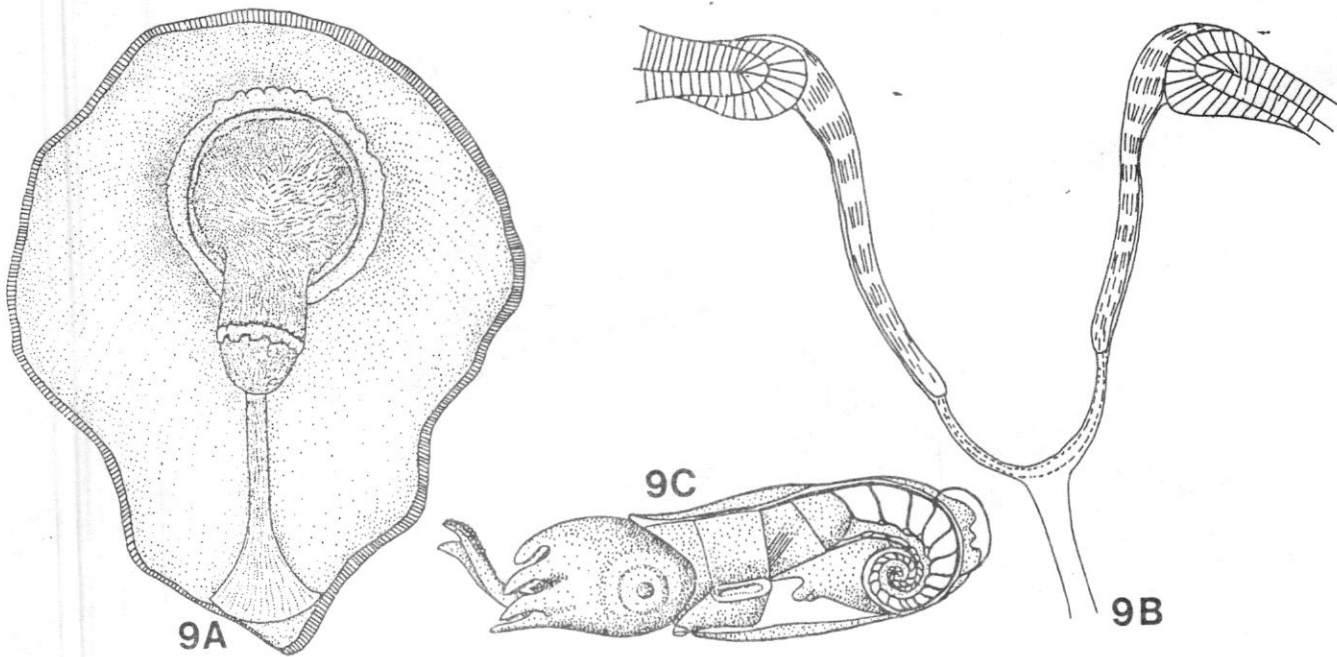


Fig. 9: *Spirula spirula* from the Atlantic Ocean near Canary Island. A: The first chamber of the *Spirula* shell opened up, exposing the earliest part of the siphuncular tube with its wrinkled surface, and its attachment to the inner wall via the organic sheet that is roughly spatulate (from Bandel and Boletzky, 1979, Fig. 5). B: The first segment of the siphuncular tube of *Spirula* ends with an organic, porous cap. The mineralized tube is attached to the walls by a mineralized ridge (from Bandel, 1982, fig. 56). C: Sketch of *Spirula* with the main retractor muscle bundle attached to the inner surface of the "living chamber" with muscle mantle that covers the liver. Muscle mantle covers the entire shell (from Bandel 1982, Fig. 59).

grow, eventually merging laterally to form the nacreous lamellae. Because of this growth mode, the nacre has a columnar appearance in vertical cross section (Nathusius-Königsborn, 1877; Schmidt, 1923).

The smallest structural units within nacre tablets measure 0.1 to 0.2 microns in diameter. These can be seen on the growing faces of the nacre tablets, but they are made visible in mature nacre only by etching (Bandel, 1977). Typical nacreous tablets are tabular and hexagonal in outline; they are known from nautiloids, ammonoids and from the outer walls of the phragmocone of belemnoids. Mutvei (1970, 1972) described the nacreous microstructure of *Nautilus* and other molluscs as consisting of small crystalline subunits. Bandel (1977) showed that the smallest components of mature nacre are round or irregular rod-like elements, which are particularly visible on the sides of growing nacre tablets. These elements combine to form tablets which are optically monocrystalline. The nacre tablets described by Mutvei (1972a) from the septum and siphuncular tube of *Nautilus* have a highly variable intracrystalline structure. This variation is particularly great in the transition from septal neck nacre to the organic siphuncular tube. Mutvei (1972a) distinguished five forms of transitional nacre in this part of the shell. Here the basic structural units are readily visible and their units assume arrangements which approach some prismatic structures. In later phases of deposition, the nacre

tablets lose their lamellar arrangement and they grade into well-developed spherulitic prismatic structure. Similar transitions between nacre and prismatic structure were noted as early as 1877 by Nathusius-Königsborn, who called such layers "prismatic nacre". Similar transitions from nacre to prismatic structure are known from many mollusks, especially in hollow spines and blisters and in shell repair structures.

In the hollow spines of the gastropod *Guildfordia*, pillars of columnar nacre extend into the space of the spine. These nacreous pillars show increasingly coarse aragonite crystals in their immature, uppermost part (Figure 10). Lamellation continues through neighbouring pillars, and the lamellae are strictly parallel to each other. During their growth the pillars are surrounded by liquids rich in calcium carbonate, and each nacre tablet grows independently of the neighboring tablets within the same nacreous lamella. According to the 'compartment theory' of Erben (1974), the union of these tablets to form continuous nacreous lamellae is evidence for the presence of membranes surrounding and defining each horizontal lamella. However, Bandel (1977) suggested that horizontally expansive lamellae of gelatinous matter, successively secreted by the epithelium, may comprise the medium in which the nacre platelets form. The chemical composition and the consistency of these gelatinous lamellae were believed to determine the composition and structure of the forming tablets. Bandel and Boletzky (1979) observed

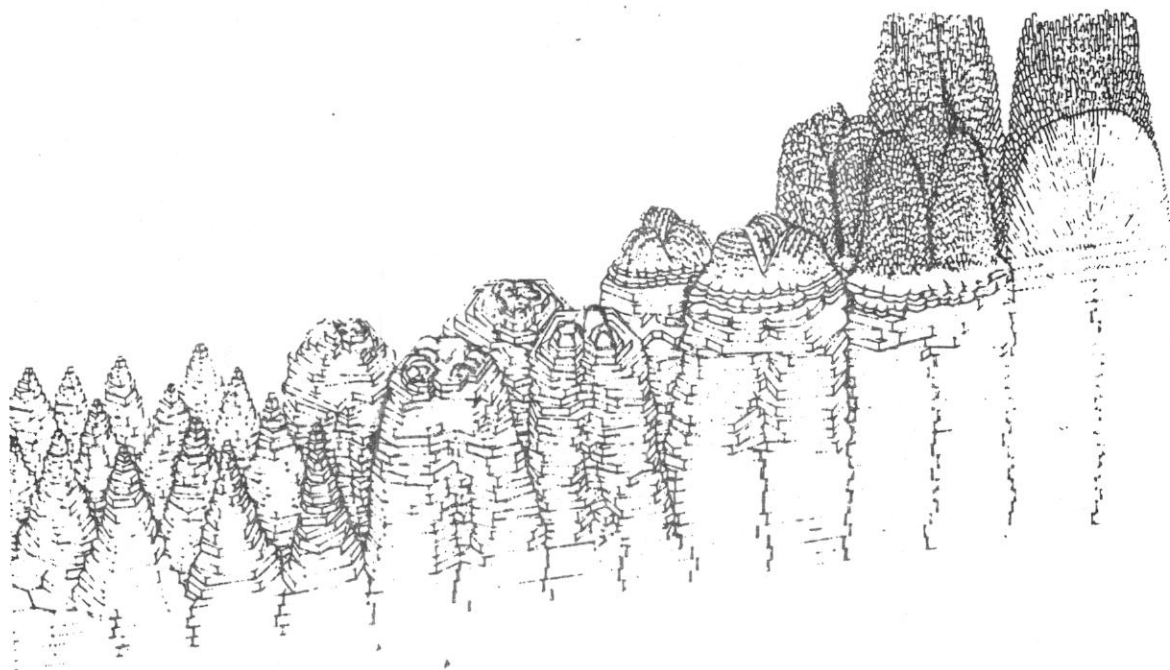


Fig. 10. Diagrammatic drawing of the succession of layers during growth on the inner surface of the shell as may be found within hollow spines, repair sections or blisters in molluscan shell with nacreous structure. At the left columns of nacre plates are oriented as single entities. At the left center three columns are intergrown with each other, and on their upper surface the growth of intermediate lamellae has started. At the right center, columns grow at their top as spherulite sectors, while on their flanks transitional plates and, further down, mature nacre are formed simultaneously. At the right, growth of spherulite sectors can be seen. From Bandel (1977, Fig. 1).

lamellar fillings of newly formed chamber sections in shells of embryonic *Sepia* (Figure 11) which confirm Bandel's (1977) interpretation.

B. Lamello-fibrillar Structure.

Mutvei (1972a) described "type 2 nacre" developed especially in the calcified septal necks of *Nautilus*. As in true ("type 1") lamellar nacre, the basic structural units here consist of granules 0.2 to 0.3 microns in maximum diameter. But in contrast to true nacreous structure, these granules are organized into dendritic crystallites or rods which comprise



Fig. 11. Schematic representation of the chamber contents of embryonic *Sepia officinalis*, with chamber liquid in a gelatinous state and exhibiting periodic striations which match the annulation of its pillars. The annulations are preserved below an organic membrane. Similar fine gel layers are responsible for the ordered growth of nacre in columnar nacreous structure. From Bandel and Boletzky (1979, Fig. 12).

lamellae rather than tablets with distinct margins. It is conceivable that this lamellar structure in *Nautilus*, as well as the structurally similar lamello-fibrillar structure of *Spirula*, are derived from nacreous structure.

Except for the first chamber, the outer shell wall of *Spirula* consists of three layers. The dorsal part of the outer layer ("ol" in Figure 12) has a nodular sculpture, and it may or may not be continuous. The ventral part of the outer layer is continuous and it consists of prismatic to spherulitic needle-like crystallites added to the shell by the muscular mantle. The main portion of the shell wall is represented by the middle or central layer ("cl" in Figure 12). In polished sections viewed under the light microscope, this appears to consist of a prismatic structure with many parallel organic lamellae crossing the prisms parallel to the inner and outer surface of the shell (Mutvei, 1964; Bandel and Boletzky, 1979). However, SEM of fractures through this layer reveal a fabric of small, granular to brick-like crystallites not arranged in vertical needles, but slightly irregularly arranged in lamellae lying parallel to the depositional surface (Bandel and Boletzky, 1979). The individual crystallites are about 0.4 microns long and 0.2 microns high and they are always enveloped by organic shell material. The lamellae of this lamello-fibrillar structure may consist of needle-like elements lying parallel to each other, of dendritic crystallites with bifurcating branches, of rods parallel or perpendicular to the plane of lamellation, and of very small, irregular units.

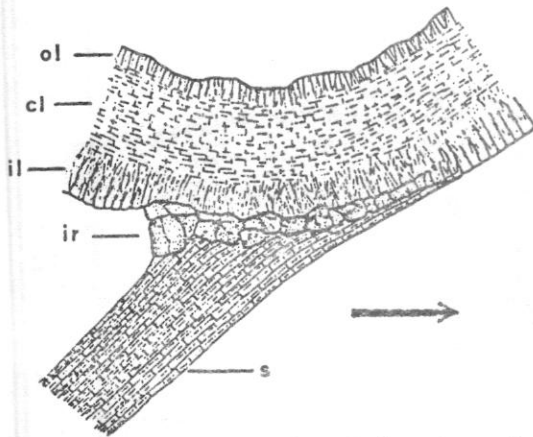


Fig. 12. Longitudinal section through the outer wall of the *Spirula* shell, at the insertion of the septum (s) on the coarsely prismatic inner rim (ir). The outer shell wall consists of an outer, irregularly prismatic layer (ol), a central lamello-fibrillar layer (cl), and an inner prismatic layer (il). The arrow points toward the aperture. From Bandel and Boletzky (1979, fig. 6).

All these components show the same rod-like basic structural units with dimensions between 0.1 and 0.3 microns. This middle layer forms more than half of the thickness of the outer shell wall. The lamello-fibrillar layer grades inward into an inner prismatic layer ("il" in Figure 12) with

somewhat variable thickness. This change is characterized by a rearrangement of the crystallites into vertical needles which increase in width toward the inner surface of the chamber. In tangential sections, these needles appear as a polygonal network (Mutvei, 1964).

The cuttlebone of *Sepia* consists of a number of organic and mineralized layers. The central layer ("cl" in Figure 13) appears earliest during embryonic development. When it mineralizes, its lateral portions remain purely organic, but its medial and ventral portions become thickened with calcareous material intercalated and interlocked with organic laminae. Thus the calcified part of the central layer is much thicker above the chambers than near the shell margins. Below this central layer, the inner layer ("il" in Figure 13) shows a lamellar structure, with the lamellae forming a low angle with the plane of the central layer. These lamellae are about 1 micron thick and they do not branch, but they decrease in thickness near the purely organic lateral zone. Each lamella within the inner layer consists of rod-like elements which are usually optically identically oriented within each layer. This optic orientation may change between different lamellae. Sometimes the needle-like crystallites which comprise the lamellae show feather-like arrangements, or they may be gently curved or branched. No distinct organic sheets appear between the lamellae, but the organic and mineralized shell materials are interlocked with one another, thus forming a composite shell deposit. Due to its high organic content, this lamellar layer in fossil sepiids like *Vasseuria* and *Spirulirostra* is commonly obliterated by boring fungi.

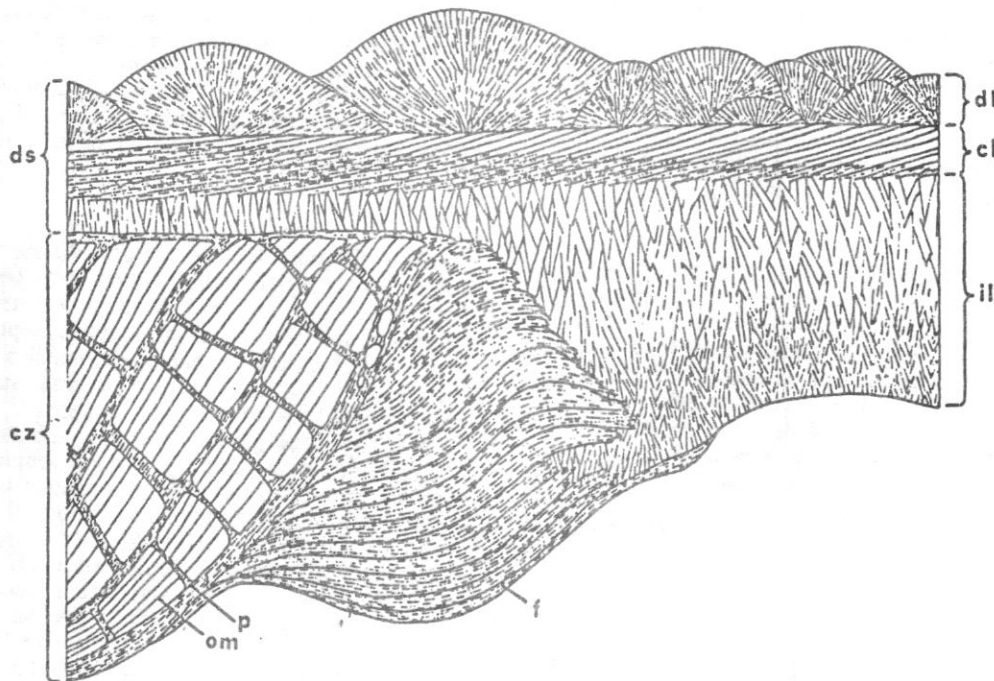


Fig. 13. Cross section through the posterior part of the *Sepia* shell, showing the insertion of the chamber zone (cz) on the lower side of the dorsal shield (ds), the latter comprising three layers: the dorsal layer (dl), the central layer (cl), and the inner layer (il). Between the marginal part of the inner layer and the chamber zone lies the fork (f). Within the chambers, organic membranes (om) are suspended between the pillars (p). From Bandel and Boletzky (1979, Fig. 2).

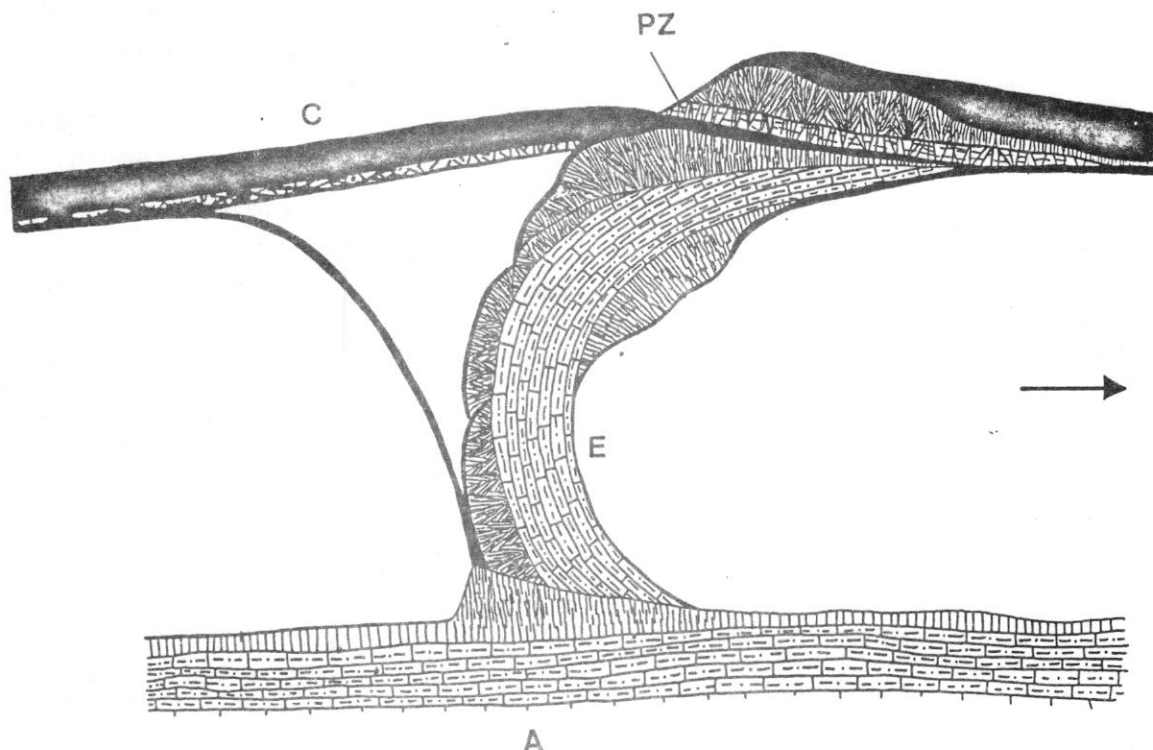


Fig. 14. Longitudinal section through the ventral half of the siphuncular tube of *Quenstedtioceras*. The arrow points toward the aperture. The horny tube (C) is attached to the first septal layers as well as to the "mural ridge" on one side of the chamber and to the septum surface and the inner side of the tube segment on the other side of the chamber. Tube attachments are represented by prismatic zones and cushions (PZ). A new chamber is initiated by the growth of organic pellicles and their attachment to the inner side of the septal neck (E), followed by rapid mineralization of the pellicles in marginal-septum positions on the outer wall (A). From Bandel (1981, Fig. 7).

Lamello-fibrillar structure differs from the crossed lamellar structure of gastropods in having more organic matrix, *i.e.*, containing as much organic material as nacreous structure (Bandel, 1979, 1989). Also like nacreous structure, lamello-fibrillar structure forms in gel lamellae (Bandel and Boletzky, 1979), with the laminae growing within a mucus layer covering the growth surface. Lowenstam (1981) indicated that "The shell wall and septa are formed by the organic matrix mediated mineralization process." However, he did not necessarily mean to imply that a mucus layer controlled crystal nucleation and growth, but rather that some epitaxial mechanism was active.

C. Septal Structures.

Septum formation in ammonites is believed to have been initiated by withdrawal of the visceral mass from the last septum to a new position, where it became attached to the walls of the living chamber just anterior to the newly forming septum. As soon as this new attachment was completed, the retractor muscle was detached, moved to a more anterior position, and there rapidly reattached. The initial septum deposits consist of an elastic organic sheet anchored to the shell walls and to the siphuncular tube by prismatic ramps

and ridges (Figure 14; Bandel, 1981). As soon as the organic septum was completed, the visceral mass became detached once again and assumed a slightly different position, deforming and stretching the organic septum somewhat. Initial crystallization of aragonitic needles (the prismatic layer) usually occurred rapidly, whereas nacre deposition continued until the septum was completed. Usually a thin prismatic layer was formed upon completion of the septum.

Ammonite septa from the second septum onwards and nautiloid septa from first septum onwards consist primarily of nacreous structure. Mutvei (1964) noted that the first septa in belemnites are composed of *Spirula*-type "nacre", *i.e.* lamello-fibrillar structure. This was confirmed by Bandel (1982), Bandel *et al.* (1984) and Bandel and Kulicki (1988). Aulacoceratids also utilized lamello-fibrillar structure for the construction of their septa, but they, like belemnites, used normal nacre for the outer wall of their phragmocone (Bandel, 1985). The shell wall of the aulacoceratid *Dictyoconites* consists of three layers: the outer layer is a thin sheet of crossed prismatic to spherulitic structure, the middle layer is nacreous, and the inner layer is blocky prismatic.

Sepiids like modern *Sepia* and *Spirula* and the fossil *Vasseuria*, *Belosepia*, and *Spirulirostra* utilize only lamello-fibrillar structure in their conch and septal walls. In *Sepia*

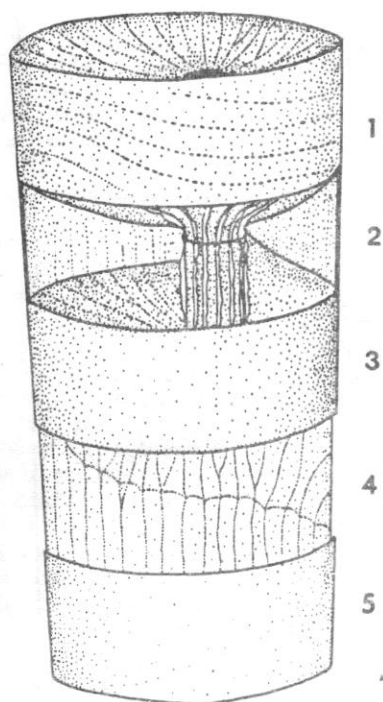


Fig. 15. Reconstructed section of the conch of Devonian *Arthrophyllum*. The first chamber (1) shows lines of growth on the shell surface. The second chamber (2) is opened and the thin sheets of its interior are removed to show the siphuncular tube with its ventral attachment membrane. The third chamber (3) has an outer wall, which in the fourth chamber (4) is omitted to show sheet attachment to the inner side of the wall. The fifth chamber (5) lies closest to the apex of the orthoceratid shell. From Bandel and Stanley (1989, Fig. 1).

the chambers are very much spread out and the septae are supported by numerous pillars and meandering walls ("cz" in Figure 13). Bandel and Boletzky (1979) observed that their growth is mediated by stratified gelatinous layers. Round pillars are initially set on the solid, mineralized ventral side of the embryonic shell. Pillars grow only by apposition of aragonite in the lamello-fibrillar structure on their tops, whereas farther towards the base, they do not increase in thickness. Between these pillars the chamber roof is usually covered by thin organic sheets which may also extend vertically between the pillars. Similar organic sheets suspended within the chamber are found in quite unrelated cephalopods with mineralized phragmocones, e.g. in the nautiloid *Lituites* (Bandel, personal observation), in the orthoceratid *Arthrophyllum* (Bandel and Stanley, 1988) (Figure 15), and in various ammonites (Schindewolf, 1967; Weitschat and Bandel, in press).

In *Sepia*, after the chamber pillars have grown to a length of 15 to 30 microns, an additional organic sheet is extended horizontally between the pillars so that each chamber has several horizontal organic lamellae between its bounding septal walls ("om" in Figure 13). When viewed from the ventral side of the shell, this sheet may cover most of the

chamber except marginally. In the first chamber of *Sepia officinalis* as well as in *S. pharaonis*, 4 to 7 organic sheets may be formed in the central part of the chamber. The actual septum is then secreted as a well-mineralized layer of lamello-fibrillar structure. This same structure also composes the pillars.

D. Siphuncular Tube Structures.

The siphuncular tube is produced by mantle cells derived from the cover of the visceral mass, of which the living siphuncular cord is an extension. Like all mantle cells, these siphuncular cells produce organic and mineralized secretions. They can also dissolve shell and deposit organic and mineralized substances within the siphuncle as endosiphuncular deposits. In addition, these cells are capable of pumping salts from their surrounding liquid and secreting liquid with salts into the siphuncular space. These liquids and salts can seep into the shell chambers and thus indirectly induce cameral deposit formation, sometimes at substantial distance from the living cells.

The siphuncular tube of *Nautilus* is the unmineralized continuation of the nacreous layer of the septum (Appellöf, 1893; Mutvei, 1972a). Each tube segment has a porous zone just before it terminates at the immediate apical septal neck (Bandel and Boletzky, 1979) ("ss" in Figure 16). Living tissue is attached in the siphuncular tubes only in the septal necks (Bandel and Spaeth, 1984). Blood vessels serve each tube segment separately, and they connect the liquid-collecting channels of the mantle pumping layer to the central siphon vessel. Liquid within the shell chamber connects with liquid in the 'pillar zone' of the siphuncular tube by means of a 'wick' which covers the internal chamber walls ("cl" in Figure 16). The 'pillar zone' is a zone of loosely meshed acicular crystallites adjacent to the porous zone of the siphuncular tube ("pz" in Figure 16).

The chalky siphuncular tube (spherulitic prismatic layer of Mutvei, 1972a), in addition to acting as a wick, also serves as a small reservoir of liquid close to the siphuncular epithelium. The chalky layer covers the exterior of the tube in its more anterior parts. Where the tube enters the aperture of the next older septum, it contacts a zone of pillars that are clearly separated by interstices. The single organic sheets which compose the horny siphuncular tube are calcified close to their apical end within the septal neck of the next older septum ("ir" in Figure 16). Here they are solidly fused with the inner side of the septal neck by a mineral ring composed of aragonitic spherulitic prismatic crystallites. The horny tube splits into thin organic sheets before it reaches the non-porous calcareous attachment ridge ("ss" in Figure 16). This part of the organic tube has interspersed irregular prismatic crystals like those present throughout the chalky layer of the siphuncular tube. However, the spongy structure of this zone is more porous and permeable than other portions of the siphuncular tube. In the pillar zone inside the septal neck, widely spaced pillars contact the spongy end of the siphuncular tube in the anterior adjacent chamber.

In comparison with *Nautilus*, the siphuncular tube of *Spirula* has a much more extended pillar zone ("pz" in Figure 17). Here the septa are similarly continuous with the siphuncular tube, but the siphuncular tube remains mineralized with lamello-fibrillar structure throughout the chamber ("sn" in Figure 17). The outer portion of the

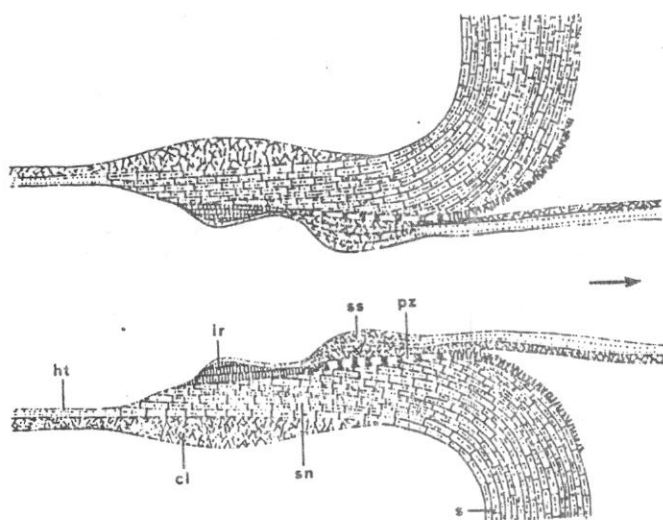


Fig. 16. Longitudinal section of the siphuncular tube of *Nautilus pompilius*. The arrow points toward the aperture. The nacreous layers of the septum (s) continue into the septal neck (sn), the organic parts of which are continuous with the horny tube (ht). The septal neck and the horny tube are covered by the chalky layer (cl) which is a porous structure consisting of needle aggregates and organic sheets. The apical end of each section of the siphuncular tube is firmly attached to the inner side of the septal neck by a solid inner ridge (ir). In front of this lies a porous spongy structure (ss) made of many discontinuous organic membranes interspersed with elements of the chalky layer. The spongy structure brings the liquid contained in the pillar zone (pz) into contact with the siphuncular tissue. From Bandel and Boletzky, 1979, Fig. 21).

siphuncular tube passes into organic sheets, the more exterior of which in newly formed chambers closes the entrance to the space in which the siphuncular pillars lie. The central portion of the siphuncular tube is continued by a zone of pillars covering the inner surface of the siphuncular tube. The more anterior pillars cover the concave surface of the septum where it meets the septal neck. The pillar zone terminates with the formation of the posterior part of a new siphuncular tube. Organic sheets extend between the pillars only in the apertural part of the pillar zone ("o" in Figure 17). Here the pillars form solid biconical structures with terrace-like annulations, each of which represents the continuation of one lamella of the anterior part of the siphuncular tube. In this position the pillar bases are fused with each other. Farther from the aperture, the pillars are more columnar in shape and they are separated by wider spaces. Pillars have straight sides on which 50 to 60 lamellar layers can be counted. Each of these lamella is continuous with a layer within the lamello-fibrillar structure of the central part of the anterior siphuncular tube ("cc" in Figure 17). The lamello-fibrillar structure of the pillars is similar to that in the central layer of *Spirula's* phragmocone wall, and consists of short needle or brick-shaped crystallites arranged perpendicular to the pillar axis. The ends of the pillars, with their radiating crystals and crystal aggregates, form a porous, interlocking

system in which numerous thin organic sheets are transversely suspended. This porous layer is covered by a smooth thick organic sheet which is the organic continuation of the inner part of the lamello-fibrillar layer of the anterior siphuncular tube. Transition from the mineralized anterior portion of the posterior organic portion of this tube is quite abrupt. The organic tube lies in contact with the living tissue of the siphuncle.

A section through *Spirula's* double-walled siphuncular tube thus shows four layers; an outer lamello-fibrillar layer, a pillar layer, a layer of interlocking needle aggregates at the internal ends of the pillars, and an inner organic layer.

Denton (1974) figured the siphuncular tube of the endoceratoid *Dideroceras*. In this animal, the mineralized portion of the siphuncular tube extends into the previously formed siphuncular tube, passing halfway into the next older chamber. In this case the permeable zone would be confined to the small region lying between the septal neck and the mineralized tube, very much as in Recent *Spirula*. In the aulococeratid *Dictyoconites* the siphuncular tube is in part double-walled and is structurally similar to that of *Spirula* (Bandel, 1985) (Figure 18; 1: nacre, 2: mineralized tube, 3: pillar zone, 4: organic tube). Similar siphuncular constructions have been reported by Fischer (1951) for a Triassic belemnoid. Miocene *Aturia* produced a double-walled siphuncular tube with an outer nacreous portion which extends the septal neck and crosses one chamber, plus an extensive wick-like inner portion which contacted the decoupled chamber liquid (Ward, 1987, Figs. 7, 18).

V. Mineralization Exterior to the Shell Walls.

A. Rostrum Function.

Modern endocochleate cephalopods have terminal or sub-terminal fins (Naef, 1928). This was certainly also the case in fossil endocochleates. Fins are anchored either directly to the shell sac or to the mantle surface, and their bases are stiffened by a cartilaginous plate. Guard and guard-like structures, whether entirely organic or mineralized, reflect the intimate junction between cartilaginous fin bases and the surface of the shell sac (Bandel and Boletzky, 1988). However, the absence of guard-like structures does not indicate a lack of fins, but rather a less massive development of fin cartilage attached to the shell sac, or even detachment of the fin cartilage from the shell sac by the formation of articulated pouches.

The application of these ideas to the Lower Devonian *Protoaulacoceras* (Bandel *et al.*, 1983) suggests that its fins were attached to a relatively long, flattened ridge on either side of the phragmocone. In belemnites, the fins are inserted behind the phragmocone, and they probably formed a closed cartilaginous tube around the guard, with fin attachment ridges resting in the longitudinal guard depressions, possibly to reduce shear stress. If this picture is realistic, the presence of a rather large phragmocone can be regarded as a buoyancy element maintained to counteract the considerable weight of the guard, rather than a passive counterweight developed in response to the tilting effect of a terminal phragmocone (Figure 19). The wide variety of guard shapes manifested in belemnite evolution may then be explained by differences in life style and swimming performance. Bandel and Boletzky (1988) considered that a massive terminal guard reflects the

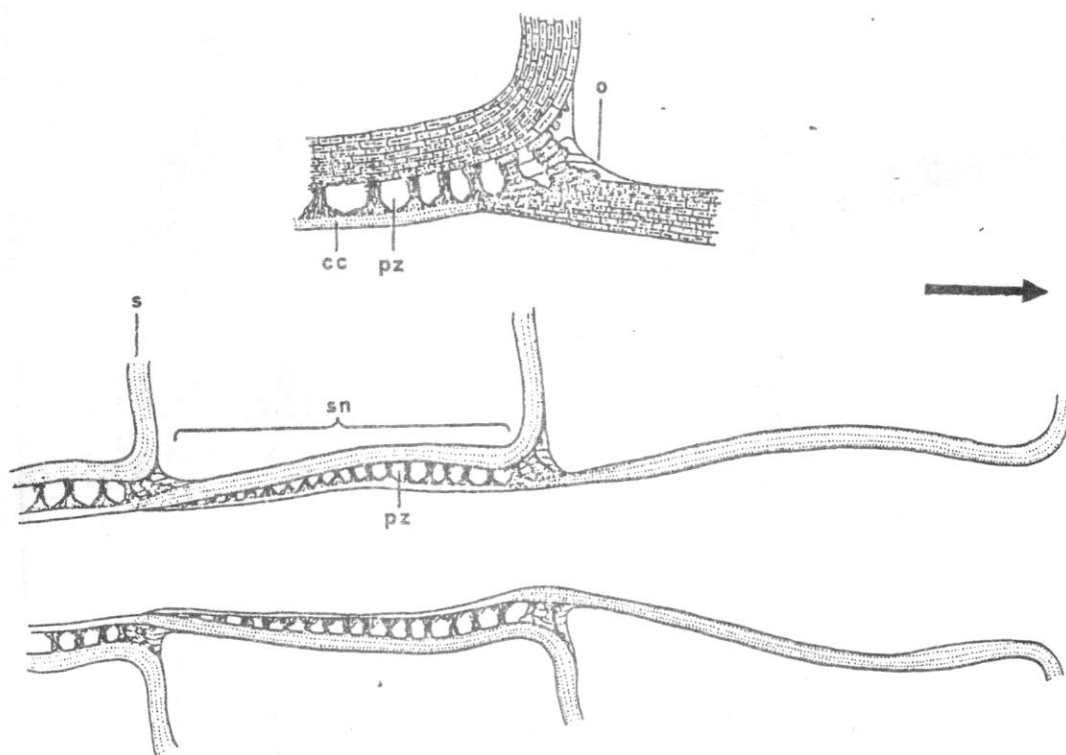


Fig. 17. Horizontal section through the siphuncular zone of *Spirula*. The layers of the septum (s) continue into the siphuncular tube. At the entrance to the septal neck of the next older septum, the lamellar layers split into organic sheets (o) that close up the pillar zone (pz). Here organic sheets and pillars of the entrance, pillars of the middle pillar zone that rest solidly on the mineral neck, and finally the organic and crystal cover (cc) of the pillar zone compose the tube. The arrow points toward the aperture. From Bandel and Boletzky (1979, Fig. 7).

presence of powerful terminal fins similar to Recent ommatostrephids. The presence of such guards in different groups, like some aulacocerids and many belemnites, can be explained by evolutionary convergence.

B. Aulacoceratid Rostra.

The rostrum of aulacoceratids such as *Dictyoconites* consists of a basal layer and overlying layers which differ in morphology and construction, but which are all aragonitic. The earliest formed basal layer covers most or all of the conch and consists of thin, sharp longitudinal ribs separated by flat interspaces. These ribs form on the growing conch of the juvenile just hatched from the egg and supplied with only a simple, short cone-like primordial rostrum. This slender juvenile rostrum initially consists of stacked, pointed cones attached to the extreme apical end of the phragmocone (Figure 20). With further growth, this rostral layer encroaches onto the phragmocone and its basal layer. The early, needle-like rostrum consists of intercalated organic and mineral layers, whereas the later, more massive rostrum is mainly calcareous. The rostrum of *Dictyoconites* was originally composed of aragonite (Bandel, 1985). The same is also true of its close relative *Austroteuthis* (Jeletzky and Zapfe, 1967).

The dorsal and ventral surfaces of the adult rostrum of *Dictyoconites* are wrinkled by three sets of ornamentation which represent imprints of the blood system of the muscular mantle. Similar features also occur on the rostral surfaces of the belemnites *Belemnitella* and *Gonioteuthis*.

C. Belemnite Rostra.

The primordial rostrum in belemnites was deposited on top of the first spherical chamber of the phragmocone. In the Middle Jurassic *Hibolithes*, the primordial rostrum of the embryonic or early juvenile consists of two portions, a lower aragonitic one and an upper (more apical) organic one (Figure 8). The organic layers grade laterally into the mineralized layers. Interruptions in the growth of regular prisms in the most apical portions of this primordial rostrum result in spherulitic growth of needles. All other aragonitic needles comprising the primordial rostrum are simple and arranged perpendicular to the surface of growth (Bandel *et al.*, 1984).

In most belemnites, with the exception of *Belemnoteuthis*, the primordial rostrum is overlain by a calcitic orthorostrum, i.e., the adult rostrum. This consists of concentric layers of calcitic needles. In fractured rostra the needles appear to continue with interruption from the phragmocone wall to the

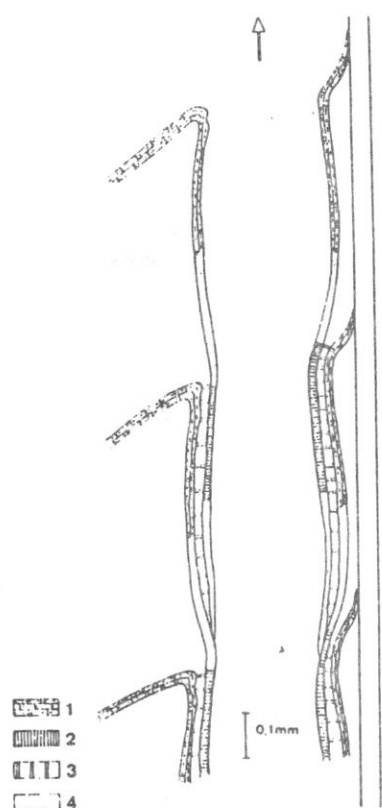


Fig. 18. Reconstruction of the siphuncular tube of the Middle Triassic aulacoceratid *Dictyoconites* from the St. Cassian Formation of the southern Alps. The longitudinal section of the tube shows that the lamello-fibrillar structure (1) of the septum continues into the long, mineral septal necks and organic tubes (4), which are attached to the inner side of the septal necks by a section of prismatic tube (2). Both walls of the tube are held apart by the prismatic pillars of the pillar zones (3). From Bandel (1985, Fig. 10).

outer surface of the rostrum (Bandel and Kulicki, 1988). Growth lines which run perpendicular to the prismatic needles differentiate layers which originally contained varying amounts of organic material.

Rostra repaired by injured individuals consist of spherulites arranged around a central axis in such a way that they reconstructed the damaged rostrum. Several steps in repair were identified by Bandel and Kulicki (1988). In the first step, the fractured phragmocone chamber is sealed over by organic sheets and thin aragonitic crusts. The rostrum itself was then reconstructed after repair and regrowth of the apical tissue of the muscular mantle. Beginning with several spherulitic centers arranged along a medial line, aragonitic spherulites grew until they touched each other and could again be covered by a continuous layer of prismatic aragonite.

Most Jurassic and Cretaceous belemnites covered the primordial rostrum with a solid, smooth, calcitic orthorostrum which, in some cases, like in Middle Jurassic *Megateuthis*, grew to more than 60 cm in length and 6 cm in

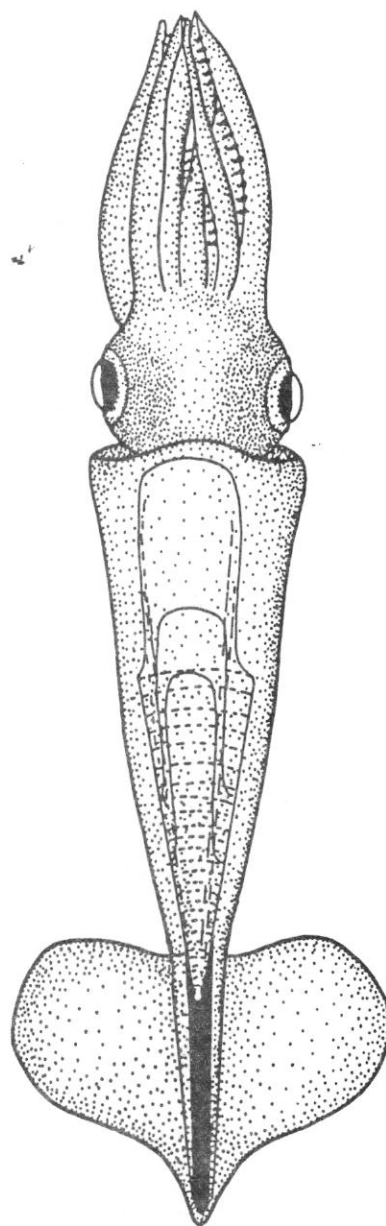


Fig. 19. Reconstruction of *Belemnites paxillosus*, a typical belemnite from the Upper Lias of southern Germany, with a shell ca 50 cm in length (total length of animal ca 70 cm). From Bandel and Boletzky (1988, Fig. 5).

width, and extended far backwards from the end of the phragmocone. In contrast, the Lower Jurassic *Nannobelus*, produced only a small, thin rostral cover over its apical phragmocone (see also Figure 21, A-C: various species of the *Belemnites acuarius* group; D: *Dactyloteuthis irregularis*; E: *Megateuthis* cf. *gigantea*; F: *Neohibolites minimus*).

The belemnite orthorostrum was originally composed of calcite, and it is generally still preserved as calcite. This

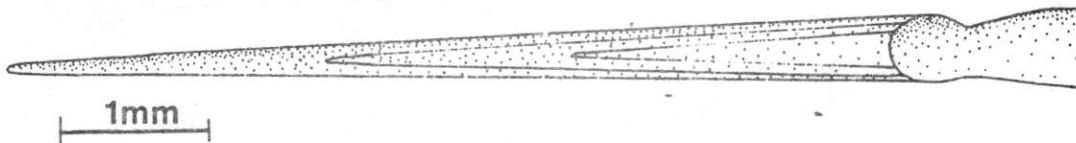


Fig. 20. Sketch of early ontogenetic rostrum of the aulacoceratid *Dictyoconites* from the Middle Triassic St. Cassian Formation. The rostrum is very slender and is attached only to the first chamber. From Bandel (1985, Fig. 24).

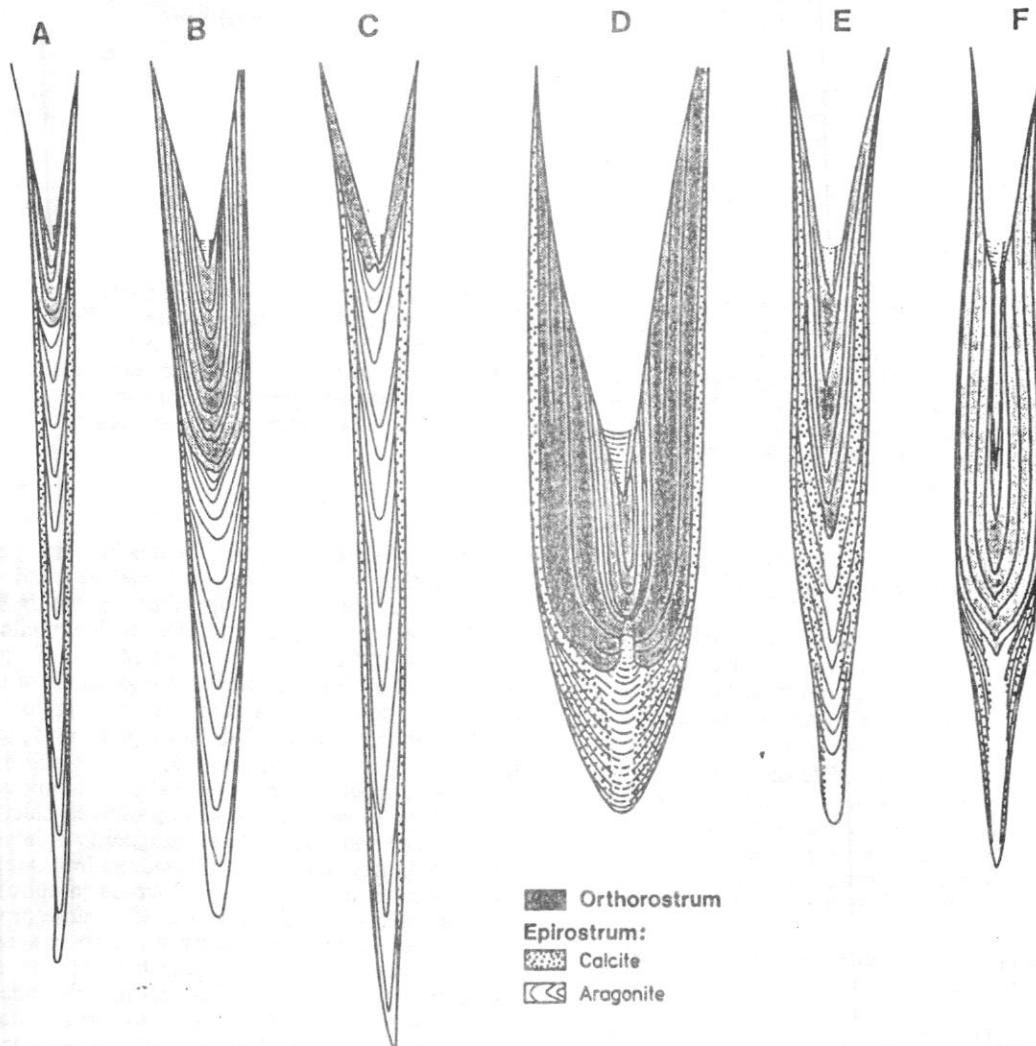


Fig. 21. A: *Belemnites acuaris longisulcata* from the Upper Lias of southern Germany, with a short orthorostrum and long aragonitic epirostrum surrounded by a calcitic cover (7 cm long). B: *Belemnites acuaris* from the Upper Lias of southern Germany, with a medium-size (5 cm long) orthorostrum connected to a slightly longer epirostrum. The calcitic cover of the aragonitic core of the epirostrum does not cover the apical portion. The aragonitic core commonly is dissolved and the rostra appear to be empty. C: *Belemnites acuaris tubularis* from the Upper Lias of southern Germany, with a thin orthorostrum and long, slender epirostrum. During diagenesis, the aragonitic core of the epirostrum collapses or recrystallizes as blocky calcite. D: *Dactyloteuthis irregularis* from Upper Lias of southern Germany has a thumb-like orthorostrum, an even broader transitional rostrum, and a short epirostrum. E: *Megateuthis* cf. *gigantea* (Middle Jurassic, northern Germany) has a 36-cm-long rostrum consisting of a purely calcitic orthorostrum and an epirostrum that is aragonitic only near its core. F: *Neohibolites minimus* (Middle Cretaceous, Northern Germany) has a short epirostrum (total length of rostrum 4 cm). From Bandel and Spaeth (1988, Fig. 1).

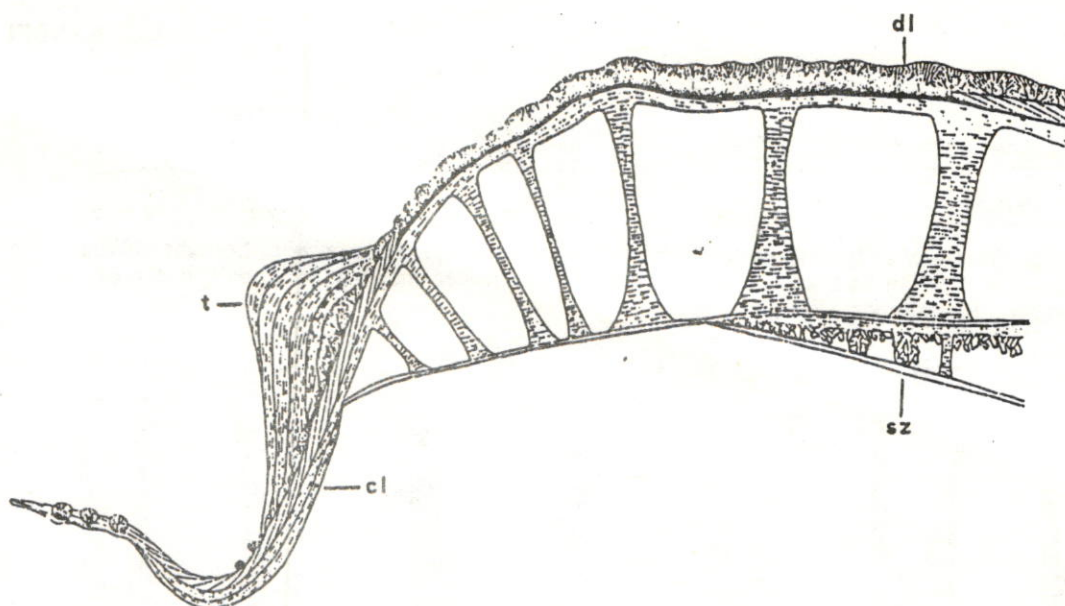


Fig. 22. Longitudinal section through the cuttlebone of the embryo of *Sepia pharaonis* from the Red Sea. Five chambers are completed and the spine (s) is present with lamellar structure. The prismatic dorsal layer (dl) forms spherulitic aggregates near the posterior rim of the shell. The central layer (cl) that is purely organic in the region of the early embryonic shell later becomes partly mineralized. In the siphuncular zone (sz) of the second chamber, the space between the pillars is partly filled with aragonitic crystals that show an inorganic type of crystal growth. From Bandel and Boletzky 1979, Fig. 14).

original mineralogy is preserved in the case of the Middle Jurassic *Hibolithes* from Lithuania (Bandel *et al.*, 1984) and recrystallization changed it very little (Dullo and Bandel, 1988). Spaeth (1971, 1975) demonstrated that much of the internal lamellar portion of the orthorostrum was unmineralized. Veizer (1974) analyzed biochemical data on belemnite rostra and interpreted their original mineralogy as low-Mg calcite, with at least 10% organic material or porosity. There is no indication that Kabanov's (1967) idea, corroborated by Dauphin (1984), is correct, that the orthorostra of all belemnites were composed of primary aragonite and that their calcite is only diagenetic. Well-preserved belemnite rostra certainly would not be as common as they are in Jurassic and Cretaceous strata if this hypothesis were correct.

The prismatic calcite in belemnite rostra was secreted in smooth layers which exactly reflected the original, smooth growth surface. Organic layers were concentrated at growth surfaces which show few or no calcitic prisms. In many belemnites, the completed calcitic rostrum (orthorostrum) was covered by an additional rostrum (epirostrum) which commonly differed in morphology, structure, and mineralogy. The epistrostrum consisted mainly of aragonite which, through diagenesis, is now commonly transformed into calcite or is dissolved, leaving a cavity filled with sediment or cement (Bandel and Spaeth, 1988). The calcium carbonate of the epistrostrum differs in both crystal structure and crystal arrangement from the calcitic rostrum. Whereas the calcitic orthorostrum grows in fine prismatic layers with parallel crystal needles, the aragonite of the epistrostrum is commonly

arranged in spherulite sectors. In the Toarcian belemnites *Salpingoteuthis*, *Youngibelus*, *Acrocoelites*, and *Dactylotheuthis*, and in the Albian *Neohibolites*, the bulk of the epistrostrum was aragonitic with exterior longitudinal ridges and furrows reflecting the construction of spherulitic prismatic growth ridges parallel to the long axis of the guard. Belemnites generally cover their aragonitic epistrostrum with an exterior calcitic layer. This layer gives evidence for the completion of the epistrostrum, and it may not have been formed in all species with an epistrostrum. Many belemnites from the Lias show a step on the preserved calcitic orthorostrum which indicates that an aragonitic epistrostrum was present but is not preserved. Transitions from aragonitic to calcitic lamellae are commonly observed in epistrostra, indicating that calcite was being deposited in close proximity to aragonite. A similar rapid transition from aragonitic into calcitic structures is also responsible for the so called 'pseudalveola' in the Upper Cretaceous belemnites *Actinocamax*, *Goniotheuthis*, and *Belemnelloccamax* (Bandel and Spaeth, 1988). The angular apertural cavity of the 'pseudalveola' is a product of postmortem dissolution of the aragonitic phragmocone and the aragonitic apertural portion of the rostrum.

D. Rostrum Homologs in the Sepiid Cuttlebone, etc.

In *Sepia*'s cuttlebone the formation of the dorsal layer beings rather late in embryonic development (Bandel and Boletzky, 1979). In *Sepia officinalis*, this layer first appears in the form of an irregular crystal cover on the organic outer

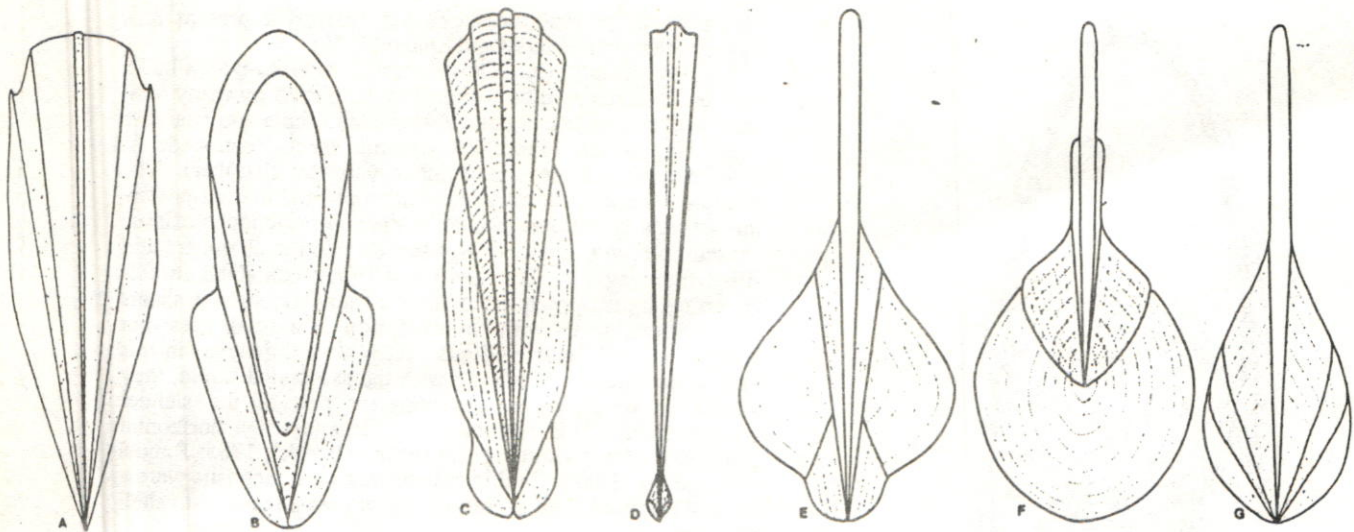


Fig. 23. Gladii of Jurassic "vampyromorph" squids. A: *Lorigosepia aalensis* from the upper Lias. B: *Trachyteuthis hastiformis* with a calcareous cover on the dorsal shield; upper Malm. C: *Leptoteuthis gigas* from the upper Malm. E: *Celaenoteuthis* sp. from the upper Malm. F: *Celaenoteuthis scutellaris* from the upper Malm. G: *Palaeololigo oblonga* from the upper Malm. Note the various forms of central and lateral fields and the more or less distinct "conus fields".

surface of the shell ("dl" in Figure 22). In *Sepia pharaonis*, the dorsal layer initially consists of nodular spherulitic structures, but with further growth spherulite sectors form on this dorsal side of the central organic layer. The dorsal layer grows over the surface of the wide central organic layer through the formation of ridge- or bump-like spherulitic structures surrounded by organic material, or with the formation of a zone of irregular fine crystal growth. This may differ among individuals as well as between growth stages of an individual.

The Jurassic vampyromorphid *Trachyteuthis* shows similar dorsal calcification. In this genus spherulitic aragonite deposited on the dorsal surface of the gladius resembles that of modern *Sepia* (Bandel and Leich, 1986). Although this squid lacks a chambered shell, the general shape of its gladius and the morphology of its fins (Figure 1) were similar to modern *Sepia* (see also Figure 23, A: *Lorigosepia*, B: *Trachyteuthis*, C: *Leptoteuthis*, D: *Plesiotheuthis*, E, F: *Celaenoteuthis*, G: *Palaeololigo*).

Returning to *Sepia* (Figure 24), the dorsal layer may be absent near the spine on the posterior part of the cuttlebone, as in *Sepia officinalis*; it may surround the spine, as in *S. orbignyana*; or it may be represented by a very thin crystal cover on the ridge which represents the spine in *S. elegans*. Structurally, this posterior spine must be regarded as part of the central layer, although it generally begins to form on the embryonic dorsal layer. The shells of *Sepia orbignyana* and *S. pharaonis* have strongly calcified, solid spines. From the margins toward the center of the spine, lamellae become continuously thicker and show an increasing amount of calcareous material. Thus the spines consist of conical layers piled upon one another. Each of these conical layers is thickest at its center and is continuous with a purely organic layer at the side of the spine. The spine itself is a purely

lamellar structure ("t" in Figure 22), whereas it is surrounded by organic continuations of its lamellae which interdigitate with calcified material of the dorsal layer.

VI. Shell Deposits within the Chambers and Siphuncular Tube.

A. Intracameral Deposits.

Intracameral deposits commonly occur in the phragmocone of fossil cephalopods, but they are unknown in *Nautilus*, *Spirula* and *Sepia*. These deposits are sometimes difficult to interpret with regard to their time of formation, and some may represent *post mortem* cementation.

The following examples illustrate the different functions and structures in cameral deposits in three fossil species which certainly formed these during their lifetime.

The phragmocone of the Middle Jurassic belemnite *Belemnoteuthis polonica* is usually free of intracameral deposits. However, intracameral deposits were formed when the animal sustained damage at the apex of its chambered shell and was obliged to repair the guard as well as the phragmocone (Bandel and Kulicki, 1988) (Figure 3). After loss of the apical chambers of the phragmocone the muscular mantle tissue healed and the terminal chambers of the phragmocone were flooded (at least 15 chambers in the studied cases). Liquid seeping into the chambers through the organic siphuncular tube came from the muscular mantle surrounding the shell as well as from the siphuncular tissue. This was apparently rich in CaCO_3 and it precipitated an aragonitic cement which coated the interior chamber walls. The siphuncular tube itself remained free of deposits, and it may later have pumped the chambers empty again after total healing of the tissue and repair of the damaged aragonitic

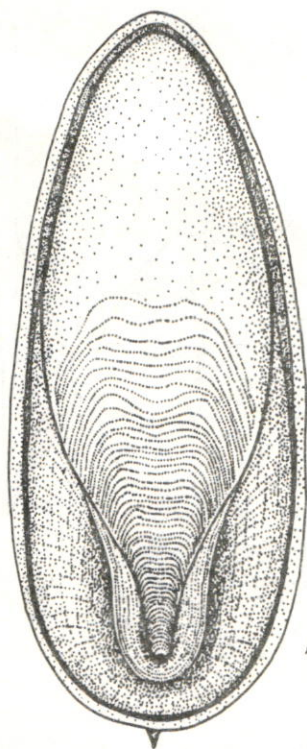


Fig. 24. Ventral view of the cuttlebone of *Sepia*, with flat chambers secreted in the depression of the dorsal shield.

guard. Near the siphuncle, the deposits are thickest; they are thinnest near the dorsal side, thus reflecting the orientation of *Belemnoteuthis* during life. Shell repair is not uncommon among belemnites but, in forms with rostra larger than *Belemnoteuthis* this usually includes only the rostrum and not the phragmocone. These large forms however, may have still reacted to shell damage by flooding of the posterior chambers of the phragmocone in order to compensate for lost posterior weight, and some may have formed cameral deposits. Cameral deposits noted by Jeletzky (1966) in many belemnite phragmocones may have originated in this manner.

However, other reported cases may merely represent *post mortem* cements (Bandel and Spaeth, 1988).

The orthoceratid (lamellorthoceratid) *Arthrophyllum* had a simple siphuncular tube which was connected by many well arranged, suspended organic sheets to the septa and chamber walls (Figure 15; Figure 25: organic sheets sectioned, A: basal chamber, B: central chamber, C: upper chamber). The chambers were apparently pumped empty and in their posterior portions later flooded again. When the siphuncular tissue ceased pumping, liquid slowly seeped into the chambers and filled them again. The Ca^{++} and CO_3^{--} contained in this returning liquid precipitated on the cameral organic sheets and chamber walls with the exception of a small area that retained a small bubble of gas. Intracameral deposits in this case were calcitic, and along with the associated liquid, they served to weigh down the posterior part of the slender conical shell. This facilitated maintenance of a horizontal position during swimming and resting (Bandel, 1985; Bandel and Stanley, 1988). In this case intracameral deposits were a normal mode of shell secretion rather than a reaction to shell damage.

In the third example aragonitic deposits were laid down during the life inside the shell chambers of Carboniferous to Upper Traissic pseudorthoceratids (Ristedt, 1971). Here prismatic spherulitic growth of aragonitic needles occurred on the inner walls of the chambers, continuously filling them. Liquid rich with calcium-carbonate must have seeped through the siphuncular tube for a long time until the posterior chambers of each phragmocone became filled with these relatively disordered chamber deposits.

B. Intrasiphuncular Deposits.

Quite a number of Paleozoic cephalopods deposited mineralized materials within their siphuncular tube. Unfortunately, the original mineralogy and structure of these deposits is still poorly known. Among modern cephalopods *Nautilus* rarely plugs its siphuncular tube with solid organic material (Bandel and Spaeth, 1984). However, this is not the usual case. Normally the siphuncle in *Nautilus* remains open and active from the first to the last chamber during the animal's entire life (Ward, 1987). Plugged siphuncles may represent a very simple solution to energy consumption of siphuncular tissue which was commonly used during the

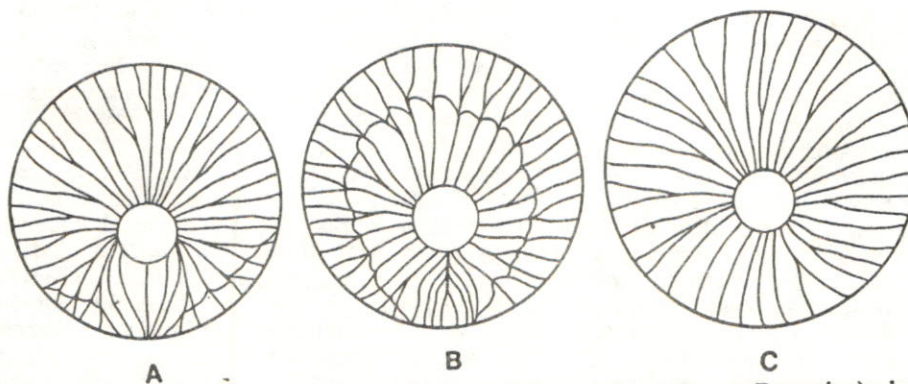


Fig. 25. Transverse sections through the chamber of *Arthrophyllum* (Lower Devonian), showing: (A) organic sheets just apertural to the previous septum, (B) organic sheets in the central position, and (C) organic sheets attaching to the lower side of the septum. From Bandel and Stanley (1989, Fig. 2).

Paleozoic. These plugs perhaps consisted of simple calcitic deposits in endoceratids and more complex ones in actinoceratids. Both examples require a much closer look before they can be adequately evaluated (see Dzik, 1984). Septae were used to close the siphuncular tube, as noted for the ellesmeroceratid *Pictetoceras* by Mutvei and Stumbr (1971).

VII. Mineralized Jaws, Brood Chambers and Statoliths.

A. Mineralized Jaws of *Nautilus* and Aptychi.

Cephalopod mandibles consist primarily of a protein-chitin complex which, in the case of *Nautilus*, is mineralized only in the exposed, oral portion of the jaws. It is not yet clear whether jaw mineralization is restricted to *Nautilus* and related genera, or whether other cephalopods developed mineralized mandibles as well (Lehmann, 1972; Tanabe, 1983; Tanabe and Fukuda, 1983; Bandel, 1988).

The aptychi of ammonites have been interpreted by Lehmann (1972) as lower jaws, although Schindewolf (1958) and Bandel (1988) prefer to reconstruct them as opercula. Aptychi consist of calcitic layers deposited over an organic base. The structure of the aptychi resembles that of the *Argonauta* brood chamber: both consist of calcitic prisms oriented perpendicular to the surface of growth. The interpretation of aptychi as lower jaws is made difficult by a non-mineralized central line, where the entire apparatus could apparently be folded. Reconstructed as opercula covering the head, the aptychi could fold and unfold periodically to permit breathing through the ventral funnel when the animal was retracted into its shell. On the other hand, Lower Jurassic ammonites such as *Arnioceras* have repeatedly been found with their upper jaw resting in the aptychus in a position resembling a lower jaw (Lehmann, 1987).

The mandibles of *Nautilus* are covered by mineral deposits only in their anterior parts near the biting edge of the jaws. A layer of spherulitic prismatic aragonite lies between the organic beak and the biting edge of the beak which consists of Mg-calcite (Lowenstam *et al.*, 1984). Crystallites in the

upper jaw are more regularly organized than those in the lower jaw, but both structures are rather coarsely textured (Tanabe and Fukuda, 1987). Personal observation of *Nautilus* beaks reveal acicular prismatic, spherulitic prismatic and spherulitic arrangements of calcite needles, in agreement with Tanabe and Fukuda (1987, Figs. 3 D-F).

B. Brood Chamber of *Argonauta*.

The shell of *Argonauta* is produced by the females as protection for the eggs, and as a refuge where the individual usually remains throughout its daily activities. Unlike normal cephalopod shells, the *Argonauta* shell is formed by a secretory epithelium situated in folds in a specialized pair of arms. These two arms extend over the posterior portion of the body when boat secretion begins, and they initially produce a cap-like first shell. This first shell is then regularly enlarged by additions to its margins (Naef, 1922).

The *Argonauta* shell is composed of three calcitic layers, the outer of which is thickest. Deposition begins with a central layer composed of fibrous organic threads into which calcitic spherulites 5 to 10 microns in diameter are dispersed. The inner and the outer layers represent continuations of the growth of the prismatic needles comprising these spherulites. With continued growth, the spherulites grade into spherulite sectors, and later into parallel needles arranged perpendicular to the surface of the shell. Fossil *Argonauta* shells from Tertiary deposits have the same structure as Recent ones (Bandel and Dullo, 1984).

C. Statoliths.

Cephalopod statocysts contain mineralized elements which, in the case of *Nautilus*, consist of numerous small spherulitic statoconia (Lowenstam *et al.*, 1984), and in modern decapods and octopods consist of a pair of statoliths with taxonomically specific shapes (Clarke, 1978). Fossil statoliths of dibranchiate cephalopods are known from Eocene strata onward. These bodies are aragonitic and spherulitic prismatic. The internal structure of the oldest statoliths reported by Clarke (1988), from the Jurassic Period, is not preserved.