Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends

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Chapter 9

Shell Structure of the Gastropoda Excluding Archaeogastropoda

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I. Introduction.

Gastropod shells consist of minute particles of calcium-carbonate intimately associated with organic material. These mineral particles are arranged in structural patterns which are indirectly rather than directly influenced by the cells of the mantle secretory epithelium. As early as 1902, Biedermann was aware of this indirect influence by the molluscan mantle on shell deposition. Bøggild (1930) described and illustrated many of the structural arrangements of mineral components in mollusc shells. Parts of his terminology are still used today, but additional terms have since been added, largely as a consequence of the introduciton of scanning electron microscopy and the easy determination of aragonite and calcite by modern X-ray techniques.

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II. Aragonitic structures.

Aragonitic crystallites occur in molluscs in two fundamentally different forms. One form consists of 0.2-micron-wide basic structural units arranged into acicular crystallites which in turn comprise crossed lamellar and a variety of related crossed, helical and prismatic structures. The other form consists of basic structural units united to form tablets and laminae in nacreous and similar structures. With few exceptions, crossed lamellar and nacreous structures do not grade into one another and they are rarely found together within a single shell.

Among gastropods, only some archaeogastropods utilize nacreous structure in their shells. All other gastropods, *i.e.*, the Neritomorpha, Heterostropha (including the Allogastropoda, Opisthobranchia and Pulmonata), Mesogastropoda (including the Taenioglossa and Ctenoglossa) and Neogastropods utilize crossed lamellar structures as their predominant aragonitic shell structure. Regarding precursors and derivates of crossed lamellar structure and similar ones of nacreous structure, a number of features are observed common to both (see section II-P).

A. Crossed Lamellar Structure.

Crossed lamellar structure was accurately diagnosed by Biedermann (1902), who noted leaf-like and plate-like first-order lamellae consisting of needles (third-order lamellae) which may be arranged into leaf-like or plate-like transverse second-order lamellae. Bøggild (1930) noted only first- and second-order lamellae. MacClintock (1967) overgeneralized that the third-order needles in aragonitic crossed lamellar structures are angular and 0.5 microns wide. The substructure of crossed lamellar layers is actually much more variable than indicated by MacClintock (1967), both in gastropods and bivalves. The structure of the basic units comprising the needles of aragonitic crossed lamellae was noted by Bandel (1979a).

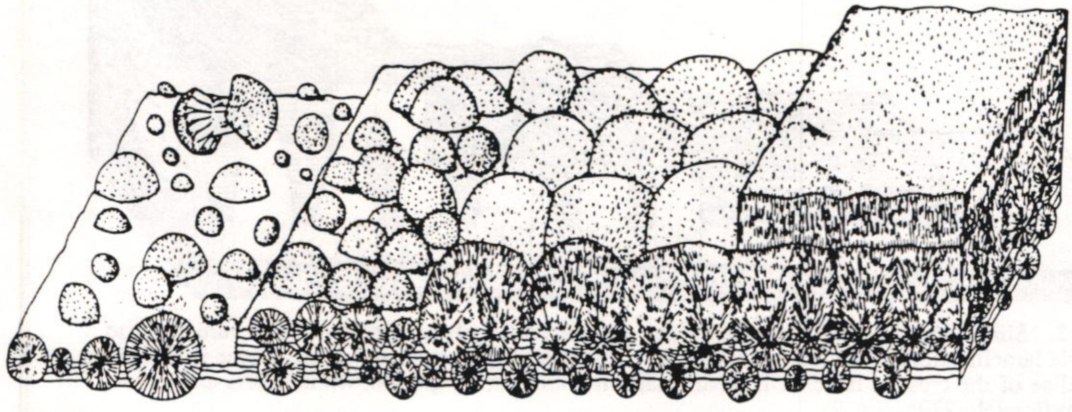

Fig. 1. Simplified drawing of the transition from spherulitic and dumbbell-like aggregates of crystallites (left side) to acicular fibrous prismatic structure. Crystallite aggregates consist of entire prismatic crystals, whereas the needles of the acicular fibrous prismatic layer are composed of basic structural units (from Bandel, 1979b, Fig. 1).

The first-order lamellae may be regular in width, as in *Charonia* and several other gastropods, or they may vary considerably in width, as in most gastropods. Second-order lamellae are usually well differentiated, but sometimes they are absent. As in simple lamellar fibrous prismatic structure, each second-order lamella consists of a single layer of needles 0.2 microns wide which are fused to each other laterally, and which have variable lengths. The third-order lamellae are needle-like and consist of 0.2-micron-wide basic elements with angular to cushion-like shapes.

B. Acicular Fibrous Prismatic Structure.

Septae formed in the apical portion of the large shell of *Charonia variegata* show a transition from acicular aragonitic crystallites 0.2 to 0.5 microns in diameter (deposited in connection with organic sheets) to crossed lamellar structure (Figures 1-2). The acicular crystallites represent the initial mineral deposits. These may unite into small aggregates in which the crystal length axes are parallel to each other, or they may grow into spherulites. The crystallite aggregates are initially interconnected by organic sheets and fibers. With later deposition, mineralization becomes denser and the crystallite aggregates grade into a more solid acicular fibrous prismatic layer in which the needle-like crystallites are mutually parallel and perpendicular to the depositional surface. In septum deposits, needle crystallites grade from forms of inorganic fabric and larger diameters into needles composed of 0.2-micron-wide basic units.

In the neogastropod *Turbinella angulata*, acicular fibrous prismatic structure also occurs in a very thin layer immediately overlying a zone of shell etching that advances onto the outer surface of the former whorl. Here the needles are usually only about 0.2 micron wide (basic structural unit dimension) throughout the layer (Bandel, 1975a Pl. 4, Figs. 1, 2). This acicular layer does not grade directly into the crossed lamellar structure, but is separated from that structure by an intercalation of more or less extended composite prisms (Bandel, 1975a, Pl. 4, Fig. 3; 1979b, Pl. 6, Fig. 12).

In the mesogastropod *Strombus*, the thick outer lip commonly shows an intercalation of acicular fibrous prismatic structure with crossed lamellar structure. The thin acicular fibrous prismatic layers appear to be structurally continuous with the overlying and underlying crossed lamellar layers. Similar intercalations of acicular fibrous prismatic structure and crossed lamellar structure occur in a great variety of gastropods representing many taxonomic groups. The needles in the acicular fibrous prismatic layers of the inner lip and of the intercalations are composed of basic structural units from the beginning of their deposition onward.

C. Simple Lamellar Fibrous Prismatic Structure.

This structure was described as "acicular lamellar" by Bandel (1979b, p. 12), and as "simple lamellar" by Archambault-Guezou (1982, p. 329, Fig. 6) and Carter and Clark (1985, p. 54, Fig. 2D). The needles of acicular fibrous prismatic structure in the septum of *Charonia variegata* (Figure 2) are sometimes organized into lamellae up to 4 microns wide, 0.2 microns thick, and over 50 microns long. Viewed on the depositional surface, these lamellae are transversely striated, indicating their substructure of needle-like elements, of which about 20 unite to form individual lamellae. In contrast to acicular prismatic structure, in which the needles are perpendicular to the depositional surface, these needles are inclined at an angle of 70 to 80 degrees to this surface. Marginally, the lamellae thin out and their basic units are arranged in a dendritic pattern.

Simple lamellar fibrous prismatic structure may also be arranged quite differently than in *Charonia*. In the freshwater pulmonate limpet *Ancylus*, the lamellae are oriented nearly parallel to the growth surface rather than almost perpendicular to it. Basic units comprising this layer grade into acicular prismatic structure by simply changing their orientation from nearly horizontal to nearly vertical. Crossed lamellar structure may grade into simple lamellar fibrous prismatic structure, either with nearly vertical simple lamellae in fill-layers in the mesogastropod *Planaxis* or with nearly horizontal lamellae in the mesogastropod *Tectarius* shell thickenings (Bandel, 1979b, Pl. 3, Figs. 1, 3, 4.).

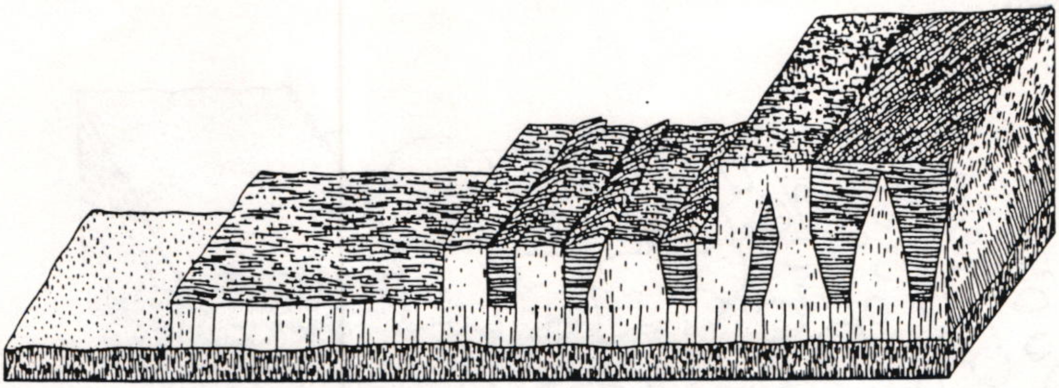

Fig. 2. Simplified drawing of the transition from acicular fibrous prismatic structure (left) to simple lamellar fibrous structure (center) and crossed lamellar structure (right). Some first-order lamellae of the crossed lamellar layer increase in width during growth, while others are stunted (from Bandel, 1979b, Fig. 2).

In the transition from the simple lamellar fibrous prismatic structure to crossed lamellar structure, some of the lamellae change the direction of their needles while others maintain their original direction. This change occurs rapidly, forming a transitional crossed lamellar layer consisting of very fine third-order lamellae (Fig. 2). This transition occurs in the septum of *Charonia* as well as in the solid shell fill of the apex of *Strombus pugilis* (Bandel, 1979b, Pl. 2, Fig. 9). Crossed lamellar structure arising by transition from simple lamellar fibrous prismatic structure is, from its inception, organized into first-, second- and third-order lamellae. However, some of the originally narrow first-order lamellae disappear farther away from the transitional zone as neighboring lamellae increase rapidly in width. In contrast to transitions from other precursors of crossed lamellar structure, the orientation of the needles in simple lamellar fibrous prismatic structure is reflected in the first-order lamellae of the crossed lamellar layer. Simple lamellar fibrous prismatic structure with needles parallel or nearly parallel to the growth surface is transformed into crossed lamellar structure by rearrangement of groups of needles (third-order lamellae) and their second-order lamellae into first-order crossed lamellae. Adjacent crystal bundles initially show only small differences in their orientation, but their needles gradually grade into a regular crossed lamellar structure (Bandel 1979b, Pl. 2, Figs. 1-6).

D. Homogeneous (Granular) Structure.

The periostracum of many gastropods is directly underlain by a very thin layer of granules about 0.2 microns wide (basic structural units) which are irregularly and densely packed into a homogeneous layer only a few microns thick. This layer commonly grades into needle-like crystallites. In the embryonic shell of the freshwater allogastropod *Valvata* (Bandel, 1977b, Pl. 2, Figs. 1,2) and below the apertural periostracum in *Columbella* (Neogastropoda) and *Orcula* (terrestrial pulmonate) and in many other gastropods as well, these granules grade into acicular crystallites arranged in spherulite columns oriented perpendicular to the depositional surface (Bandel, 1979b, Pl. 3, Figs. 6, 7). Granules may also grade into composite prismatic structure (in some neritids), into dendritic structure (in the repaired shell of some pteropods), or into crossed acicular structure (in many archaeogastropods and heteropods).

E. Blocky Prismatic Structure.

When *Neritina* (Neritomorpha) repairs its shell, the first mineralized layer consists of 0.3- to 0.5-micron acicular elements which form blocky prismatic structure. With shell growth, the blocky prisms grade into spherulite sectors. This blocky prismatic structure initially lacks minute basic structural units, but it later contains them. Very similar arrangements may be present in the inner prismatic shell layers inside many molluscs (Bandel, 1979b, Pl. 4, Figs. 10 and 11; Pl. 5, Fig. 7).

F. Composite Prismatic Structure.

In *Columbella* and *Neritina* spherulitic prismatic structure grades into composite prismatic structure by organization of the needles into bundles in which prism axes are mutually parallel to each other. Adjacent composite prisms are oriented in inclined position toward the depositional surface but not parallel or radial to each other. This structure may grade into crossed lamellar structure by selection of two bundle orientations which unite to form the first-order lamellae (Figure 3). Transitions from composite prismatic structure to crossed lamellar structure can be observed in almost all gastropods with crossed lamellar structure (Bandel 1979, Pl. 4, Figs. 1, 5, 6, 9). The needles within the composite prismatic layer are usually not fused into second-order lamellae, but they combine to form second-order lamellae as they pass into crossed lamellar structure.

In the initial mineral deposits of the organic embryonic shell of *Buccinum* and *Turbinella* (Neogastropoda), spherulitic aggregates grow unevenly and form the crystal bundles of the composite prismatic structure. Only two of the needle directions in this structure continue into the first-order lamellae of the adjacent crossed lamellar layer (Bandel, 1975a, Pl. 1, Figs. 1, 3; Pl. 4, Figs. 1, 2). The second-order lamellae form later during the growth of the crossed lamellar layer and are not present in the transitional zone between the spherulitic and crossed lamellar structures.

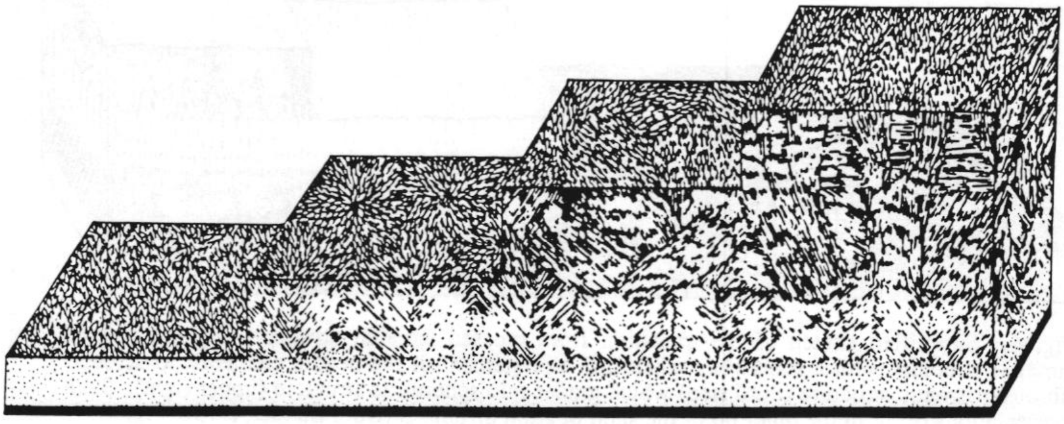

Fig. 3. Simplified drawing of the transition found in the neogastropod *Columbella mercatoria* from homogeneous (granular) structure (left) below the periostracum to spherulite sector structure (second step), composite prismatic structure (third step), which grades into crossed lamellar structure (right, upper step) (from Bandel, 1979b, Fig. 3).

Transitions from crossed lamellar structure to simpler structural types may also pass through composite prismatic structure. This occurs when crossed lamellar layers are intercalated with prismatic or spherulitic prismatic structures (Bandel, 1979b, Pl. 5, Fig. 6). Composite prismatic structure is transitional between crossed lamellar structure and acicular prismatic structure in polyplacophoran shells (Haas, 1972a) and bivalve shells (Kennedy *et al.*, 1970; Taylor *et al.*, 1969; Kobayashi, 1964; Wise, 1971). It may also occur as an intermediate layer between simpler structures and crossed prismatic structure which, in turn, can grade into nacre. Composite prismatic structure represents, in part, the "complex crossed lamellar" structure as applied by some students of gastropod shell microstructure (see *Glossary*, this volume).

G. Dendritic Structure.

The apical fill layers in the strombid *Lambis* and other mesogastropods may consist of dendritic branching needles oriented parallel or nearly parallel to the depositional surface (Bandel, 1977b, Pl. 4, Fig. 6). In the embryonic shell of *Valvata* this dendritic layer is very thin and forms a transition between granular structure and crossed lamellar structure (Bandel, 1977b, Pl. 2, Fig. 1). A transition from dendritic structure to spherulite sectors, with radially oriented acicular dendritic elements, occurs in shell thickenings of the land snail *Zonites* (Bandel, 1977b, Pl. 4, Fig. 7). During shell repair, some pteropods form dendritic structure as a transition between granular and helical structures (Bandel, 1977b, Pl. 3, Figs. 9, 10).

H. Spherulite Sector Structure and Spherulitic Prismatic Structure.

The neogastropod *Buccinum undatum* secretes, from its third whorl onward, crossed lamellar structure near the aperture and, farther back in the shell, a layer of vertically oriented columnar sectors consisting of radially arranged needles. In the latter structure, acicular structural units radiate toward the depositional surface from a longitudinal prism (column) axis. The individual needle-like crystallites show radially arranged, pointed heads on their smooth depositional surface (Bandel, 1975a, Pl. 7, Figs. 1-6). Bøggild (1930) called this layer of the *Buccinum*-shell the "composite prismatic structure" because he noted differences in the dimension of the sectors composed by the needles. Similar spherulitic prisms are found in various shells in the transition from nacreous to prismatic structures (Erben *et al.*, 1968; Erben, 1971; Bandel, 1977a). Haas (1972a) noted that in some polyplacophoran shells, spherulitic prismatic structure grades into crossed lamellar structure, just as noted in *Buccinum* and in the stromboid *Aporrhais* by Kessel (1933).

In the transition from crossed lamellar structure to spherulitic prismatic structure, the first-order lamellae first pass into composite prisms, and the latter then become arranged into concentrically constructed spherulitic prisms. When viewed on the growth surface, this transition is easily recognized from the striped appearance produced by the heads of the growing needles of the crossed lamellar layer, the irregularly oriented groups of needles in the composite prismatic layer, and finally the more and more regularly arranged heads of the growing needles towards the layer of spherulitic prismatic structure (Bandel, 1975a, Pl. 7, Fig. 4; 1979b, Pl. 6, Fig. 11). There is no change in the shape and composition of the individual needles and their dip angles throughout these transitions; only their orientations change relative to one another.

Where prismatic layers are intercalated with crossed lamellar layers, acicular fibrous prismatic structure may grade into spherulitic prismatic structure. Thinner prismatic layers between the crossed lamellar layers tend to remain acicular, but in thicker prismatic layers the needles tend to deviate from the vertical direction and form bundles of needles that meet in a line which is almost vertical to the growth surface (composite prisms of Carter and Clark, 1985, p. 55). As with other prismatic structures consisting of acicular subunits, the needles in this spherulitic prismatic structure consist of basic structural units so that individual needles are never very long (Bandel, 1979b, Pl. 6, Figs. 5, 6,

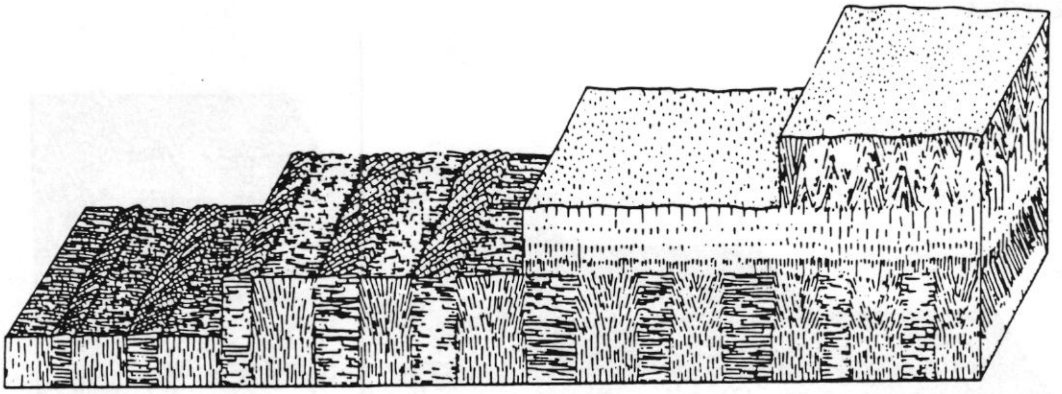

Fig. 4. Simplified sketch of the transition from crossed lamellar structure (left) to crossed lamellar structure with a somewhat spherulitic arrangement of the needle elements, to acicular fibrous prismatic structure (third step) which grades into spherulitic structure (upper right). Such intercalations occur in the outer lip of the shell of adult *Strombus* (from Bandel, 1979b, Fig. 4).

8). The composite structural type of the spherulitic prismatic structure commonly occurs in shells with predominantly crossed lamellar structure where the shell is thickened, for example on the apertural lips and within the shell interior. (Figure 4).

In the case of the terrestrial pulmonate *Perforatella*, spherulitic prismatic structure comprises the first calcified layer of the embryonic organic shell (Bandel, 1979b, Pl. 8, Fig. 2). A similar sequence of early spherulitic prisms grading into crossed lamellar structure can be observed in the tectibranch *Haminoea* and in the internalized shell of the *Aplysia* (both opisthobranchs).

I. Helical Structure.

In the pelagic pteropod *Cavolinia* the newly hatched animal has a horn-like shell which grows into a flat, wide bilaterally symmetrical juvenile shell. The body then continues to grow while shell growth is stunted until the tentacle-like appendages and sheet-like mantle cover the exterior of the shell. A very drastic and rapid change then occurs in which *Cavolinia* dissolves the mineral portion of its shell, leaving only its periostracum. The periostracal margins are then enlarged to make a more spacious, elastic shell. The mantle epithelium adheres to the exterior, and the mantle with its muscle attachment lies at the interior of this organic shell. The outer muscular mantle and the internal shell muscles then deform the shell to produce the characteristic rounded conch of the adult. During this deformation, but mainly after its completion, an aragonitic layer with predominantly helical structure is deposited on the inner surface of the periostracum. This metamorphosis of the juvenile to the adult shell is unique among gastropods (Bandel and Hemleben, 1990) and is found only in representatives of the living genera *Diacria* and *Cavolinia* as well as in the fossil genus *Vaginella*.

Pteropod helical structure was initially described by Bé *et al.* (1972) and Rampal (1973, 1975). Bé *et al.* (1972) suggested that pteropod helical structure represents a new architectural plan evolved by initially unmineralized opisthobranch ancestors. They believed that this unusual orientation of aragonite needles reflects in some mysterious way the helical structure of collagen. However, Bandel (1977b) demonstrated that pteropod helical structure is derived from crossed acicular structure, which is in turn closely related to crossed lamellar structure.

J. Crossed Acicular Structure.

In the heteropod *Atlanta peronni* the first layer below the periostracum consists of a special type of crossed structure in which the first-order lamellae are only as thick as the third-order lamellae. Otherwise the orientation of the constituent needles is like that in the underlying crossed lamellar layer. The transition between these two structures merely involves thickening of the first-order lamellae from the crossed acicular to the crossed lamellar layer (Bandel, 1977b, Pl. 2, Figs. 3, 4). Crossed acicular structure also occurs in the outer layer of the early post-embryonic shell of the gastropod *Cittarium pica* (Erben, 1971, Pl. 2, Fig. 4) and in certain pteropods (Bandel 1977b, Pl. 2, Figs. 6, 7).

In the pteropod *Cuvierina* the periostracum near the adult shell margin is underlain by an extremely thin layer of minute granules (basic structural units) which pass inward into crossed acicular structure. The basic structural units of the granular layer become aligned into single needles and bundles of needles arranged in two directions and dipping 30 to 40 degrees relative to the depositional surface. The needles thus intersect each other at angles of 120 to 150 degrees. The dip directions of the two needle systems are parallel to each other and to the plane of the shell aperture. Bundles of two to four acicular third-order elements sometimes aggregate into first-order lamellae. However, unlike the first-order crossed lamellae in *Atlanta*, the first-order lamellae in *Cuvierina*'s crossed acicular layer are very short or absent and consist of platelets made up of fused acicular elements up to 2 microns long, 8 microns wide and 0.2 microns thick. The needles and needle bundles dipping in opposite directions touch, displace and surround each other and commonly branch in two, but they never penetrate each other, as in dissected crossed prismatic structure (see below).

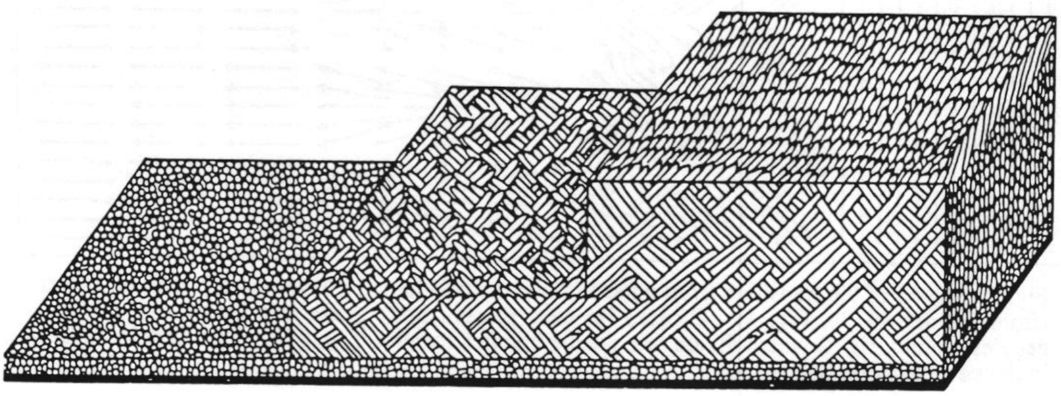

Fig. 5. Simplified drawing of the transition from homogeneous (granular) structure (lower left) to helical structure (upper right). The homogeneous layer covers the organic periostracum and grades into crossed acicular structure (center). Needles of crossed acicular structure turn into those of helical structure (from Bandel, 1977b, Fig. 1).

K. Transitions between Crossed Acicular, Helical, Dendritic and Crossed Lamellar Structure.

Crossed acicular to helical structure. In the transition from crossed acicular to helical structure, needles turn away from their inclined orientations and twist into the new spiral direction (Figure 5). In helical structure, the basic structural units are added to the needles in such a way that each needle comes to lie almost parallel to the depositional surface, and the needles spiral in helical coils. In changing from crossed acicular to helical structure, adjacent needles assume the same dip angle and (changing) dip direction and they grow parallel to one another. The needles of the helical layer appear regularly bent and arranged into low spirals which meet the growth surface at a very low angle. The spiral needles continue to consist of cushion-like basic structural units about 0.2 microns wide (Bandel 1977b, Pl. 1, Figs. 1-9).

Dendritic to helical structure. Shell repair in *Cavolinia* shows that helical structure can also develop from an initial dense layer of dendritic crystallites arranged parallel to the depositional surface (Bandel 1977b, Pl. 3, Figs. 2-10). The initial shell repair deposits are granular, and these grade into the dendritic layer consisting of branching needles. These branching needles consist of basic structural units about 0.2 microns wide. With continued shell deposition, the individual needles assume helical orientations with both right and left coils, and the spirals become wider. The first needles comprising the spirals show remnants of the dendritic structure, but the later-formed needles become more regularly shaped, and left-handed spirals are discontinued in favor of right-handed spirals. The regular helical structure is rapidly attained in the repair of damaged shell. The initial formation of both left and right spirals demonstrates that, at this stage of development, organic matrix does not predetermine the growth of right spirals only, contrary to Bé *et al.* (1972). However, this possibility cannot be excluded for the later growth of right-handed helical structure. Regardless of the controls, the right-handed helices appear to gradually eliminate the left-handed helices as the structure develops, thereby increasing the orderliness of crystal growth within the extrapallial fluid.

Helical structure between two crossed lamellar layers. Shell material secreted by the neogastropod *Murex* during the construction of a new varix consists mainly of outer and

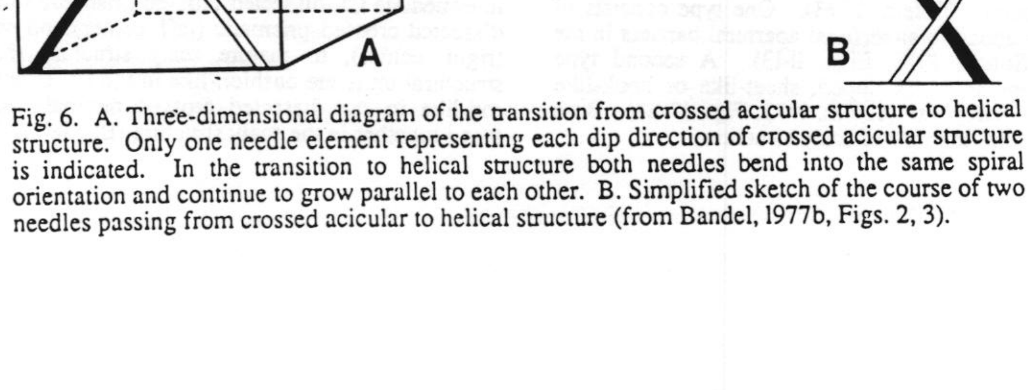

Fig. 6. A. Three-dimensional diagram of the transition from crossed acicular structure to helical structure. Only one needle element representing each dip direction of crossed acicular structure is indicated. In the transition to helical structure both needles bend into the same spiral orientation and continue to grow parallel to each other. B. Simplified sketch of the course of two needles passing from crossed acicular to helical structure (from Bandel, 1977b, Figs. 2, 3).

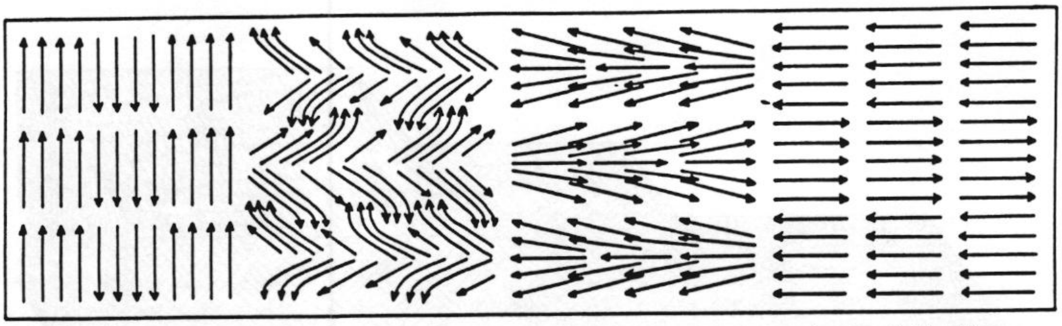

Fig. 7. Sketch of the transition from outer to inner crossed lamellar layers in the shell of *Murex* (from Bandel, 1977b, Fig. 4). Crossed lamellar plates (right) grade into plates with inclined needles (center, right) which divide into needle bundles (center, left), which then turn in helices in the new direction (left).

inner crossed lamellar layers differing in dip direction by an angle of 90 degrees. Between these layers, the third-order needles twist in a right angle as they pass from one crossed lamellar layer to the next. This is accompanied by spiral growth of the first-order lamellae which contain these aragonitic needles. One half of each first-order lamella thus grows into a right-handed spiral while the other half grows into a left-handed spiral (Figure 7). When the new growth position in the adjacent crossed lamellar layer is reached, helical growth ends and the needles once again assume a straight shape (Bandel, 1975a, Pl. 3, Fig. 1; 1977b, Pl. 4, Figs. 1, 2, 4). Thus each first-order lamella in one crossed lamellar layer is structurally continuous with halves of two first-order lamellae in the adjacent crossed lamellar layer. Sets of crossed lamellae in the two crossed lamellar layers differ in their dip angle by 110 to 120 degrees relative to each other.

L. Scaly Structure.

The apertural inner lip of many pulmonate gastropods and some mesogastropods, such as *Erato*, *Cypraea* and certain melaginellid neogastropods, is covered with inclined, scale-like mineral deposits. These species are united by the common presence of a narrow, high aperture. Solem (1972, 1973) and Solem and Lebryk (1976) described this so-called micro-armature for many land snails with scaly apertural lips, and thus concluded that this feature provided additional information regarding systematic placement. These apertural scales apparently serve as holdfasts for mantle tissues when the animal is active. The scales are weakly inclined away from the aperture and they are steeply terraced on the depositional surface, thereby preventing slippage of the mantle back into the shell when the animal holds its shell above the foot. Scaly structure is derived from crossed lamellar structure through crossed prismatic transitional structure (Figure 8).

This scaly layer is common only among land and freshwater gastropods, but it occurs in a wide variety of taxonomic groups. Small pulmonates show two types of scaly micro-armature (Solem, 1973). One type consists of triangular points added to superficial apertural barriers in the Endodontidae (Solem, 1973, Figs. 11-13). A second type consists of triangular, blunt tipped, sheet-like or hook-like denticles in the Charopidae (Solem, 1973, Figs. 17-22). Both types represent modifications of scaly structure.

M. Dissected Crossed Prismatic Structure.

In many adult mesogastropods, such as *Stombus*, *Modulus*, *Cassis*, and *Distorsio*, the thickened shell and the apical shell fill materials commonly show acicular elements with two needle directions which, in contrast to crossed acicular structure, dissect and penetrate each other (Bandel, 1977b, Pl. 4, Fig. 5). Similar structures also occur in pleurotomariid archaeogastropods (Erben and Krampitz, 1972), but they have

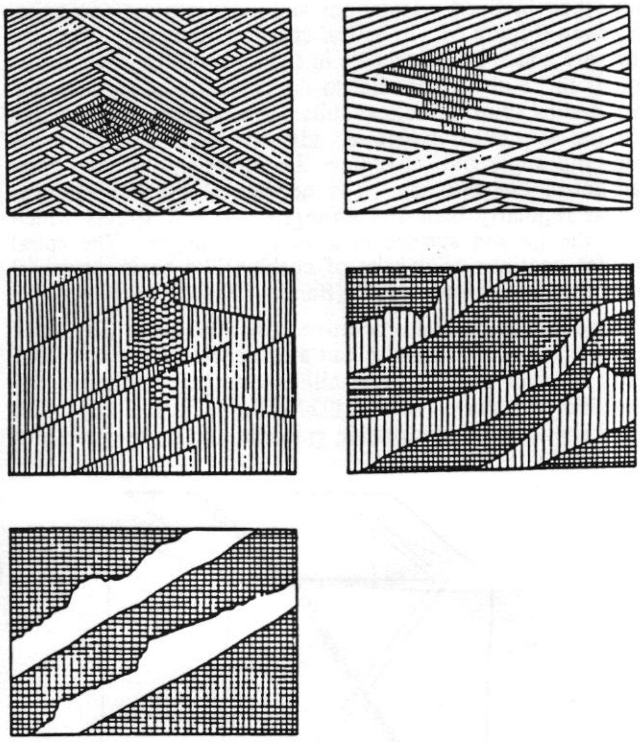

Fig. 8. Sketch of transition from CL structure (upper left) to intermediate CL/dissected crossed prismatic (upper right), to dissected crossed prismatic (left, center) and scaly structure (right, center), to mature scaly structure (base). Basic structural units are cushion-like in the CL structure, cube- to rod-like in the dissected crossed prismatic structure, and fused together in the scaly structure (Bandel, 1979b, Fig. 5).

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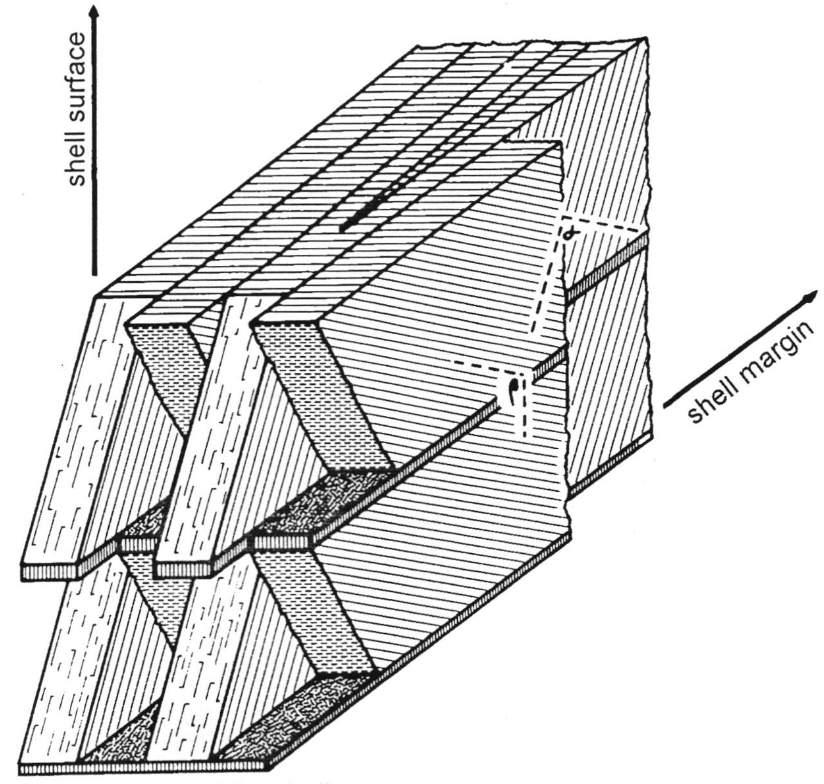
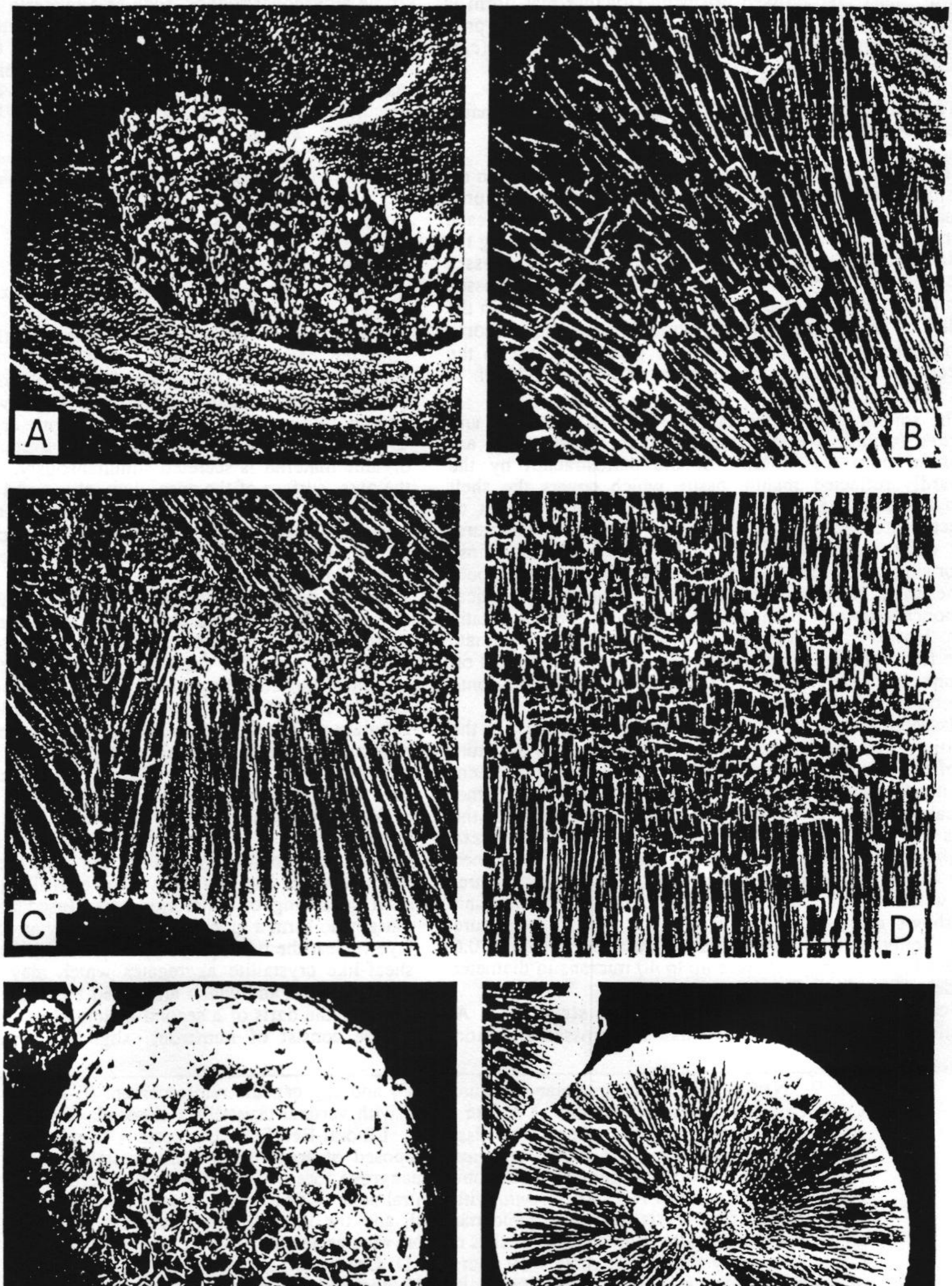

shell surface
α
β
shell margin
plane of symmetry of the shell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been misinterpreted as deposits laid down during early shell growth. Dissected crossed prismatic structure may form in the juvenile shell of certain nacreous archaeogastropods prior to the ontogenetic appearance of the nacreous structure (*e.g.*, in *Calliostoma*; Bandel, 1977a, Pl. 1, Fig. 8).

N. Transitions between Scaly, Dissected Crossed Prismatic, Crossed Acicular and Crossed Lamellar Structures.

Crossed lamellar to crossed prismatic structure. In the transition from crossed lamellar to dissected crossed prismatic structure, the inclination of the needles relative to each other decreases, and the basic structural units comprising the needles change from cushion-like shapes in the crossed lamellar layer to rod-like shapes in the dissected crossed prismatic layer. These units are arranged serially within the needles of the crossed lamellar structure, but they become oriented nearly perpendicular to the growth surface in the dissected crossed prismatic structure (Bandel, 1979b, Pl. 7, Figs. 6-8).

The smooth, outer shell layers of *Trivia*, *Cyphoma* and *Cypraea* (triviid, ovulid and cypraeid mesogastropods) are deposited onto the exterior of the periostracum by the outwardly reflected mantle tissue which covers the shell when the animal is active. These outer layers consist of dissected crossed prismatic structure with basic structural units quite a bit larger (0.3 - 0.6 microns) than those comprising the normal crossed lamellar structure in the bulk of the shell below the periostracum. In adults, vertical components dominate in this dissected crossed prismatic layer. However, in juveniles, inclined components dominate in the first mineral deposits observed on the aperture and on the inner lip, which consist of scales deposited directly onto the periostracum (Bandel, 1979b, Pl. 8, Figs. 7, 8).

Dissected crossed prismatic to scaly structure. In the transition from dissected crossed prismatic to scaly structure one of the directions of inclination becomes more prominent until needle interpenetration disappears. At the same time, vertical structural elements fuse with each other until the scales are present. In the small pulmonate gastropod *Aplexa hypnorum*, the smooth surfaces of the scales are inclined about 40 degrees to the growth surface. The basic structural units within each scale are fused into a solid crystalline unit that shows undulating fracture surfaces similar to mature nacre. Individual scales in this scaly structure are up to 0.6 microns high and may measure up to 40 microns in diameter (Bandel, 1979b, Pl. 8, Fig. 5).

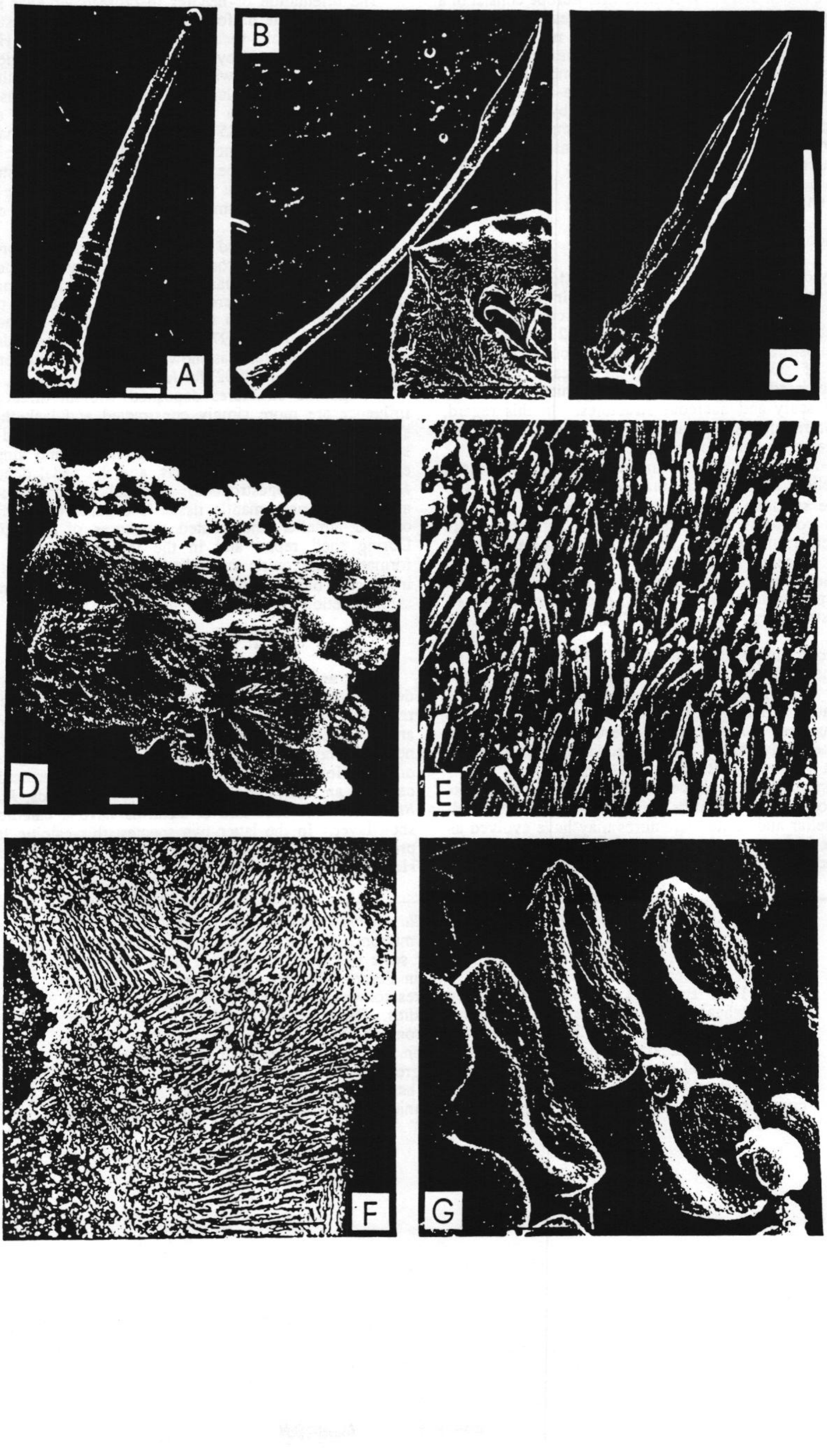
Scaly to dissected crossed prismatic structure. A transition from scaly structure to dissected crossed prismatic structure is associated with nacre in the inner shell layers of some archaeogastropods, such as *Seguenzia* (Bandel, 1979b, Pl. 3, Figs. 2, 7). This transitional structure was called "dissected crossed -acicular" and differs from dissected crossed prismatic structure only in its intergradation with nacreous structure. Gainey and Wise (1975) called a similar structure "oblique prismatic", and Erben (1971, Pl. 3, Figs. 1-4; 1972, Pl. 2, Figs. 3-6) considered it to be a modification of nacreous structure. In the Cephalopoda, some of these structures are united under the term "wrinkle layer".

O. Opercular and Helicid Dart Structures.

Opercular structures. The opercula of neritomorph gastropods such as *Nerita*, *Neritina*, *Theodoxus*, *Smaragdia*, and *Puperita* and of naticid mesogastropods such as *Natica* are mineralized with aragonite. The crystallites deposited onto the organic operculum by the pedal epithelium are simply arranged in patterns which resemble inorganic crystal growth. Here, aragonite deposition begins with spherulites or dendritic crystallites interlayered with organic laminae. Crystallite growth remains somewhat irregular as long as organic material is secreted simultaneously. In contrast, on the outer surface of the operculum, above and away from the surface of the foot and on the margins of the operculum, vertically oriented prismatic needles 1-4 microns wide are deposited which show uniform optical crystallographic orientation (Figure 9).

Helicid darts. Pulmonates of the family Helicidae secrete one or two mineralized darts which they use as stimulants during copulation. Copulation in these gastropods can last up to 24 hours. The darts form within a special gland sac, and each dart consists of a tube with a closed, pointed end and a wider, open end. New darts are secreted for each act of copulation. The darts consist of aragonitic needles less than 1 micron wide and of variable lengths. These needles are arranged within more or less well-ordered spherulites, spherulitic ridges, or sheaf-like aggregates. Darts from different helicid species may be quite different in shape, and this difference is also reflected in the arrangement of their fascicular aragonitic crystallites. For example in a Mediterranean helicid, the two darts show eight longitudinal ridges each consisting of spherulitic rows fused along their thin margins to form a tube that is covered by an exterior organic layer. Near the tube aperture the spherulitic ridges grade into sheaf-like crystallite aggregates which may be marginally fused together and which are joined by organic material. In contrast, the darts of a second helicid species from southern France consist of numerous, slightly spherulitic rows of

Fig. 9. Neritid aragonitic opercular structure (A-D) and egg capsule reinforcement (E-F). A: Central portion of the operculum of *Nerita polita* with vertical crystallites exposed. Growth starts from organic surface that has been dissolved. Littoral Red Sea. Bar scale = 10 microns. B: Fractured operculum of *Neritina virginea* composed of aragonitic needle crystallites in a somewhat spherulitic arrangement. Colombian mangrove forest. Bar scale = 10 microns. C: Fractured operculum of *Nerita peloronta* with central zone of operculum (near the internal peg) consisting of fine crystallites in organic material, and the internal peg consisting of coarse aragonitic prisms. Operculum body consists of more regular needles (upper part and Figure 9D). Columbian rocky shore. Bar scale = 10 microns. D: Operculum of *Nerita peloronta* consisting of coarse, regular, aragonitic rods. Bar scale = 10 microns. E: Aragonitic sphere of the egg cover of *Nerita versicolor* from the Columbian coast. Bar scale = 10 microns. F: Fractured sphere of the egg cover of *Nerita peloronta* from the Columbian coast shows simple aragonitic needles. Bar scale = 10 microns.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needles which are so close together they almost form a prismatic layer. This dart has a spear-like point with sharp ridges (Figure 10).

Darts of *Cepaea* and *Helix* from central Europe consist of a round tube with four sharp, exterior ridges. These darts consist of interlocking spherulites which radiate outward toward the outer surface of the dart. The apertural end has a head piece which resembles a half-closed umbrella cut off at its pointed end. The ridges of the umbrella-like head piece consist of aragonite needles held together by organic shell layers (Figure 10). Despite the rather complex shapes of helicid darts, they all show simple patterns of aragonitic mineralization which resemble in shape and size the crystallites and crystal aggregates in the initial deposits associated with shell repair and internal septa.

P. Discussion of Aragonitic Structures.

A variety of structure types appear to be closely related to crossed lamellar structure by virtue of their intergradation with crossed lamellae and their similar composition of clearly visible basic structural units about 0.2 microns wide. Different substructures occur only in nacreous structure, in the plates of scaly structure and, to a lesser extent, in dissected crossed prismatic structure, which sometimes grades into scaly and nacreous structures. In this regard, scaly structure shows a homogeneous substructure more similar to nacreous than crossed lamellar structure.

In terms of their mutual intergradation, aragonitic crossed lamellar, helical, and scaly structures are closely related. The intermediate structure from crossed lamellar to spherulitic structure is composite prismatic; to helical structure it is crossed acicular; and to scaly structure it is dissected crossed prismatic. Presently unknown are direct transitions from crossed lamellar and helical structures to nacreous structure. However, spherulitic prismatic, scaly, and dissected crossed prismatic structures may grade directly into nacreous structure.

No gastropod is presently known in which nacreous and crossed lamellar structures occur within the same shell. In this respect gastropods may differ from bivalves. Among bivalves, nacreous and crossed lamellar or complex crossed lamellar structures are associated in certain members of the Crytodontacea, Mytilacea, Aviculopectinacea, Trigoniacea and Myacea (Newell and Boyd, 1975; Carter, 1980a,c).

When gastropods first evolved from the limpet-like ancestors of all conchiferan molluscs during the Cambrian Period, crossed lamellar and related structures may have evolved as an early alternative to nacreous structure. There is presently no reason to believe that, within the Gastropoda, nacreous structure is simpler than crossed lamellar structure and therefore evolved prior to crossed lamellar structure, as commonly stated in text books dealing with molluscs.

The orientation of needles in crossed lamellar structure may remain quite uniform and may be characteristic of an individual shell of a species, or a group of species. However, as was demonstrated by Bandel (1979b), needle orientations may also be variable within a single crossed lamellar layer. In the mature crossed lamellar structure of most gastropods, the dip angles form a mutual angle between 90 and 130 degrees. A survey of 85 gastropod species proves that needle angle and arrangement in more or less regular crossed lamellar structure can be of no help in gastropod systematics. A preliminary survey of gastropods from the Middle Triassic Alpine St. Cassian Formation indicates that this is also true for fossil shells.

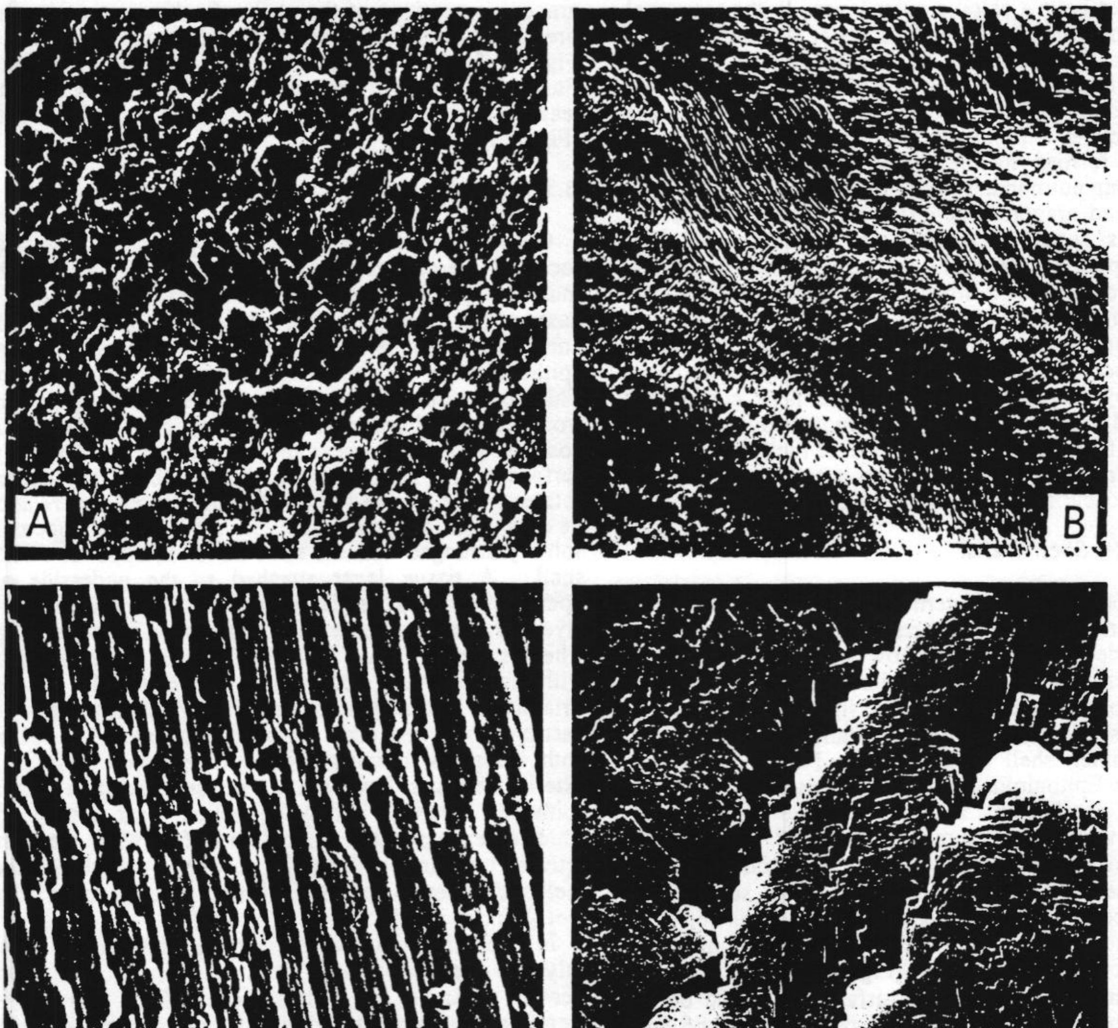
The initial mineralized shell deposited under the protective periostracum usually consists of basic structural units like those in crossed lamellar structure. Transitions from these initial deposits into crossed lamellar structure may be extremely abrupt, as in the embryonic shells of neogastropods (Bandel, 1975a, 1979b), or they may be gradual and visible in thin sections, as shown by Kessel (1941b) for *Natica* and by Biedermann (1902) for *Helix*.

Aragonitic structures deposited without direct mantle influence are more simply constructed and lack the basic structural units characteristic of crossed lamellar and related structures. This includes opercula, neritid and ampulariid egg shell deposits, helicid darts, and the pedal deposits of *Hipponix* (Mesogastropoda; personal observations). It appears that only mantle tissue is capable of forming the crossed lamellar and related structures of the Mollusca. During shell repair and in the initial layers of septum formation, aragonitic crystallites of "inorganic" habit grade into "true" biocrystallites with increasing mantle control on shell secretion.

III. Calcitic Structures.

X-ray analysis utilizing the Debye-Scherrer method has documented calcite in the outer shell layer of *Nerita* and related marine Neritidae, in the outer shell layer of *Neritina* and *Theodoxus* among the brackish water and freshwater neritids, and in the egg capsule of the *Nerita (Tliostyra) albida*. However, similar deposits in many other neritid egg capsules are aragonitic. Among mesogastropods, *Littorina littorea*, *L. obtusata* and *L. saxatilis* have a calcitic outer shell layer. In the latter two species, this calcitic layer is present in shells newly hatched from the egg. Among the Heteroglossa, *Epitonium lamellosum*, *Scala communis* and

Fig. 10. Helicid dart structure. A: Dart of *Helicella conspurcata* (southern France) is of simple shape (see structure in 10D,E). Bar scale = 100 microns. B: Dart of *Chilostoma desmoulinsi* from southern France with spear-like head. Bar scale = 1 mm. C: Dart of *Helix aspera*, a common European helicid. Structure is shown in Figure 10F and crystal growth surface in Figure 10G. Bar scale = 1 mm. D: The crystallites composing the dart of *Helicella* consist of simple wheat grain aggregates and spherulitic bodies. Bar scale = 10 microns. E: The inner surface of the tube forming the dart of *Helicella* consists of pointed heads of aragonite needles that mineralize the dart walls. Bar scale = 1 micron. F: This fractured wall of the dart of *Helix* shows spherical crystal aggregates that have intergrown with each other into a solid wall. Bar scale = 10 microns. G: Growth surface of the base of the dart of *Helix* demonstrating the complex shapes produced by the inhibiting organic mucus covering the growing spherulitic crystal aggregates. Bar scale = 10 microns.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Janthina exigua have a calcitic outer layer. In the terrestrial mesogastoropod *Tudora* and the freshwater *Bithynia* only the operculum is calcitic. Among the Neogastropoda, *Trophon*, *Neptunea* and *Nucella* have species with a calcitic outer shell layer. In *Nucella lapillus* the initial mineralization of the embryonic shell is entirely aragonitic, but a calcitic outer shell layer is formed by the young hatches from its egg capsule. Among pulmonates, species of the slug *Parmacella* have calcite and aragonite deposits, whereas in *Deroceras* only calcite is deposited beneath the organic shell. The eggshells of pulmonates such as *Helix*, *Cepaea*, *Discus*, *Zonitoides*, *Monacha* and many other genera are calcitic (personal observations).

Calcitic shell deposits in *Neritina*, *Littorina*, *Janthina*, *Epitonium*, *Nucella*, *Rapana*, *Trophon*, and *Neptunea* were documented by Bøggild (1930), and are here confirmed. Bøggild noted the occurence of homogeneous, grained, prismatic, and foliated structures in calcitic molluscan shells. These same structural types, with the exception of foliated structure, also occur in aragonitic deposits.

A. Calcitic Outer Shell Walls.

Bøggild (1930) applied the term "homogeneous structure" to aragonitic or calcitic shell layers which, when viewed in thin section under ordinary light, show no apparent structural organization, but which show extinction in one direction over large portions of the layer in polarized light. Even with the electron microscope, the smallest crystalline units comprising calcitic outer shell layers in the Neritoidea, some *Littorina*, some Epitonioidea, and in *Neptunea* and *Nucella* appear rather nondescript and demonstrate little order regardless of whether fractures or polished and etched sections are viewed. Sometimes irregular spherulitic sectors can be seen oriented parallel to the depositional surface (in *Velates*, an Eocene neritid) or perpendicular to this surface, but more commonly Bøggild's observation can be confirmed that no apparent structure is present (Figure 11).

In many cases the depositional surface of calcitic outer shell layers (on the inner surface of the outer lip of the aperture) shows patterns of crystal faces. Large crystal units with small rectangular to pyramidal laths have similar orientations within each larger unit, but the orientation differs from unit to unit. The term "homogeneous structure" might be applied to these calcitic layers, which may be structurally equivalent to some "granular" layers described for bivalves by Taylor *et al.* (1969). Organic material may be enriched along some growth surfaces, much more so than in aragonitic portions of the shell. Such layers commonly are preserved during diagenesis (Bandel and Weitschat, 1984, Figs. 6, 8, 9), even when the shell is totally recrystallized. Fungi feed on such organic layers intercalated with calcite, leaving strange marks which might be difficult to interpret (Figure 11).

B. Calcitic Opercula.

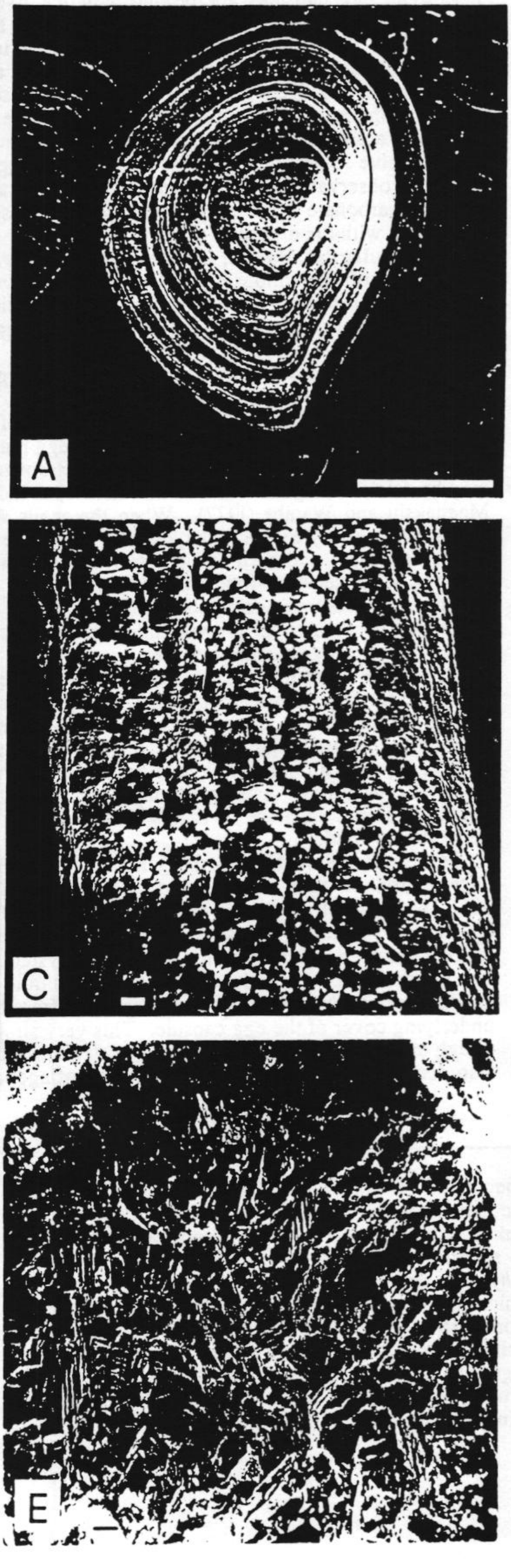
Gastropod opercula lie on the upper side of the posterior foot and are connected to a branch of the shell-attachment muscle. Kessel (1941b) studied operculum growth in many gastropod species in detail. According to his data, during embryonic growth the foot differentiates a glandular epithelial area which initially secretes a round operculum. This operculum is fully attached at first, but it later detaches from the epithelium and is then enlarged by secretions from a zone of gland cells near the columellar side of the upper surface of the foot. In the simplest case, the operculum rotates on the foot and new opercular secretions are added to its edge near the gland zone. Thus the simplest opercula are spirally arranged with the spire direction opposite that of the shell. A tissue layer attached to the underside of the operculum covers the gland secretions with a smooth exterior layer. Opercula of most Caenogastropoda are purely organic, whereas those of most Neritomorpha are mineralized, many with aragonite (see above) and with calcite in the case of Triassic to Recent *Neritopsis*. The Mediterranean archaeogastropod *Astraea* adds calcareous layers to its operculum both along its margins and on its exterior surface. The exterior deposits, however, are not secreted by a permanent epithelial covering, but by epithelium near the operculum which extends over the operculum surface when the animal is actively crawling. When the gastropod withdraws into its shell and closes its aperture, this epithelium is retracted to the foot (Bandel, 1988).

In opercula with concentric rather than spiral structure, only the depositon of the basal epithelium (shell finish of Kessel) enlarges the primary operculum. In one-sided accretion the operculum grows away from the gland zone as material is added only to one side.

The epithelial layer which covers the organic operculum after its first deposition can deposit calcitic shell material, as in freshwater bithyniids and in the land snails *Cyclostoma* (Cyclophoridae), *Tudora* (Chondropomidae), and *Pomatias* (Pomatiasidae) (Figure 12; personal observations).

In *Bithynia* from European lakes, spherulitic crystal aggregates are incorporated into the organic operculum

Fig. 11. Calcitic outer shell wall structures. A: Growing surface of the outer apertural lip of *Neptunea decemcostata* (north Atlantic) consists of small, angular, calcitic growth fronts within the organic mucus (now dissolved). Bar scale = 10 microns. B: Growth surface of the outer lip of a juvenile *Nucella lapillus* from the coast of the North Sea, with growth facets of larger crystal units of calcite that each represent one optical unit. Bar scale = 10 microns. C: Growing facets of one optical unit in the outer lip of *Littorina littorea* from the shore of the North Sea with a regular arrangement within each unit. Bar scale = 1 micron. D: Growth surface of the apertural margin of a growing *Nucella lapillus* with fairly coarse growing edges of different crystal units. Bar scale = 10 microns. E: Fractured shell of the fossil neritid *Velates schmideli* (Eocene, Paris Basin) with calcitic outer shell layer of unusual structure, and with aragonitic crossed lamellar inner shell layer (lower part). Bar scale = 10 microns. F: The organic layers that follow increments of growth in the calcitic outer shell layer of *Nerita tesselata* (Caribbean shore) have been digested by fungi, leaving meandering dissolution tracks. Bar scale = 10 microns.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formed by the very young animal. Further enlargement occurs as accreted organic rims, which also include spherulites. On the upper side of the operculum these crystal aggregates grow into larger, irregularly formed calcitic crystallites. The initial spherulites eventually unite into polygonal blocks in which neighboring crystallites show identical optical orientation. The growth surfaces of these opercula present an uneven surface due to the presence of incompletely united blocks, which join at depth into large units with the same optical properties. Hubendick (1948) described the epithelium which secretes the operculum in *Bithynia*. Opercular growth is discontinuous and the operculum-secreting cells are not attached to the operculum. The organic components of the operculum are produced by tall epithelial cells, whereas the mineral components are deposited by shorter cells. The shrub-living *Tudora* sp. from Curaçao (West Indies) produces simpler opercula which lack the organic layers and crystal spherulites. Here layers of coarse calcite are deposited on top of each other, apparently through periodic secretion of calcifying mucus by the pedal gland. In this case, larger crystal units containing similarly oriented cyrstallites show no pattern of common orientation relative to neighboring structural units. These calcitic prisms show transverse striations which follow accretion lines. According to Bøggild's (1930) terminology, the operculum of *Bithynia* consists of grained structure in its central portion and prismatic structure in its marginal rims. The operculum of *Tudora* is prismatic throughout. Its prismatic structure consists of rather coarse crystallites with characteristic calcite cleavage faces; it is therefore quite different from aragonitic prismatic structure but similar, in this respect, to the calcite prisms of the pterioid bivalve *Pinna*.

C. Eggshells.

Many neritaceans, some ampullariids (Architaenioglossa) and many pulmonates lay eggs with calcified egg capsules. In the genus *Nerita* from warm rocky intertidal shores, the lid of the cup-shaped egg capsule contains numerous calcareous spheres. The mineralogy of these spheres varies from species to species: these are aragonitic in *Nerita versicolor*, *N. peloronta*, *N. tessellata* and *N. fulgurans* from the Caribbean Sea, but calcitic in *Nerita polita* from the Red Sea (Bandel, 1982). The aragonitic spheres are well-rounded, whereas the calcitic ones are pill-shaped with two cup-like ends and a short central cylindrical portion. Crystallites in both types are arranged in a simple concentric spherulitic structure (Figures 9E,F; 13E,F).

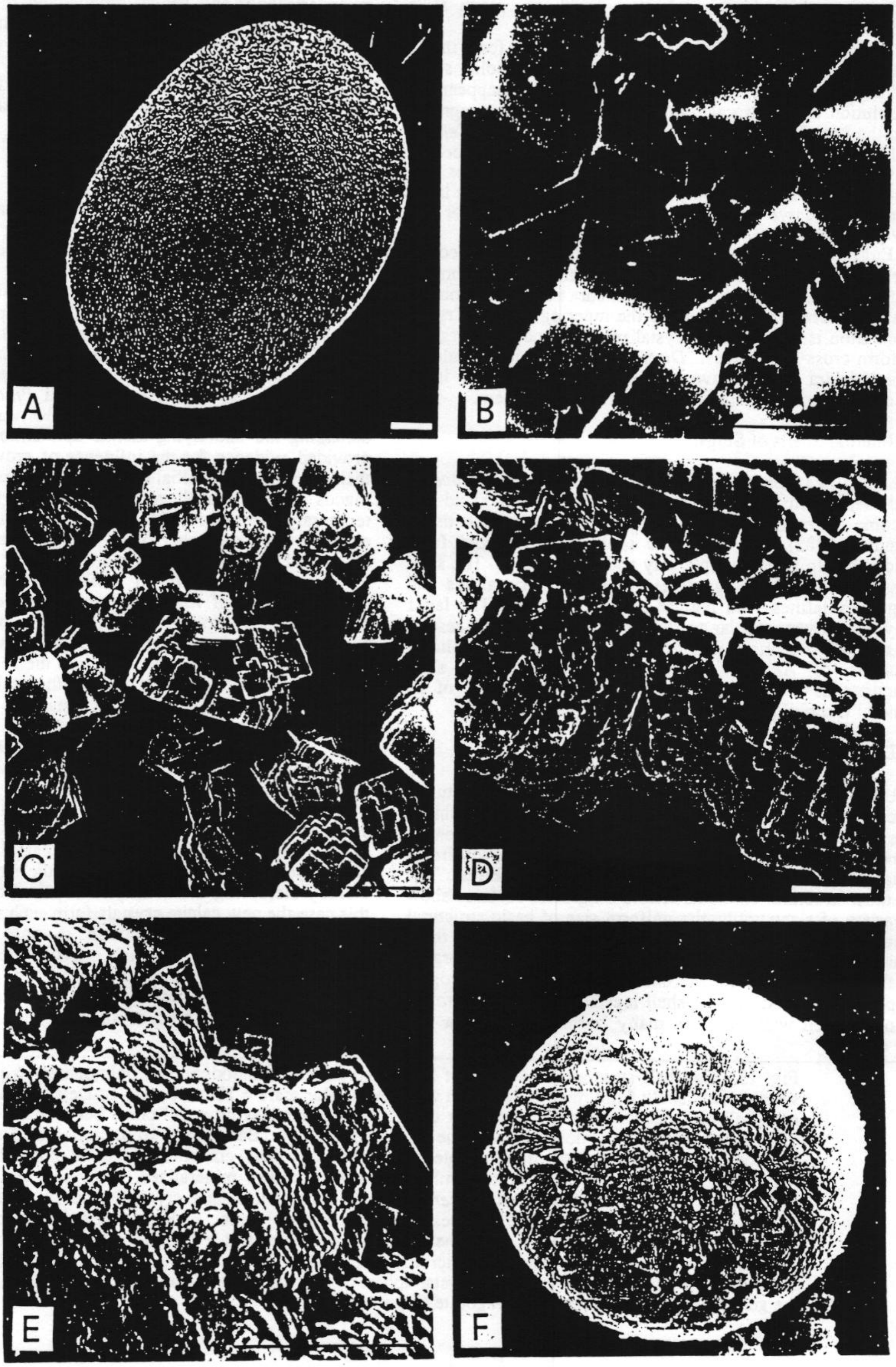
According to Andrews (1936) the calcareous spheres of neritacean egg capsules are produced in the liver and are collected in a special sac near the capsule gland. Meenakshi and Watabe (1977) reported that similar spheres in different portions of the body of *Ampullarius* are utilized as calcium reservoirs which dissolve before the snail deposits its egg mass. Spheres of this type extracted from the tissue of *Viviparus* are calcitic with a radial construction, but they are less massive than those reinforcing *Nerita* egg capsules (personal observations). Many freshwater prosobranchs have calcium carbonate spheres in their visceral mass, usually associated with the digestive gland.

The ampullariids *Marisa*, *Lanistes* and *Ampullarius monticolus* have soft, gelatinous egg masses, whereas *Ampullarius porphyrostomus* from South America, other species of this genus from southeast Asia, and species of the genus *Pila* from Africa have hard, mineralized egg masses. Females ready to spawn leave the water and crawl onto vegetation at least 10 cm above the water surface. The freshly formed egg masses are soft but they harden after a few hours of exposure to the air (Bandel, 1976b). The walls of the egg mass consist of a mucus with small crystals of calcium carbonate. These may be calcitic, aragonitic and even vateritic, as indicated by Meenakshi and Watabe (1977). When the snails within the egg mass are ready to hatch, they eat the entire interior walls of the egg mass and then fall or crawl down to the water. The egg walls serve as food for the hatchlings as well as a calcium carbonate provision for reinforcing their shells, as evidenced by their rapid growth and numerous fecal pellets shed by the freshly hatched juveniles.

Tompa (1967a) found that the outer surface of the eggshell of the terrestrial stylommatophoran *Anguispira* consists of calcite crystal facets about 10-15 microns in maximum diameter. Fractured eggs reveal three layers: an outer layer of large crystals, a thicker middle layer, and a thin inner layer of small crystallites. A jelly-like layer surrounds the entire eggshell. Some eggs are so lightly calcified that they have no structural rigidity.

Terrestrial pulmonates of the genera *Cepaea*, *Helix* and *Discus* produce eggs with a solid calcareous shell (Figure 13). The eggshell commonly calcifies after oviposition. The egg leaves its parent still soft, often quite transparent, and lacking calcareous crystals on its cover. Crystallization of the eggshell occurs with evaporation of liquid from a gelatinous outer layer that is clearly separated from the actual underlying cover of the egg capsule. This very simple mode of egg calcification by desiccation of a gelatinous outer layer also occurs in other organisms, such as dinoflagellate cysts,

Fig. 12. Calcitic opercular structures. A: Operculum of *Bithynia tentaculata* with central portion composed of calcitic spherules in organic matrix, as shown in B, and marginal portions with calcitic growth as in C and D. European lakes. Bar scale = 1 mm. B: Central portion of the operculum of *Bithynia* composed of calcite spherules in organic shell. Bar scale = 100 microns. C: Growth on operculum margin in *Bithynia* is similar to growth of calcitic outer shell layers in *Nucella* (Figure 11D). Bar scale = 10 microns. D: Calcitic growth in the operculum of *Bithynia* forms larger units with uniform optical orientation forming a mosaic pattern. Bar scale = 10 microns. E: Transverse fracture of the calcitic operculum of *Tudora* from Curaçao shows an almost purely mineral composition with the growth of larger crystal units. Bar scale = 10 microns. F: Growing surfaces of the operculum of *Tudora* show similar features as in shell layers of *Nucella* and *Littorina* (Figure 11), forming a coarse pattern of crystallites with differing optical orientations. Bar scale = 10 microns.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and the resulting biominerals may look very much alike (Bandel and Keupp, 1985).

In *Monachoides* the calcitic crystallites which form in the gelatinous egg cover do not unite to form a solid shell. Before the embryo hatches, the crystallites disappear by dissolution and their calcium carbonate becomes integrated into the growing shell of the young snail. In *Helix*, *Cepaea* and *Discus* the interior of the calcified eggshell becomes only partly etched prior to hatching. This demonstrates that gastropod egg shells are only partly protective, and to a large extent they serve as calcium carbonate reservoirs for the developing embryo.

Eggshells in terrestrial pulmonates are characterized by irregular intergrowths of angular to acicular calcite rhombohedra. In *Helix* the rod-like rhombohedra are initiated on the basal membrane of the cover of the inner egg case. Crystal orientation is random and crystal rods commonly intergrow to form cross-like shapes. *Discus* eggs have blocky calcitic rhombohedra which have one edge contacting the inner membrane, but these likewise show a random pattern.

D. Internal Shells of Slugs.

As in all gastropods, the naked pulmonate slugs *Deroceras* and *Arion* form a shell, but only after the shell gland has become internalized by a covering muscular mantle tissue (Bandel, 1982). This organic shell is mineralized from below, but in a very simple way and with calcite. The shell consists of irregular aggregates of calcitic crystallites and larger crystallites with regular surface patterns. The latter may show a very regular crystal growth surface which resembles the fibrous prismatic structure of *Mytilus* or the foliated structure of *Anomia*. This internalized calcitic shell functions as a calcium carbonate reservoir, and all of its mineral is mobilized when eggs are laid (Fournié, 1979).

E. Discussion of Calcitic Structures.

Unlike aragonitic crossed lamellar and related structures, calcitic structures in gastropod shells do not contain cushion-like basic structural units. Instead, calcitic structures consist of needles, rods and plates which represent the growth fronts of larger structural units with uniform optical properties. The smallest structural elements visible on growth surfaces show a variety of sizes unlike the uniform size of basic structural units in aragonitic structures. The morphology of these structural units is commonly influenced by associated organic shell deposits. With the exception of some archaeogastropods, gastropod calcitic shell layers are generally limited to outer shell walls (*e.g.*, in many Neritomorpha, in a few mesogastropods and neogastropods, and in the internalized shell of pulmonate slugs). Calcite also occurs in the opercula of many unrelated gastropods, in the egg capsule of some Neritidae, and in the mineralized eggs and diaphragmata of pulmonates. Among non-archaeogastropods, highly organized, complex calcitic structures are apparently absent.

IV. Transplantation Experiments: Implications for Biomineralization

One approach to understanding the processes of shell formation is to observe transitions leading from one structural type to another, especially in association with shell repair and in experiments with shell deposition on transplanted materials. Reaumur (1709, in Biedermann, 1902) broke pieces from the shell of *Helix* and replaced them with fine leather to observe the mineral deposits on its surface. Similar experiments were conducted by Bandel and Keupp (1985), who transplanted fresh shell material from the bivalves *Mytilus*, *Pinna*, *Anomia* and *Pinctada* onto large *Helix* shells in which a shell window was made without damaging the underlying mantle epithelium. The research provided evidence for the influence of growth surfaces and their covering extrapallial fluid on mineralization. *Helix* uses mucus for rapid shell repair and in the formation of its temporary operculum (diaphragma). The mucus forms cystallites of variable shape and orientation which are connected by organic sheets and fibers.

When the depositional surface of the calcitic simple prismatic layer of *Pinna* is transplanted onto *Helix*, new calcitic crystal growth follows *Pinna*'s prismatic surface faithfully, with somewhat more rapid growth at the prism margins. This occurs whether or not the *Pinna* shell surface was cleaned of extrapallial fluid with a solution of sodium hypochlorite. Small, triradiate crystallites with their c-axis perpendicular to the surface form on the *Pinna* prismatic layer, reflecting directions within a spherulite prisms on the transplant shell. Untreated or cleaned calcite folia from *Anomia* induce growth along the step-like growth edges of the blade-like units of this structure. However, the large surfaces of the folia remain free of new crystallites. In *Mytilus* the sheet-like flat rods of the calcitic prismatic outer shell layer are strongly inclined to the surface of growth, thereby increasing the density of exposed crystal edges. In this case the new calcite crystals form such a dense layer that little of the original structure is apparent except for conservation of the original optical orientation. These experiments demonstrate that introduced growth surfaces, regardless of their mineralogy and microstructure, can serve as matrices for ordered crystallite growth in host shells

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Fig. 13. Eggshell structures. A: Egg of *Discus rotundatus* (Endodontidae, pulmonates) with solid calcitic shell; from middle European woodlands. Bar scale = 100 microns. B: Detail of the egg shell of *Discus* with heads of regular calcitic crystallites leaving small pores between each other that connect the atmosphere with the interior of the egg. Bar scale = 10 microns. C: The egg cover of *Perforatella* (small pulmonate from German gardens) contains aggregates of calcite which dissolve when the shell of the embryonic snail becomes mineralized. Bar scale = 10 microns. D: The eggshell of *Helix aspera* is rather solid but calcite crystallites show quite irregular growth patterns. Central Europe. Bar scale = 10 microns. E: Fractured egg shell of *Discus rotundatus* is composed of a fine-grained inner layer and a columnar outer layer of calcitic crystal growth. Bar scale = 10 microns. F: Egg capsules of *Nerita polita* from the rocky shore of the Red Sea contain calcitic crystal spheres, whereas those of most other members of the genus *Nerita* are composed of aragonite (Figures 9E,F).

regardless of their presence or absence of original extrapallial fluid.

Not only the structure and orientation but also the mineralogy of the crystallites is determined by the implanted depositional surface. When the depositional surface of *Pinna* nacre is transplanted, aragonitic crystallites form. With transplanted aragonitic nacre from *Pinna*, *Pinctada* and *Mytilus*, new crystal growth begins primarily at the nacre tablet margins. Only actively growing (incomplete) nacre tablets induce new crystal growth over their entire surface. No difference is seen when the surficial extrapallial fluid is removed from the transplant. The new growth of this nacre brings out previously hidden directions of crystal arrangement within the tablets. It becomes evident that mature nacre is characterized by two crystallographic orientations which resemble crossed prismatic structure. Immature nacre induces the growth of small tablets or acicular crystallites with more than two directions, revealing a pattern transitional to spherulitic prismatic structure. Significantly, transitions from nacre to crossed acicular structure and to spherulitic prismatic structure are common in nacreous molluscs (Bandel, 1977; Erben, 1974).

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

Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends. Volume I. Joseph G. Carter, editor. Van Nostrand Reinhold, New York.

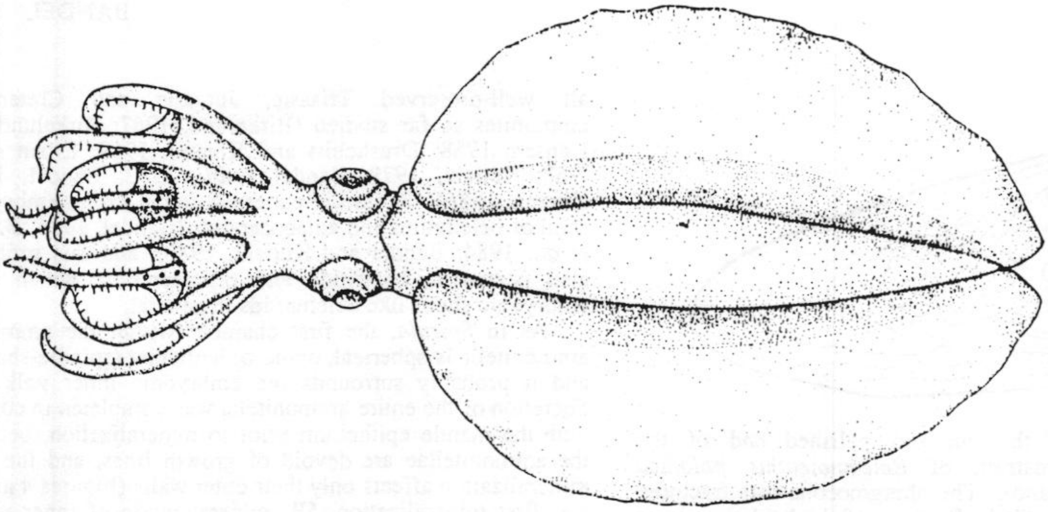

Fig. 1. Reconstructed *Trachyteuthis hastiformis* seen from above. The vampyromorph squid was up to 53 cm long and lived near the lagoons of the Solnhofen area (southern Germany) in the shallow northern margin of the Tethys Ocean during Upper Jurassic times. From Bandel and Leich (1986, Fig. 20).

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 intracameral deposits such as those in pseudorthoceratids (Ristedt, 1971). One might well call these pseudorthoceratid intracameral deposits a cement which formed while the animal was living. During shell repair, similar prismatic cements are known to have been deposited by *Belemnoteuthis* (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 intracameral 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

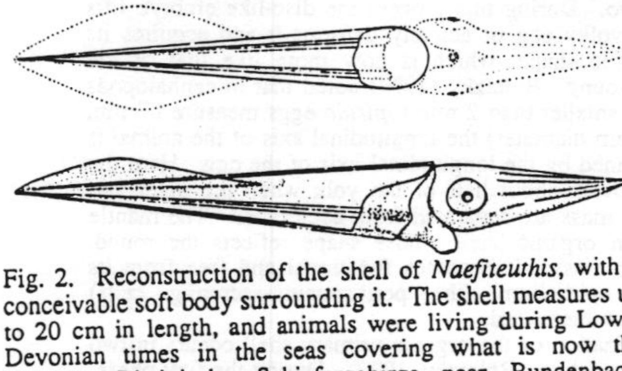

Fig. 2. Reconstruction of the shell of *Naefiteuthis*, with a conceivable soft body surrounding it. The shell measures up to 20 cm in length, and animals were living during Lower Devonian times in the seas covering what is now the southern Rheinische Schiefergebirge near Bundenbach, Germany. From Bandel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

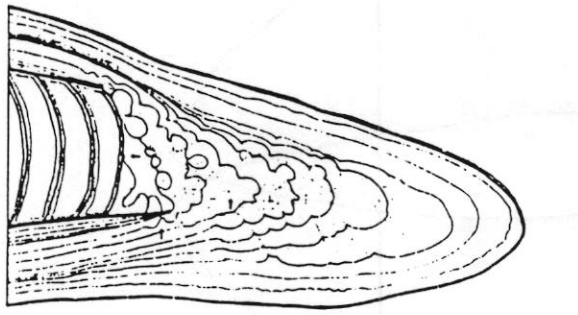

Fig. 3. Sketch of the cut and polished end of the phragmocone and rostrum of *Belemnoteuthis polonica* (Middle Jurassic, Poland). The phragmocone was fractured during life but then healed. Portions of the healed rostrum show spherulithic structure (arrows). Chambers close to the repair are partly filled 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 yolky 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 bactritids and orthoceratids, which have embryonic shells like belemnitids 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 mineralizaiton 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 tubercules is present, the crystallites show their spherulitic orientation best within these tubercules.

Interestingly, archaeogastropods 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.

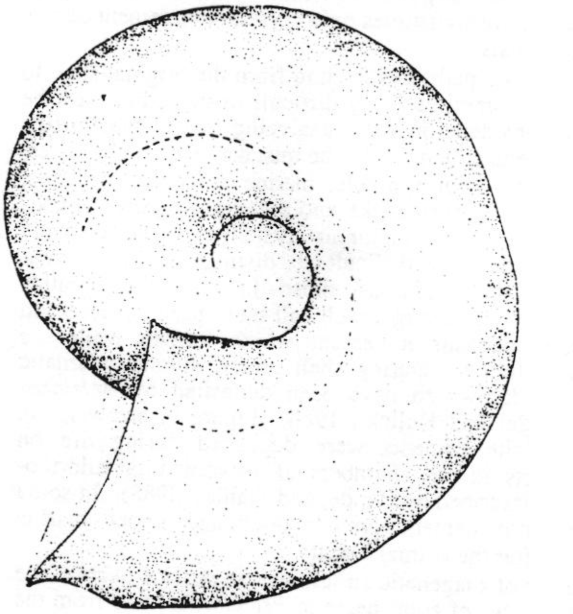

Fig. 4. The outer shell of the ammonitella, already detached from the gland cells of the mantle edge, but before mineralization has covered much of its initial shell cup (indicated by the stippled line). The ammonitella was initially unmineralized. From Bandel (1982, Fig. 40).

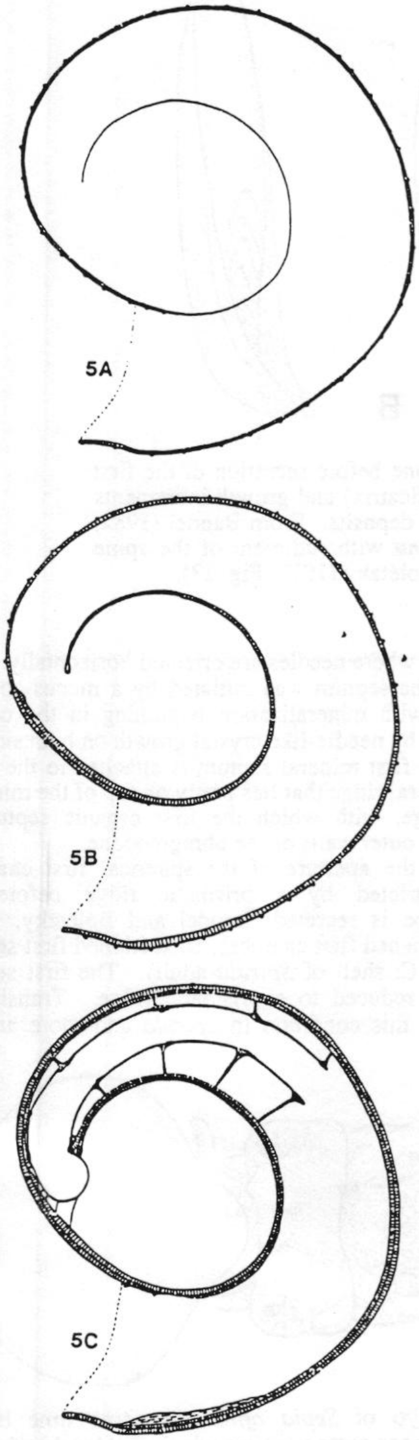

Fig. 5. Stages in the mineralization and construction of the first chambers in the ammonitella of *Quenstedtoceras* from the Middle Jurassic of Poland. A: Median section through an ammonitella after mineralization of the outer shell walls. B: Ammonitella after deposition of the first inner prismatic 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 *Natuilus* 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

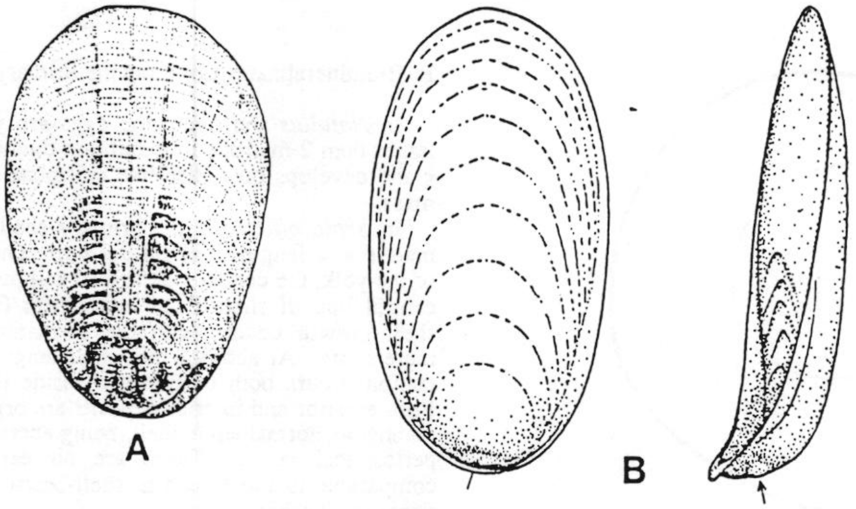

Fig. 6. Cuttlebone of young *Sepia*. A: *Sepia officinalis* cuttlebone before secretion of the first mineral layer on the inside shows the scar on the primary shell (cicatrix) and growth increments on the secondary shell. These are later covered by outer mineral deposits. From Bandel (1982, Fig. 55). 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 proseptum is prismatic whereas the second septum is nacreous (Kulicki, 1979; Bandel, 1982; Landman and Bandel, 1985). The microstructure of the proseptum 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 proseptum 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 proseptum.

This type of prismatic proseptum, 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 belemnitids) have a similar prismatic septum which differs in shape from the later nacreous septa. But belemnies 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 belemnitid 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

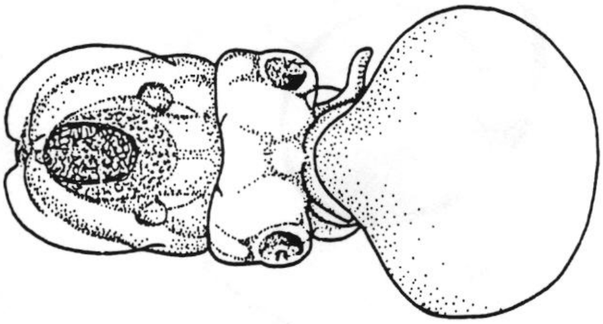

Fig. 7. Embryo of *Sepia officinalis* some time before hatching, with large outer yolk sac which will be absorbed by the time of hatching. At that time, the animal will have doubled in size. The shell has two complete chambers, and the third is being formed. The first-formed chamber has been emptied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

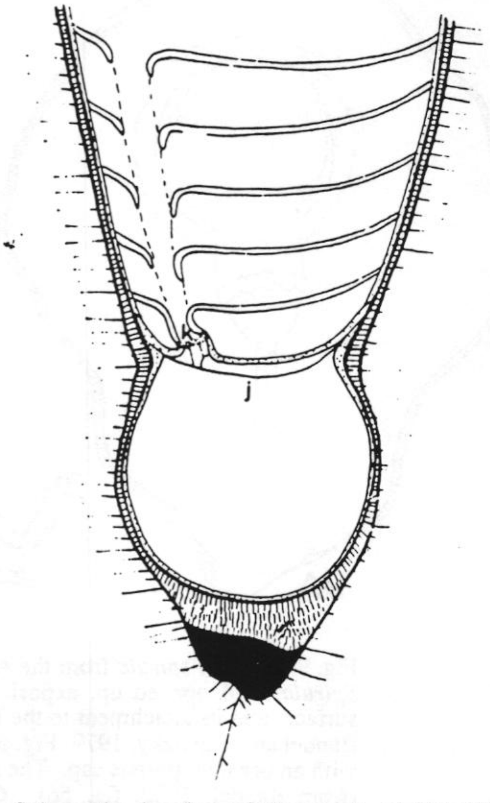

Fig. 8. Schematic drawing of the conch of *Hibolithes* as contained within the calcitic rostrum. The first septum (j) is organic, while the following second septum is prismatic and the third and later ones are nacreous and mineralized. The primordial rostrum is in part aragonitic, prismatic and organic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

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 polycrystaline aggregate. The nacre tablets are usually deposited in discrete stacks on the depositional surface. These stacks expand laterally as they

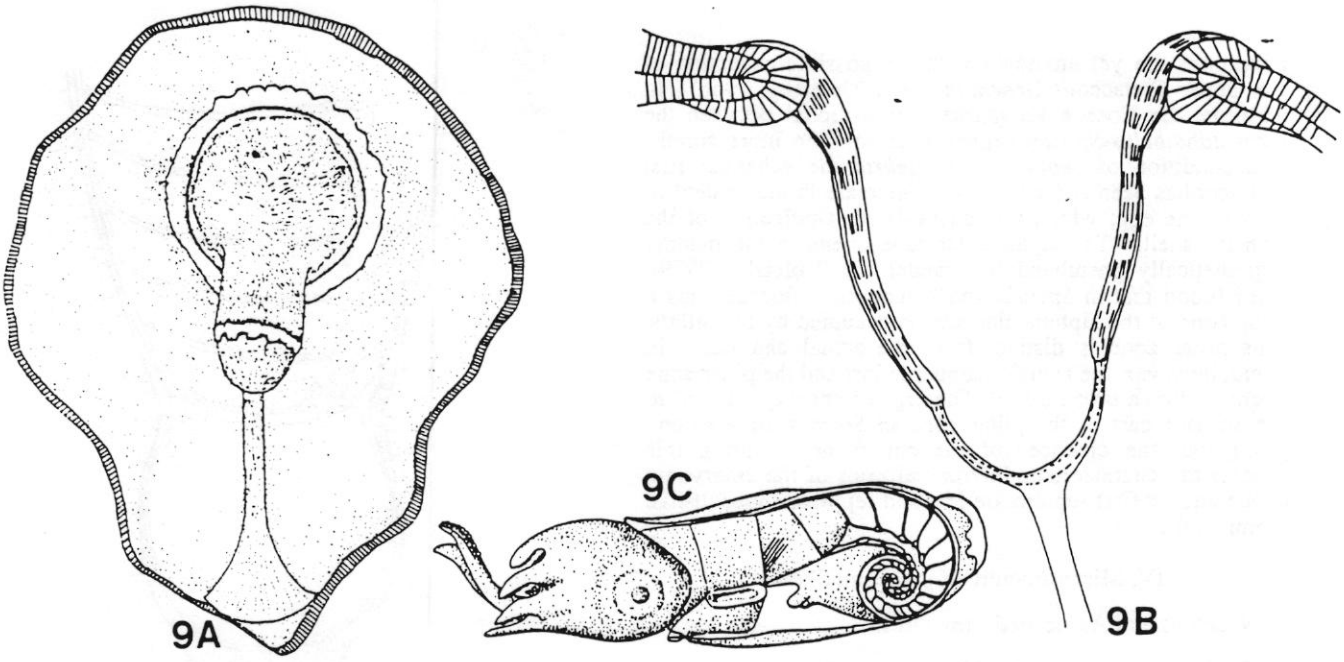

Fig. 9: *Spirula spirula* from the Atlantic Ocean near Canary Island. A: The first chamber of the *Spirula* shell opened up, exposing the earliest part of the siphuncular tube with its wrinkled surface, and its attachment to the inner wall *via* the organic sheet that is roughly spatulate (from Bandel 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

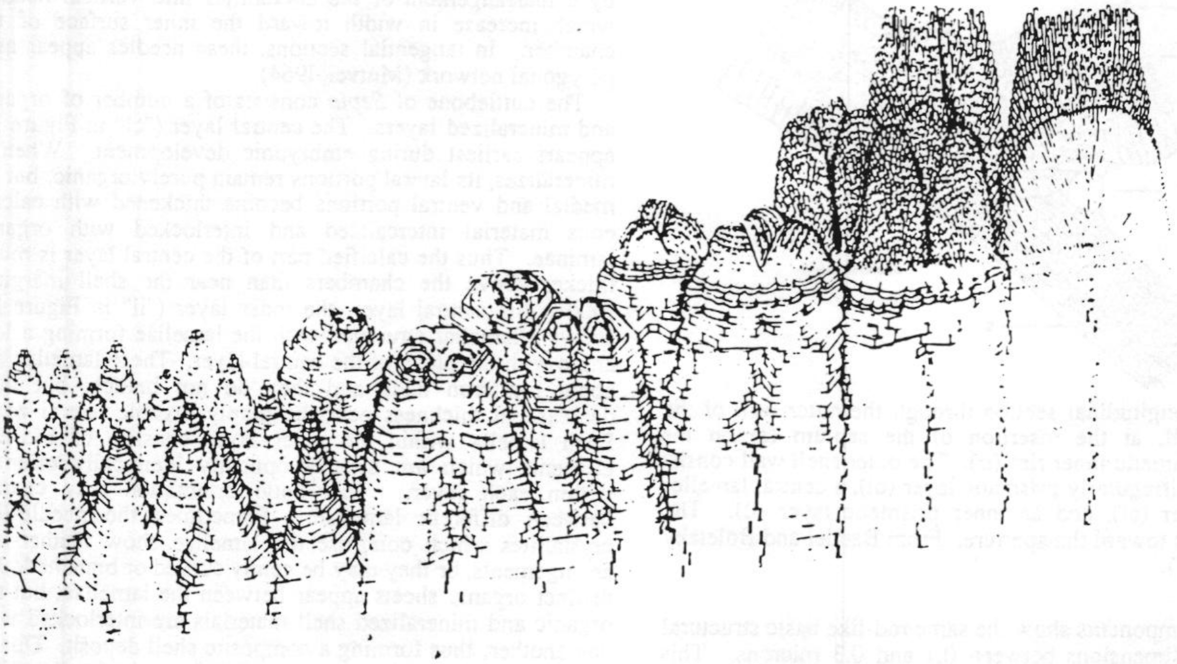

Fig. 10. Diagrammatic drawing of the succession of layers during growth on the inner surface of the shell as may be found within hollow spines, repair sections or blisters in molluscan shell with nacreous structure. At the left columns of nacre plates are oriented as single entities. At the left center 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 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.

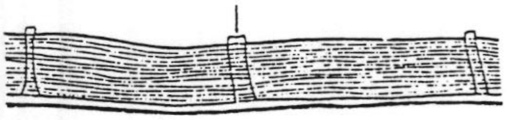

Fig. 11. Schematic representation of the chamber contents of embryonic *Sepia officinalis*, with chamber liquid in a gelatinous state and exhibiting periodic striations which match the annulation of its pillars. The annulations are preserved below an organic membrane. Similar fine gel layers are responsible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

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.

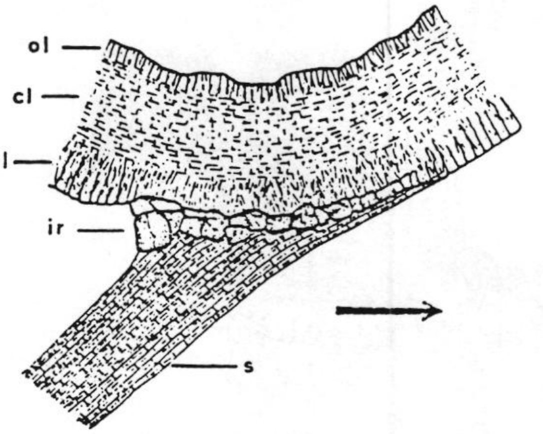

Fig. 12. Longitudinal section through the outer wall of the *Spirula* shell, at the insertion of the septum (s) on the coarsely prismatic inner rim (ir). The outer shell wall consist of an outer, irregularly prismatic layer (ol), a central lamello-fibrillar layer (cl), and an inner prismatic layer (il). 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.

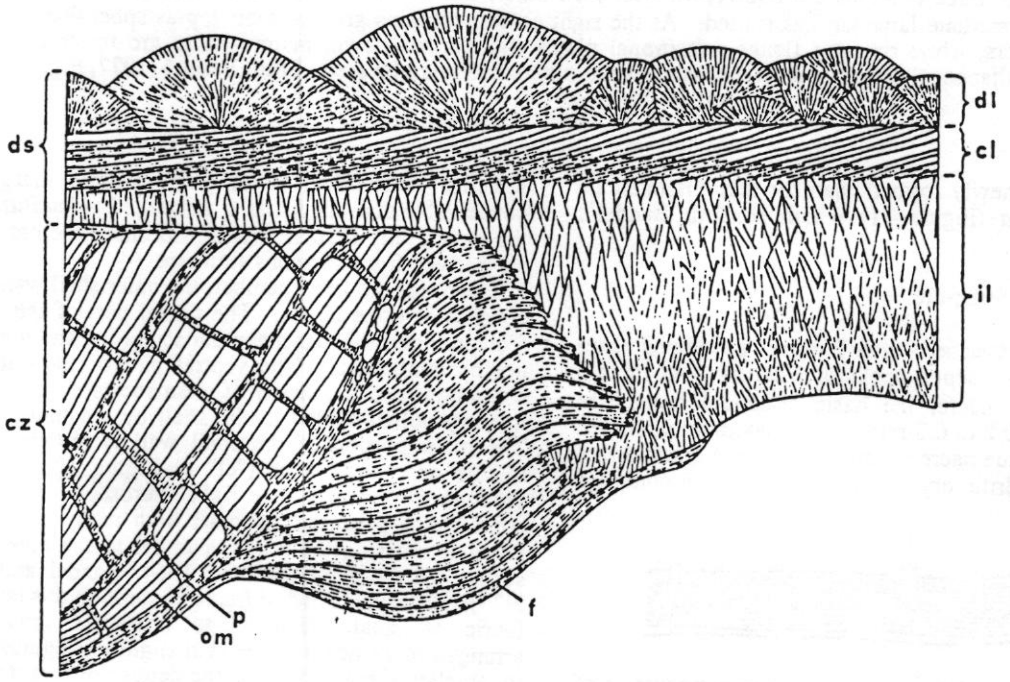

Fig. 13. Cross section through the posterior part of the *Sepia* shell, showing the insertion of the chamber zone (cz) on the lower side of the dorsal shield (ds), the latter comprising three layers: the dorsal layer (dl), the central layer (cl), and the inner layer (il). Between the marginal part of 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).

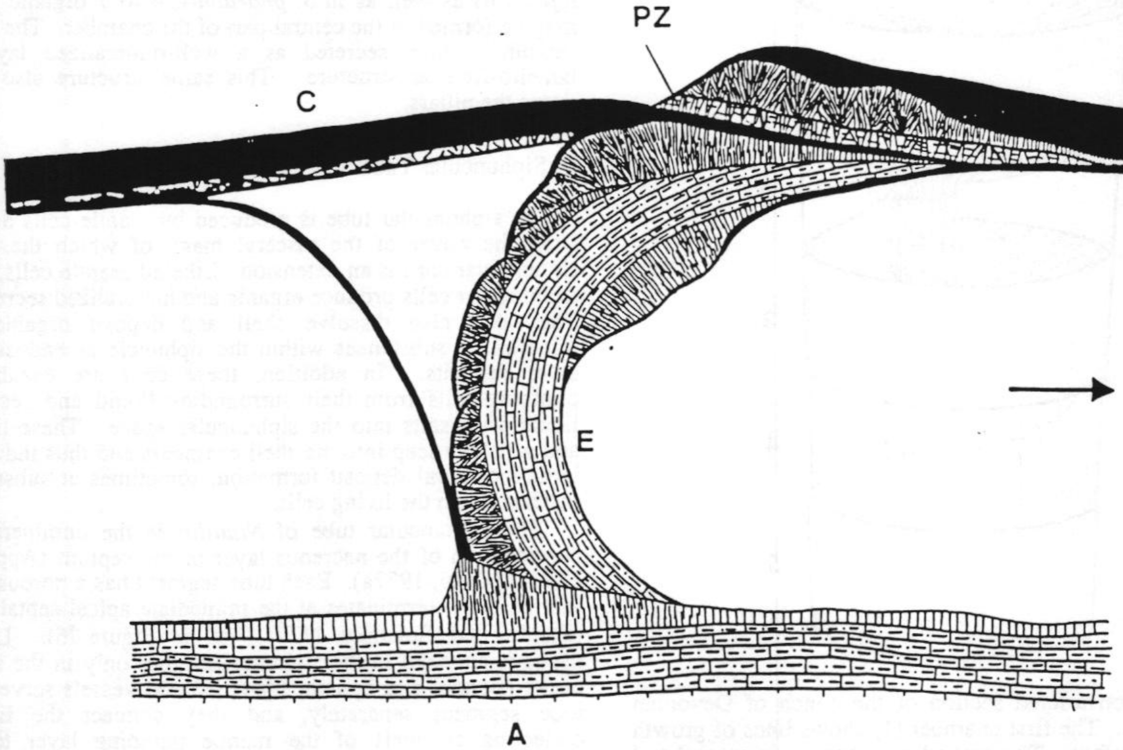

Fig. 14. Longitudinal section through the ventral half of the siphuncular tube of *Quenstedtoceras*. The arrow points toward the aperture. The horny tube (C) is attached to the first septal layers as well as to the "mural ridge" on one side of the chamber and to the septum surface and the inner side 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*

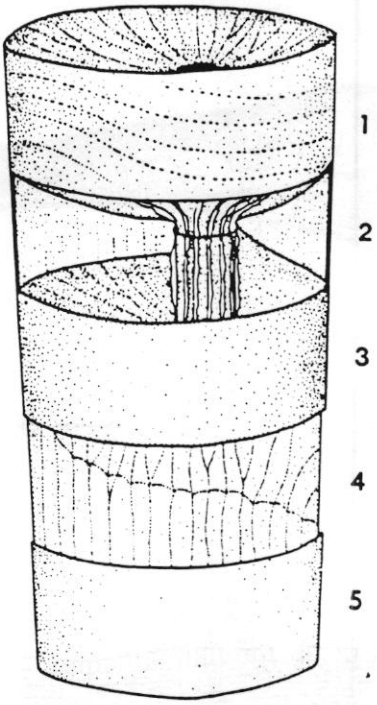

Fig. 15. Reconstructed section of the conch of Devonian *Arthrophyllum*. The first chamber (1) shows lines of growth on the shell surface. The second chamber (2) is opened and the thin sheets of its interior are removed to show the siphuncular tube with its venteral attachment membrane. The third chamber (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 sipho 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 chalkly 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

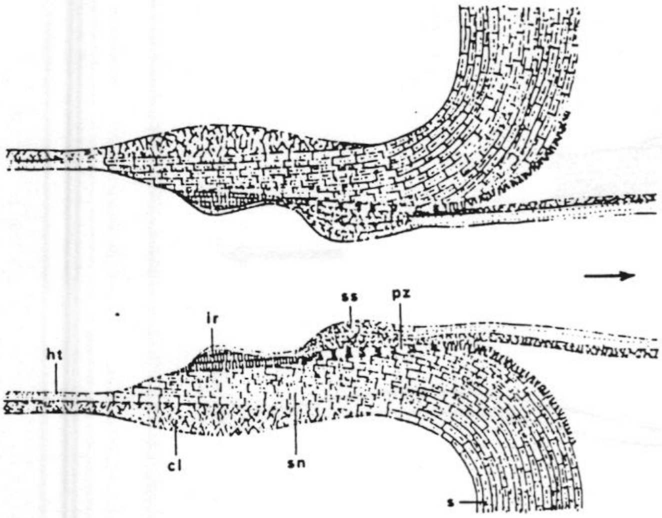

Fig. 16. Longitudinal section of the siphuncular tube of *Nautilus pompilius*. The arrow points toward the aperture. The nacreous layers of the septum (s) continue into the septal neck (sn), the organic parts of which are continuous with the horny tube (ht). The septal neck and the horny tube are covered 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 siphunucular 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 biconcial 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 subterminal 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

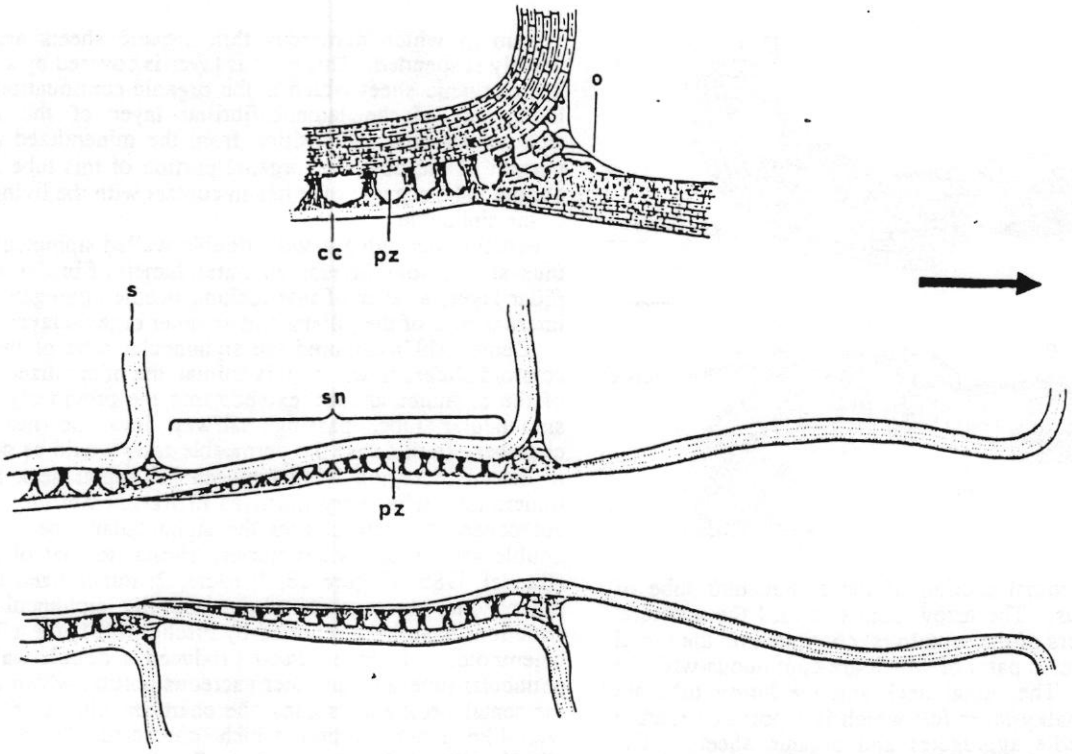

Fig. 17. Horizontal section through the siphuncular zone of *Spirula*. The layers of the septum (s) continue into the siphuncular tube. At the entrance to the septal neck of the next older septum, the lamellar layers split into organic sheets (o) that close up the pillar zone (pz). Here organic sheets 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

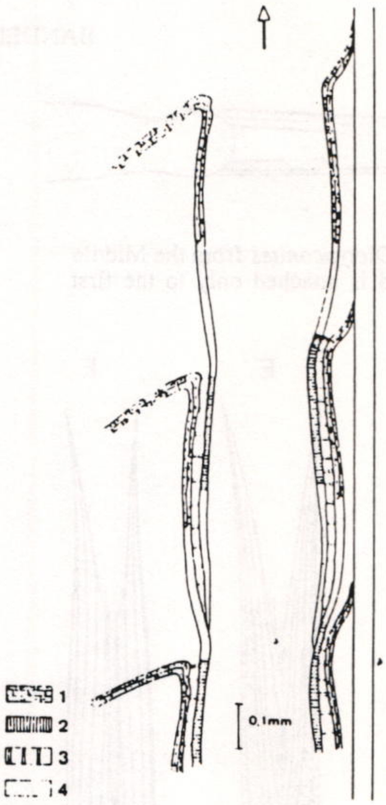

Fig. 18. Reconstruction of the siphuncular tube of the Middle Triassic aulacoceratid *Dictyoconites* from the St. Cassian Formation of the southern Alps. The longitudinal section of the tube shows that the lamello-fibrillar structure (1) of the septum continues into the long, mineral septal necks and 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).

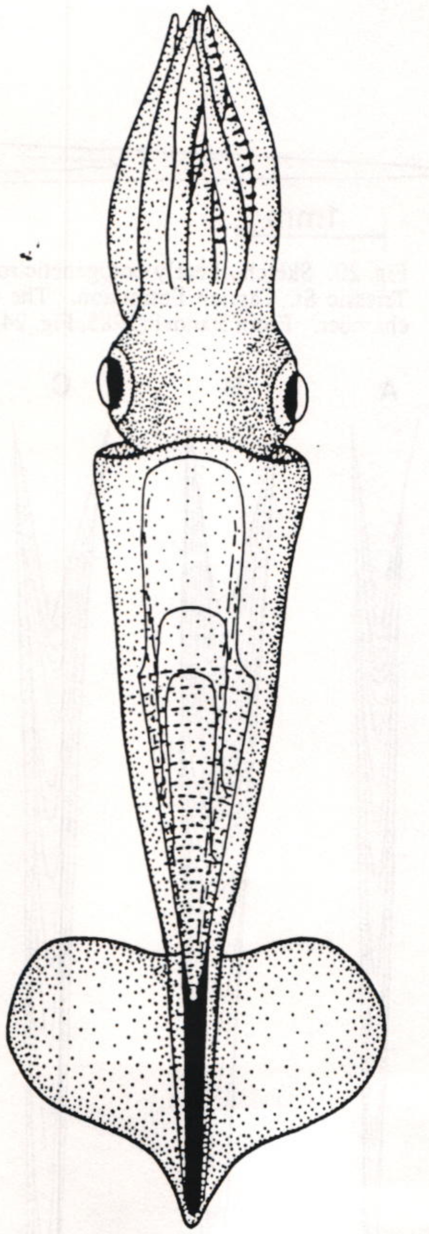

Fig. 19. Reconstruction of *Belemnites paxillosus*, a typical belemite from the Upper Lias of southern Germany, with a shell ca 50 cm in length (total length of animal ca 70 cm). From Bandel and Boletzky (1988, Fig. 5).

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

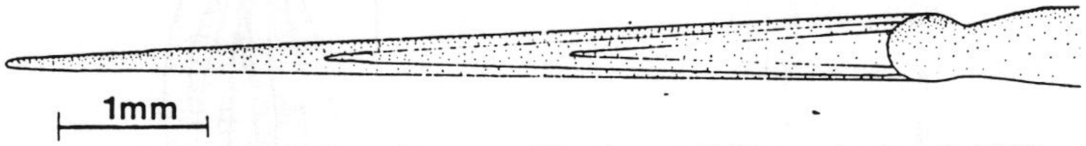

Fig. 20. Sketch of early ontogenetic rostrum of the aulacoceratid *Dictyoconites* from the Middle Triassic St. Cassian Formation. The rostrum is very slender and is attached only to the first chamber. From Bandel (1985, Fig. 24).

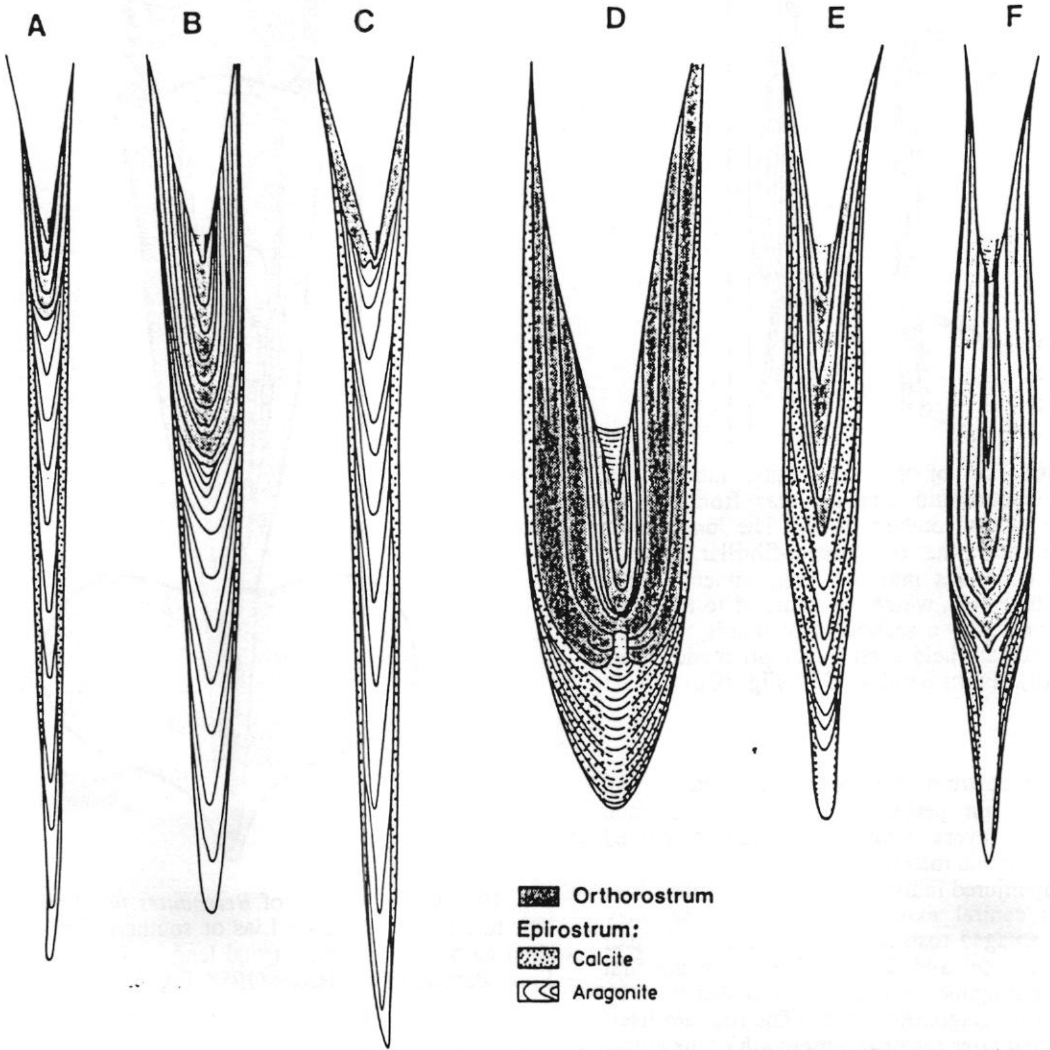

Fig. 21. A. *Belemnites acuarius longisulcata* from the Upper Lias of southern Germany, with a short orthorostrum and long aragonitic epirostrum surrounded by a calcitic cover (7 cm long). B. *Belemnites acuarius* from the Upper Lias of southern Germany, with a medium-size (5 cm long) orthorostrum connected 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 acuarius 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: *Neohibolithes minimus* (Middle Cretaceous, Northern Germany) has a short epirostrum (total length of rostrum 4 cm). From Bandel and Spaeth (1988, Fig. 1).

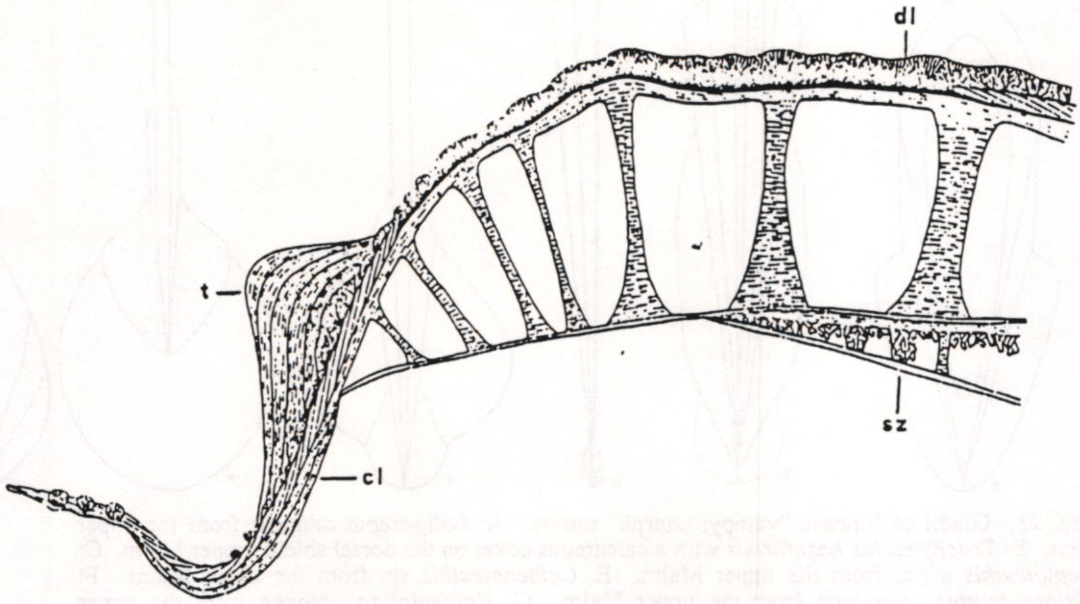

Fig. 22. Longitudial section through the cuttlebone of the embryo of *Sepia pharaonis* from the Red Sea. Five chambers are completed and the spine (s) is present with lamellar structure. The prismatic dorsal layer (dl) forms spherulitic aggregates near the posterior rim of the shell. The central layer (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 epirostrum 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 epirostrum differs in both crystal structure and crystal arrangement form the calcitic rostrum. Whereas the calcitic orthorostrum grows in fine prismatic layers with parallel crystal needles, the aragonite of the epirostrum is commonly arranged in spherulite sectors. In the Toarcian belemnites *Salpingoteuthis*, *Youngibelus*, *Acrocoelites*, and *Dactyloteuthis*, and in the Albian *Neohibolites*, the bulk of the epirostrum 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 epirostrum with an exterior calcitic layer. This layer gives evidence for the completion of the epirostrum, and it may not have been formed in all species with an epirostrum. Many belemnites from the Lias show a step on the preserved calcitic orthorostrum which indicates that an aragonitic epirostrum was present but is not preserved. Transitions from aragonitic to calcitic lamellae are commonly observed in epirostra, 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*, *Gonioteuthis*, and *Belemnellocamax* (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

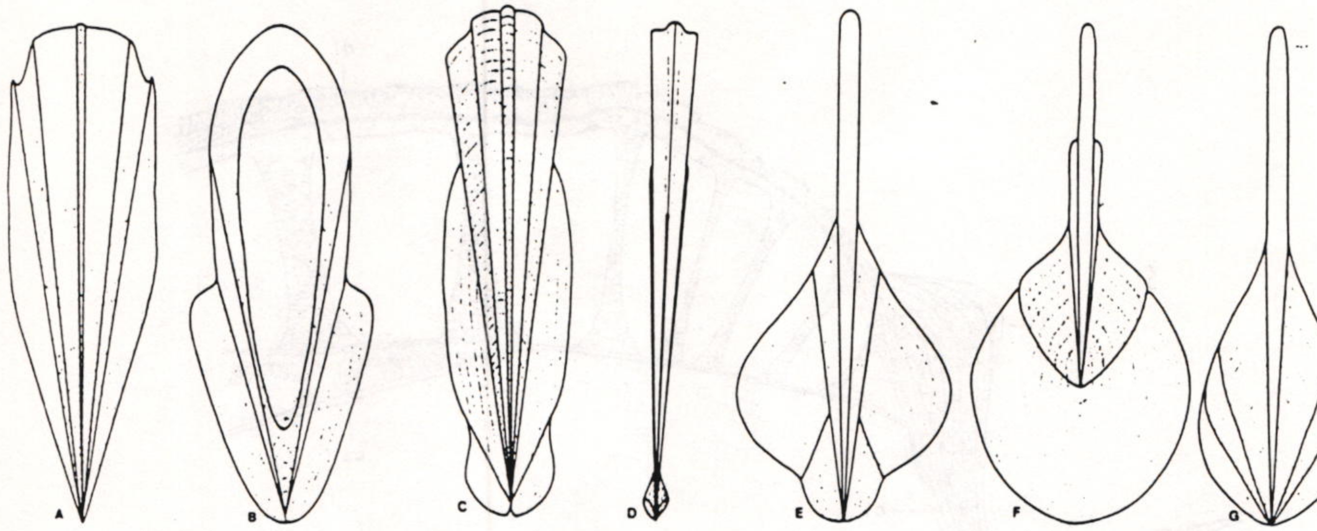

Fig. 23. Gladii of Jurassic "vampyromorph" squids. A: *Loligosepia aalensis* from the upper Lias. B: *Trachyteuthis hastiformis* with a calcareous cover on the dorsal shield; upper Malm. C: *Leptoteuthis gigas* from the upper Malm. E. *Celaenoteuthis* sp. from the upper Malm. F: *Celaenoteuthis scutellaris* 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: *Loligosepia*, B: *Trachyteuthis*, C: *Leptoteuthis*, D: *Plesioteuthis*, 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*; or 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 continous 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

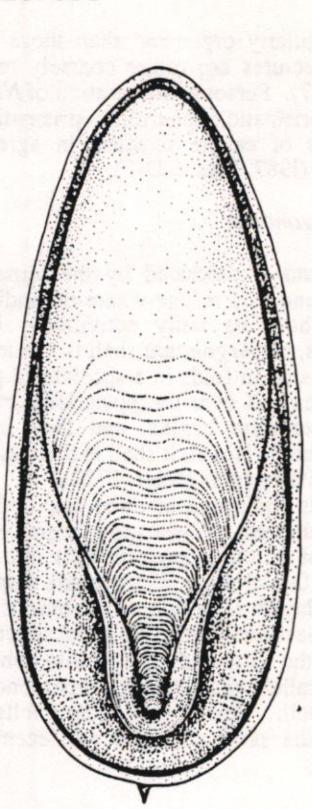

Fig. 24. Ventral view of the cuttlebone of *Sepia*, with flat chambers secreted in the depression of the dorsal shield.

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

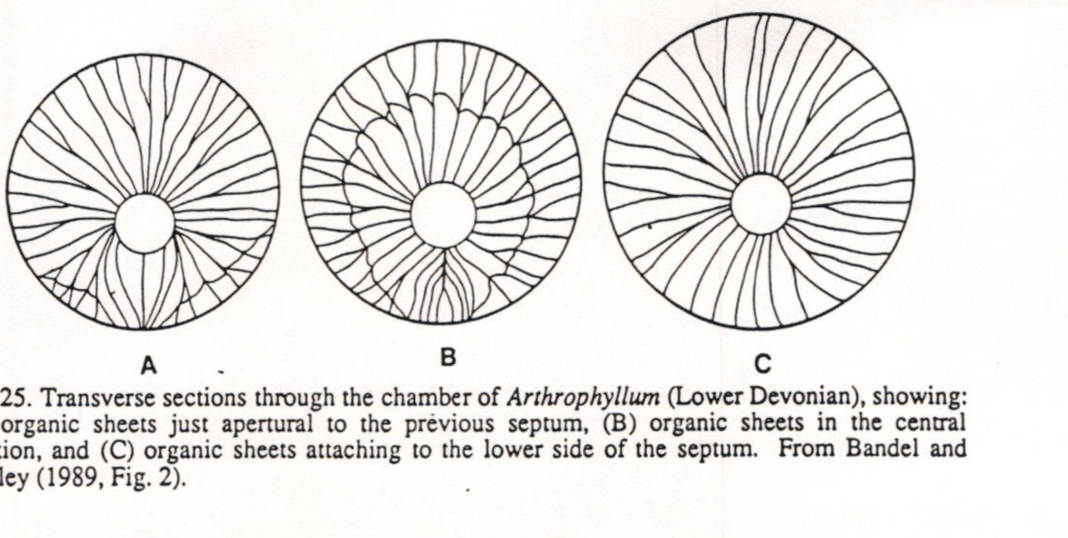

Fig. 25. Transverse sections through the chamber of *Arthrophyllum* (Lower Devonian), showing: (A) organic sheets just apertural to the previous septum, (B) organic sheets in the central position, and (C) organic sheets attaching to the lower side of the septum. From Bandel and Stanley (1989, Fig. 2).

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 adquately evaluated (see Dzik, 1984). Septae were used to close the siphuncular tube, as noted for the ellesmeroceratid *Pictetoceras* by Mutvei and Stumbur (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 positon 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. Depositon 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.