

The ammonitella: a model of formation with the aid of the embryonic shell of archaeogastropods

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Recent archaeogastropoda secrete their first conch (primary shell) without producing increments of growth. This conch remains attached to the epithelium responsible for its production until completed. Only afterwards does tissue detach from the edge of the shell and the conch begins to function as a protective exoskeleton. After a potential swimming phase by the veliger larva, the organic primary shell is deformed by mechanical means through muscular tension from the inside and the outside of the conch. It then becomes mineralized by aragonitic crystallites and, thus, functional for the use of a benthic animal. The embryonic conch of ammonites (ammonitella) is devoid of increments of growth. The inner lip (dorsal side) of the aperture became flattened after the evenly rounded primary conch had been secreted. The primary organic shell was mineralized by aragonitic crystallites from within. All these features of the formation of the ammonitella can be interpreted in the light of early shell formation of recent archaeogastropods. □ *Molluscs, ammonites, early ontogeny, shell structure.*

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Formation of the shell in conchiferan molluscs is characterized by several features common to all representatives of the group. One is the presence of a shell gland or mantle rudiment differentiated from ectodermal cells of an area of the embryonic body that lies close to the rudiment of the hind gut. Another is the differentiation of these cells into three regions of the molluscan mantle that are characterized by cells of different shape and by different functions. Shell production is initiated by cells secreting organic fibres and substances binding them together to a first conch (primary shell). These cells grow across the visceral mass and finally comprise the periostracal groove or grooves found near the growth edge of each conch. Behind this layer of gland cells of the periostracal mantle, the visceral mass is covered with mantle cells that are responsible for the formation of the mineral shell (shell mantle). Anterior to the periostracal cells, a muscular mantle forms that is responsible for the shape of the conch and provides a base for shell secretion in the periostracum-gland zone. In some molluscs the mantle grows into ridges that cover the shell margin and may even enclose the shell.

Usually the first shell formed in conchiferan molluscs (primary shell) is attached to the soft tissue by cells of the gland zone that produces it. This zone represents the only attachment between shell and soft tissue (Bandel 1982). Later,

new connections from the body to the shell develop and the mantle edge becomes detached from the shell margin. Only after this independence of the shell from its secreting epithelium is a continuous layer of the mineral deposit added to the organic conch from the inside.

The mode of shell formation in archaeogastropods, described in detail by Bandel (1982), can be utilized for understanding the early shell deposition, shaping and mineralization of the ammonitella, and the embryonic shell of ammonites. The chambered interior of the conch cannot be explained using this model, but knowledge of ontogenies of recent cephalopods with chambered shell (Bandel & Boletzky 1979) can be utilized or comparison can be made with fossil cephalopods such as belemnites (Bandel *et al.* 1984).

Large numbers of nuclear whorls of different ammonites have been studied and described in the literature by several authors. Extensive reviews on older publications can be found in Erben *et al.* (1968), Kulicki (1979), Drushchits & Doguzaeva (1981) and Bandel (1982). A number of models proposed for the formation of the ammonitella have been reviewed in detail by Bandel (1982).

An amazing uniformity of ammonitellae of different ammonites throughout their existence can be found and has been well documented by Er-

ben *et al.* (1968). The ammonitella can be considered a factor uniting all ammonites and differentiating this group clearly from all other cephalopods. It developed within the root stock of ammonites during Lower and Middle Devonian times (Erben 1964, 1966) and remained basically unchanged until the extinction of ammonites at the end of the Cretaceous. The great uniformity of shapes and structure of the ammonitella throughout the existence of ammonites indicates that all ammonite embryos developed basically in the same way, independent of the taxonomic position of their progenitors and of whatever differences may have existed in their life history.

The ammonitella

Morphology. – Erben (1964, 1966) stated that all ammonitellae known have two morphologic constrictions. One is located near the apertural end of the initial chamber ('protoconch') (Fig. 1A, 1B), the other marks the apertural end of the ammonitella ('nepionic constriction' of Hyatt 1872) (Fig. 2). The initial chamber is wider than high and almost as wide as the whole ammonitella is high, and is covered in large part by a planispiral whorl coiled tightly around it (Fig. 1A, 1B).

The first constriction actually consists of the flattened inner lip of the ammonitella aperture. It is the ventral wall of the initial chamber (Fig.

1B). The dorsal side of the initial chamber, in contrast, is smoothly rounded. The flattened inner lip can usually be noted in median section, as for example in numerous plates in Drushchits & Doguzaeva's book on ammonites (1981, Pls. 15, 18, 19, 26, 28, 29, 31, ... 40). It is, therefore, a general feature of the embryonic shell of the ammonites.

The second constriction lies near or at the end of the ammonitella. The primary shell always differs from the subsequent shell in both ornamentation and shape (Fig. 2). The second constriction is located above the flattened inner lip of the aperture marking the first constriction. It is conspicuous from the outside of the shell and, even more so, in steinkerns, because it is accompanied by a thickening of the shell which, in turn, produces a groove on its cast.

The surfaces of all ammonitellae that have been studied and that have the original shell preserved lack growth lines, although exceptions can possibly be found among the earliest ammonites (Erben 1964, 1966, pers. comm. 1983). Up till now, well-preserved surfaces have shown a more or less regular sculpture or tubercles (Bandel *et al.* 1982; Bandel 1982; Landman & Bandel 1985), as is figured here in the case of *Baculites* from the Upper Cretaceous of Jordan (Fig. 1A). The sculpture is found on all outside walls of the ammonitella and ends abruptly with the second constriction. Following whorls have a different sculpture (Fig. 2).

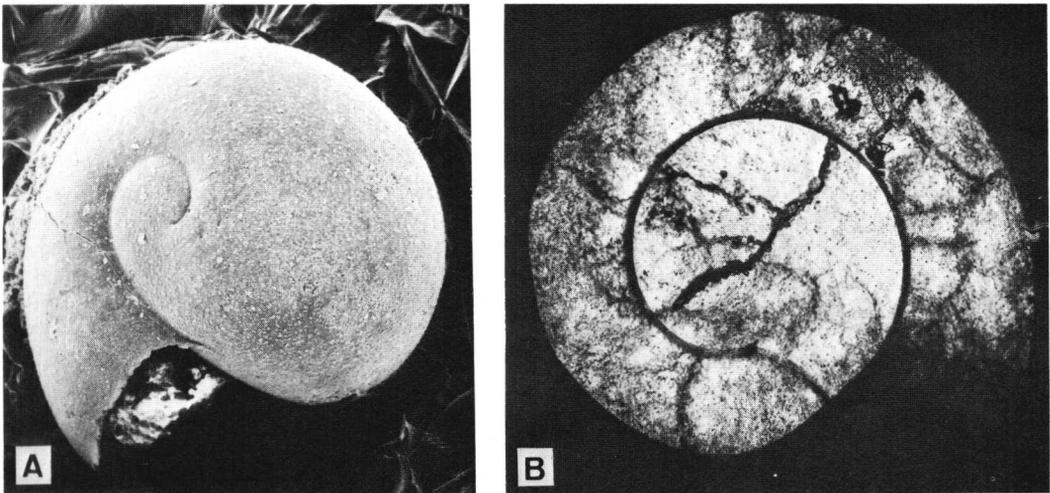


Fig. 1. □ A. Ammonitella of *Baculites* from the Campanian (Upper Cretaceous) of Jordan. The embryonic shell of an ammonite consists of two whorls. $\times 70$. □ B. Section of ammonitella of *Vallites* from the lowermost Namur C (Carboniferous) of West Germany. The planispiral whorl is coiled tightly around the initial chamber. The inner lip of the ammonitella is flattened. $\times 80$.

Fig. 2. Shells of two juvenile individuals of *Reticuloceras* from the Namur C of West Germany show the change in the sculpture from ammonitella to juvenile shell as well as the thickening (nepionic constriction) of the end of the ammonitella. $\times 15$.



Phragmocone. – The ammonitella contains inner walls which separate a chambered part of the conch (phragmocone) from the living chamber that held the bulk of the soft body. These two regions of the conch are connected to each other by the siphuncular tube, which contains the siphuncle, as in recent *Nautilus* and *Spirula*. We can safely assume that the siphuncle of ammonites corresponds in composition and function with that of these living cephalopods and that it represents an extension of the visceral mass. Like its recent counterparts, it was provided with a cover of mantle cells. These functioned as a pumping epithelium that could actively extract salt from extrapallial liquid neighbouring the siphuncular tube (Denton & Gilpin-Brown 1966; further lit. see Bandel & Spaeth 1984). Liquid from the chamber adjacent to this salt-poor extrapallial liquid was therefore sucked from the chamber. Penetration of liquid through the tube was perhaps facilitated by porous zones (Bandel & Boletzky 1979; Bandel 1981, 1982).

The first septum (proseptum of Schindewolf 1954) differs from later septa not only in shape and structure but also in its independence from the siphuncular tube. It was formed before the first segment of the siphuncular tube and before the tissue of the body detached from its anchorage within the first chamber. After septum completion, the tissue became reattached in two spots on the apertural side of the septum (Fig. 3).

Differences in the morphology of the first sep-

tum are present among different ammonite species. These differences are of three types: (1) the course of the septum in relation to the inner lip; (2) the size and shape of the foramen, and (3) the width and height of the whorl. The size and shape of the foramen may be simple, as in the Jurassic *Quenstedtoceras*, or may be extended into a forwards-bent septal neck, as in the Upper Carboniferous *Vallites* (Fig. 4A). This septal neck may form a tube equal in length ventrally and dorsally; it may be longer on one side than the other, and it may be of the same diameter throughout or expand into bulbous shape. Where the neck comes into contact with the inner wall, a suture forms that could be mistaken for an independent second septum with the same structure as the first.

The first segment of the siphuncular tube is attached to the margins of the foramen of the first septum. This attachment is mineralized and consists of prismatic aragonite crystallites. Within the initial chamber, in contrast, the short blindly ending tube (caecum) is anchored with organic sheets that may have a variety of shapes. They may be similar to the long sheets, as present in the recent *Spirula* (Bandel & Boletzky 1979), or may be short and numerous. The range in morphology within a single species may be large, as in the cases of *Quenstedtoceras* (Kulicki 1979; Bandel 1982) and *Scaphites* (Landman & Bandel 1985). The formation of the first blind segment of the siphuncular tube after completion of the first septum is not only documented by tissue attach-

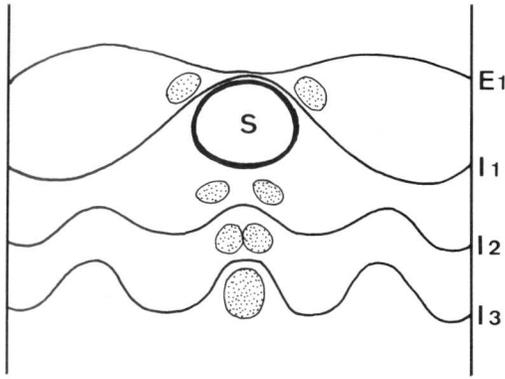


Fig. 3. Sketch of the scars left by the forwards migrating retractor muscles of *Quenstedtoceras* from the Middle Jurassic of the Balticum. The inner lip (E1) is the basal support of the first septum (I1, proseptum). Second septum (I2) and third septum (I3) close four chambers and the migrating muscles left paired scars until uniting from fifth chamber onwards. S = siphuncular tube. Redrawn from original photographs presented by Bandel (1982).

ment scars, but also by attachment sheets glued to the first septum, to the inner lip, and to the outer wall of the initial chamber.

The second septum is nacreous (Birkelund &

Hansen 1967; Kulicki 1979; Bandel 1982). It is continuous with the siphuncular tube that crosses the lumen of the second chamber and attaches to the foramen of the first chamber. It forms by the same process that formed the chamber and its tube section. Differences in its morphology are attributed primarily to three factors: (1) the distance to the first septum; (2) the composition, position and size of the siphuncular tube belonging to it; and (3) the line of attachment to the ammonitella walls (primary suture of Schindewolf 1954).

The second septum may be totally independent of the first and, in which case, may have a complete suture. It may also rest, however, in part or largely on the surface of the first septum, and thus produce an incomplete internal suture or no internal suture at all. The tube segment may be attached to either the dorsal or the ventral wall. Its mineralized apical end may come in contact with the wall, thus forming a small suture that can easily be mistaken for a second prismatic septum (Erben *et al.* 1969). The tube can be totally free, subcentral or submarginal. The septal necks can be turned backwards as in *Nautilus* or they can twist forward as in adult *Quenstedtoceras*

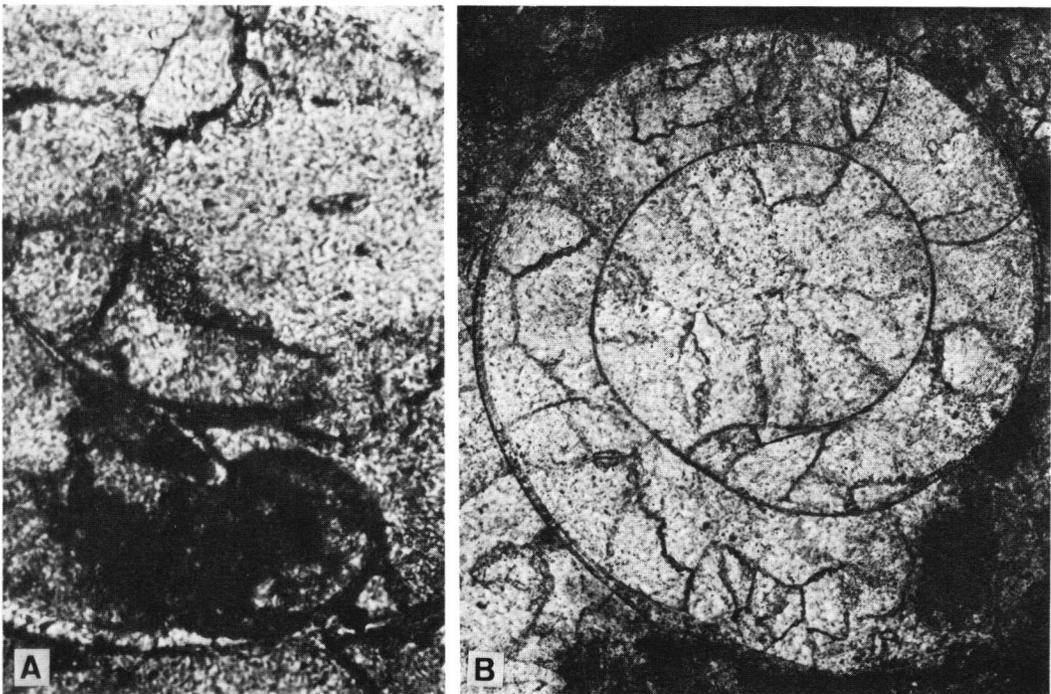


Fig. 4. □ A. Section through the blind end of the siphuncular tube of Carboniferous *Vallites*. This caecum is attached to a tube-like septal neck. ×220. □ B. Initial two whorls of *Vallites* with first septa just below the flattened inner lip of the ammonitella. ×100.

and, thus, a porous zone can be present either at the apical or apertural end of the second chamber (Bandel 1981, 1982).

In subsequent chambers the morphology of the siphuncular tube in different ammonites may be even more diverse. Nacreous septal necks may increase in length, and, connected to them, double tubes similar to those of recent *Spirula* in some clymeniids or long prismatic attachment rings with extended porous zones may form between them. Later septa resemble the second septum, but their attachment to the walls may become more complex. The ammonitella may have only one septum as in an American *Baculites* (Landman 1982) or the Carboniferous *Reticuloceras*, or it may have several septa as in *Quenstedtoceras* (Kulicki 1979; Bandel 1982) and *Baculites* from Jordan.

Shell structure. – The ammonitella is composed of organic and aragonitic shell material. The microstructure of the aragonite is prismatic and nacreous. The second and consecutive septa are nacreous while all other walls, including the first septum, are prismatic. After the second constriction,

the walls are composed of a central nacreous layer covered by an inner and an outer prismatic layer (Erben *et al.* 1969).

The outer prismatic layer of the ammonitella formed by spherulitic prisms growing outward through the primary organic shell into the tubercles of the sculpture (Fig. 5A). This outermost, first formed, mineral layer was deposited only on the outer walls of the ammonitella and totally impregnated the organic shell with aragonitic material. The inner walls and the inner side of the outer shell of the ammonitella were covered afterwards by one to several layers of prismatic structure. The most apical portion of the ammonitella has only one such layer. From the end of the initial chamber to its apertural area several layers are deposited one on top of the other having grown in an inward direction. A maximum wall thickness is reached in the prismatic ridge that forms the base of the first septum.

Each of the prismatic layers ends abruptly, such that a step-like structure is formed on the inner wall of the initial chamber (Fig. 5A). If this is preserved on the surface of the steinkern, distinct lines are seen on the initial chamber that closely

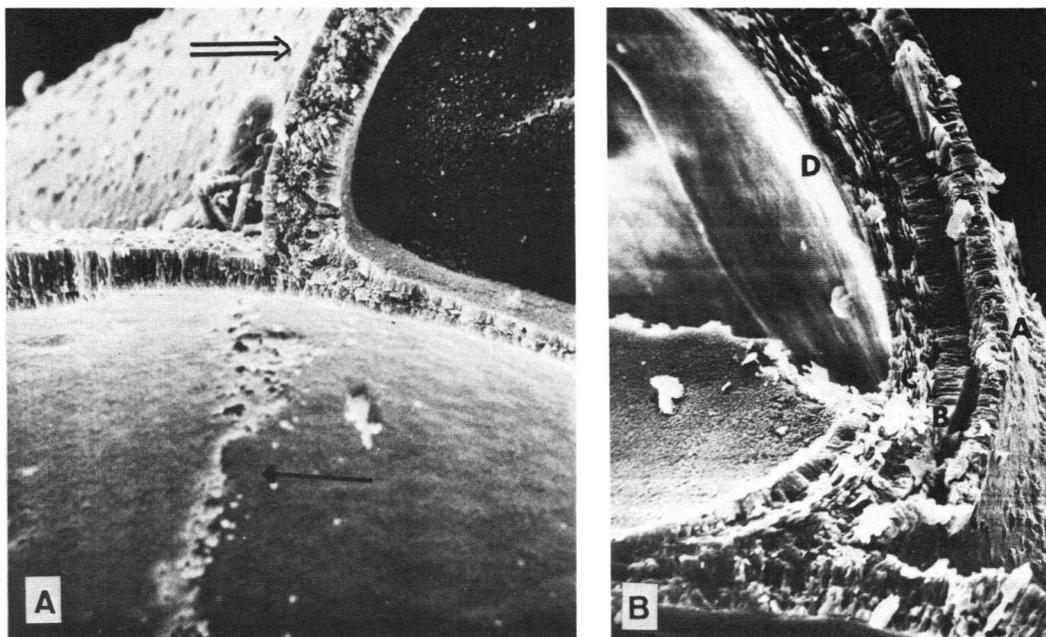


Fig. 5. □ A. The fractured ammonitella of *Quenstedtoceras* shows the step-like end of the inner prismatic layer (arrow) as well as the continuous outer prismatic layer (double arrow). $\times 1000$. □ B. The fractured attachment of the juvenile shell to the shell aperture of the embryonic shell in *Quenstedtoceras*. The prismatic layer of the outer aperture of the ammonitella (A) is underlain by the characteristic adult shell layers consisting of the outer prismatic (B), the central nacreous (C) and the inner prismatic (D) layers. $\times 1000$.

resemble growth lines (Erben 1966; Bandel 1982).

The first septum is prismatic throughout. It, thus, closely resembles the first mineralized septum in the Jurassic *Hibolithes* (belemnite) (Bandel *et al.* 1984) and in the Triassic *Dictyocornites* (Bandel 1985). The second septum is nacreous, as are the following ones. The zone of attachment of the septum to the wall is prismatic, with a transitional change into nacreous structure as shown for *Nautilus* by Mutvei (1972) and, in general, by Bandel (1977).

The inner wall surface of each chamber was covered by a mucous layer during life. This mucous layer functioned as a wick and thus connected the liquid in the chamber with small amounts of liquid present in the porous zones of the septal necks. The mucous layer in recent *Nautilus* has been studied by Bandel & Spaeth (1984). During early diagenesis, mucus is commonly transformed into thin phosphatic crusts that cover all surfaces in each chamber. Organic structures such as the siphuncular tube and its attachment sheets may also be mineralized secondarily (Bandel 1981, 1982). Diagenetically altered mucous layers and organic sheets have been interpreted erroneously as additional primary septa, tubes and branching structures (for detailed discussion of literature see Bandel 1982), or have been regarded as original apatitic deposits secreted by the ammonite (Hewitt & Westermann 1983).

The primary conch of archaeogastropods

Formation. – The early ontogenetic shell of archaeogastropods is formed in a way that is different from that in all other gastropods. The exclusion also holds the Neritacea, which represents an own order of gastropods separate from both archaeogastropods and higher prosobranchs (Bandel 1982).

Early in the embryonic development, just after ectodermal and endodermal epithelia have been differentiated; a region of ectodermal cells is transformed into the shell gland. An organic shell in the shape of a regular concave cap is secreted by this shell gland (Fig. 6A). The mantle epithelium (shell gland) spreads rapidly across the apical portion of the body of the embryo, secreting shell with its anterior margin. The gland cells at this anterior margin, which represent the rudiment of the periostracum groove, are of columnar shape and remain attached to the shell margin. Cells behind the gland area are of different shape and represent the mantle cells typical for the cover of the visceral mass.

When the primary conch is completed it is large enough to cover the retracted soft body. Two things then happen: firstly the shell becomes attached to the soft body behind the apertural area; and secondly, the shell aperture detaches from the gland cells. The new attachment is formed by mantle cells in the apical region of the

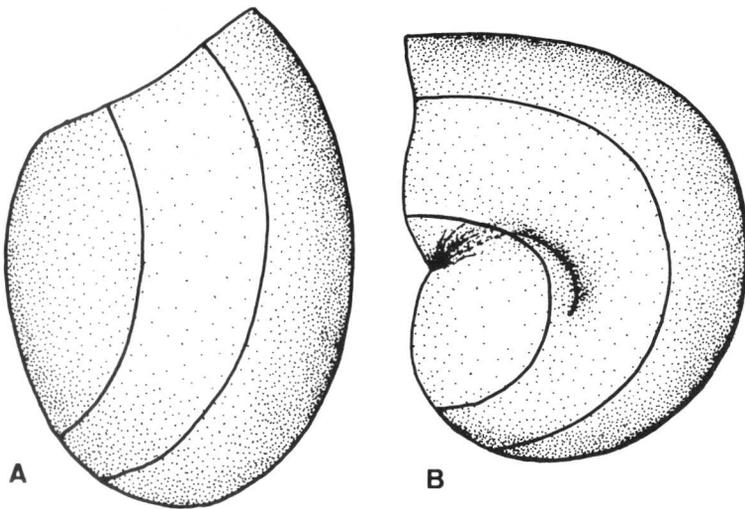


Fig. 6. Sketch of the embryonic shell of an archaeogastropod before (A) and after deformation (B) by the force of the soft body.

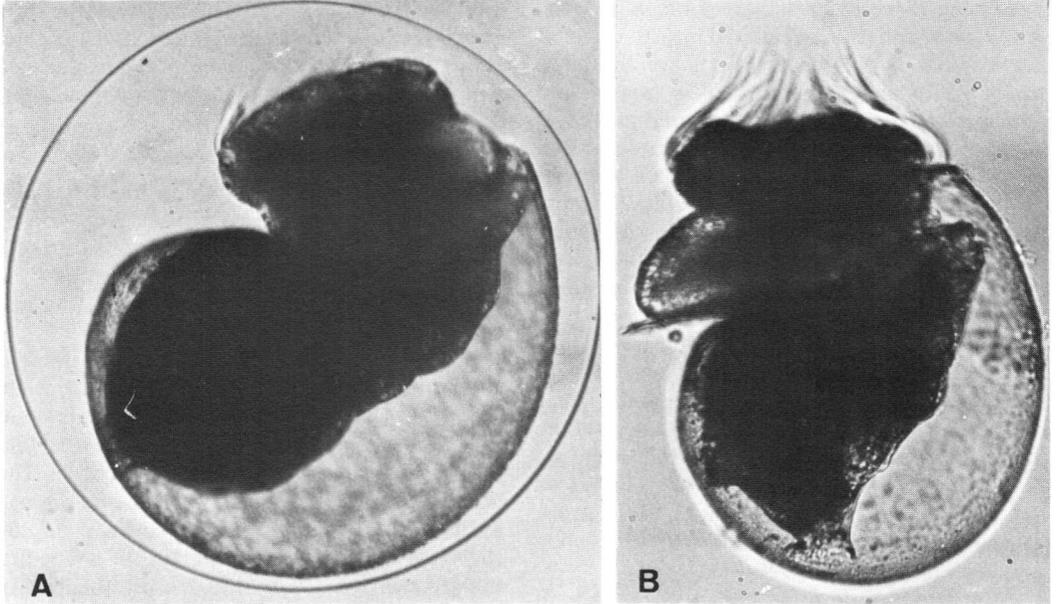


Fig. 7. □ A. The embryo of *Cantharidus* (Trochacea, Archaeogastropoda) during onset of body torsion. The soft body is attached to the shell only with muscles. $\times 280$. □ B. The embryo of *Gibbula* (Trochacea, Archaeogastropoda) after completion of body torsion and before shell mineralization. $\times 300$.

conch (Fig. 7A). Here cells covering the visceral mass are transformed into palisade-like cells (Bandel & Spaeth 1984). These attach the visceral mass to the conch by thin organic threads that extend from the interior of the cell through extrapallial space to the shell (Fig. 8). The palisade-like cells of the mantle are underlain by connective tissue that serves as a holdfast for muscle fibres. Two separate sets of muscle fibres grow from mesenchymal cells until a retractor apparatus is formed.

After formation of the secondary body attachment to the shell interior, the primary attachment to the shell margin is dissolved. The body of species that pass this phase of development during an actively swimming larval stage can be totally retracted into the shelter of the primary conch. At this stage of development the rudiment of the foot represents a low hump below the head bearing the velum (Fig. 7A). The withdrawn animal closes the aperture of its conch by folding cilia of the velum down onto the head.

During further embryonic development, the visceral mass begins to become torted and the foot differentiates, secreting an operculum. This process leaves the primary shell and tissue attachments unaffected. Torsion of the visceral mass is

trochospiral, which results in a passive rotation of the anterior portion of the body. The growing foot therefore moves from its dorsal into lateral position (Fig. 7B). The energy for cell growth and morphological changes in the veliger larva of archaeogastropods is derived from the egg yolk, and no other sources of food are available until benthic life has started.

When the veliger larva is fully developed, the upper side of the foot has secreted an operculum which can close the aperture tightly when the animal is retracted. The transitional phase from

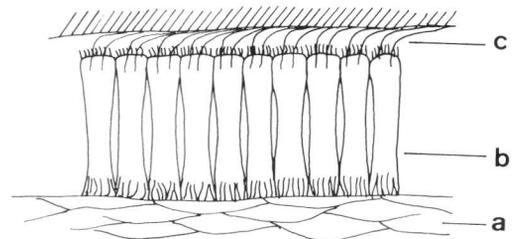


Fig. 8. Sketch of the shell-body attachment tissue as found in molluscs in general. Organic threads (c) are glued to the shell and continue into palisade-like cells (b) that are attached to connective tissue (a) which, in turn, can serve as holdfast for muscle fibres.

swimming to creeping mode of life is reached when the foot has differentiated into an organ of locomotion. In this pediveliger stage the bilaterally symmetrical organic shell is twisted into trochospiral shape by both the internal attachment of the visceral mass and by inward pressure of the foot outside the shell. The shell becomes trochospiral with a right hand coiling because muscles attach the visceral mass to the shell interior at a central and a right position in the veliger with velum-head upwards (Fig. 7B). If one views the shell the other way around in the crawling animal with head-foot towards the substrate, muscles attach in central and left positions. Because of the pressure of muscular tissue from the inside and the outside of the shell the dorsal side of the conch becomes bent and the lateral sides are folded (Fig. 6B). The lateral position of the foot is helpful too, and after deformation of the conch its new position is well fitted for a stable crawling on substrate.

After completion of the enforced trochospiral coiling of the bilaterally symmetrical primary conch the foot has found a new position and the attachment of the body to its shell is rearranged. The central attachment of the visceral mass to the shell is dissolved and only the columellar muscle remains. It is now the only muscle responsible for rapid retraction of the body into the shell. At the same time the shell is mineralized throughout and fixed in shape. With completion of the changes the pediveliger stage, during which the animal can swim with the velum-sail and creep

with its foot, is at an end; velum is resorbed, and purely benthic life begins. Shell growth is resumed only after the gastropod has become firmly established in its living environment and is successfully feeding.

Morphology. – The primary conch consists of a bilaterally symmetrical cup with an inclined round to oval aperture. It has a long side and a short side. The surface is usually covered by a sculpture consisting of ribs, tubercles, pits and crests and groove network (Bandel 1982).

As a consequence of the deformation also the external morphology of the shell is changed. On the sides of the aperture, starting from its base, folds develop, one deeper than the other, so that the result is a trochospirally coiled conch. The original sculpture becomes stretched and pressed during this deformation most strongly on the short side below the folds (Fig. 9A, 9C). The primary conch with its species-specific shape, size and ornamentation differs in all these features from the following secondary shell (Fig. 9B).

Shell structure. – The organic shell is totally mineralized by aragonitic prisms after its deformation. The formerly elastic organic shell is transformed by the process into a rigid conch. Crystallites of 0.1 to 0.2 μm thickness penetrate and replace organic shell from the inner surface into the sculpture during mineralization (Bandel 1979a).

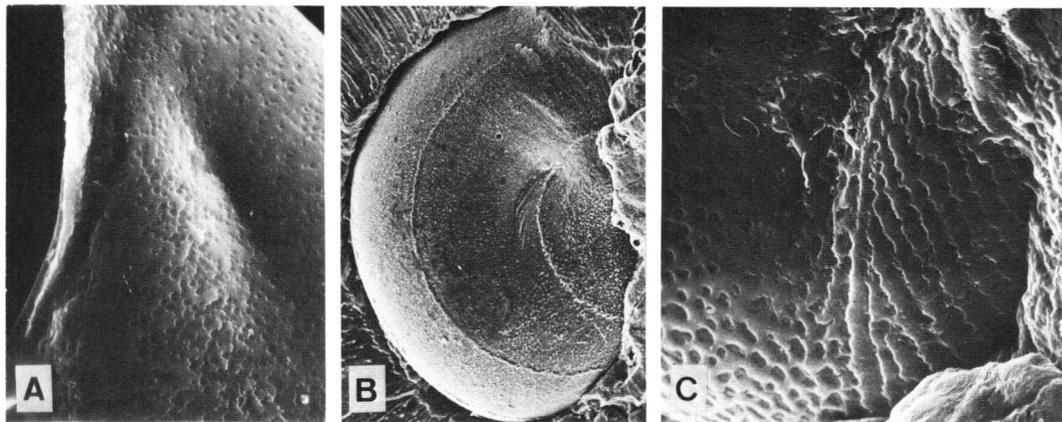


Fig. 9. □ A. Fold of the embryonic shell of *Diodora* (Fissurellacea, Archaeogastropoda) formed during secondary deformation of the shell. $\times 250$. □ B. Original sculptural elements cross the fold in the case of the embryonic shell of *Galeoastrea* (Trochacea, Archaeogastropoda). The adult shell differs completely from the embryonic shell. $\times 200$. □ C. In the case of *Fissurella* (Fissurellacea, Archaeogastropoda) the stretched and folded area near the inner lip of the embryonic shell shows a different sculpture from the neighbouring shell. $\times 650$.

The structural characteristics of the adult shell are established when the secondary shell becomes secreted. The lumen of the primary conch may later become filled by secondary shell material secreted by the mantle of the visceral mass. Such fillings can provide no clues regarding the ontogeny or phylogeny of shell structure as was assumed by Erben & Krampitz (1972). The primary conch may also be sealed off from the later formed shell lumen by septum, and will usually be eroded or, as in many fissurellids, resorbed (Bandel 1979b, 1982).

Reconstruction of the ammonitella formation

The whole external conch of the ammonitella, like the primary shell of the archaeogastropods, was formed in uninterrupted contact between gland cells of the mantle margin and the shell margin. Growth lines are therefore absent. In both cases the end of mantle growth across the yolk-filled visceral mass is indicated by a constriction of the aperture (Figs. 2, 4B, 5B). The primary shell was purely organic and elastic. The contact between gland cells and shell margin dissolved after the completion of the primary shell and after the tissue of the body had reattached itself in a more apical position. In both cases this attachment is paired, but is bilaterally symmetrical in the ammonitella in contrast to archaeogastropods. The shell was mechanically deformed before it became mineralized and rigid. This deformation of the ammonitella resulted in a flattening of the inner lip at the aperture. The functional significance of this morphological change could lie in the very limited space available for the ammonite embryo in a round egg (Fig. 10). The flattened area increases the room needed for the operculum—head—beak—tentacles and, perhaps, an external yolk sac. In the case of archaeogastropods, deformation of the primary conch transforms the bilaterally symmetrical conch of a free-swimming veliger into the trochospiral shell needed by the crawling benthic snail.

Initial mineralization was rapid and penetrated and replaced the elastic organic shell with aragonite needles from the interior surface into the sculptural elements. The functional significance of this change in the case of the archaeogastropods is related to benthic life, while in the case of ammonites it is a prerequisite for the construc-

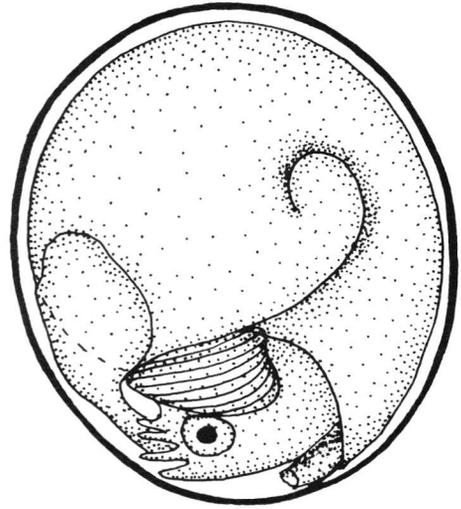


Fig. 10. Sketch of a possible ammonite embryo in its egg prior to hatching.

tion of the phragmocone. The archaeogastropod model can thus help in the reconstruction of the formation of the ammonitella. It does not improve our understanding of the later additions of the internal features of the chambered part. Only rather general data on septa formation in gastropods provide some information (Bandel 1979b; Bandel & Hemleben 1975), but data valuable for the function of the ammonitella can be gathered from living and fossil cephalopods (Ward & Bandel 1985). The attachment of the end of the siphuncular tube to the walls of the initial chamber can be compared with those produced by recent *Spirula* (Bandel & Boletzky 1979). The function of the siphuncle in relation to the liquid-filled chambers can be understood by studying *Nautilus* (Ward 1979). The shape of the first septum can be related to that of the first mineral septum in fossil belemnites and septum formation can be understood with the help of the recent *Sepia*, *Nautilus* and *Spirula*.

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