

The Structure and Formation of the Siphuncular Tube of *Quenstedtoceras* compared with that of *Nautilus* (Cephalopoda)

By

Klaus Bandel, Erlangen

With 9 figures in the text

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Abstract: The mode of formation of new chambers of the ammonite *Quenstedtoceras* was analysed in detail and compared with that of *Nautilus*. The siphuncular tube formed independently from the septum and was attached to the ventral shell wall. The septum was fixed in shape by rapid mineralization and the nacreous septum formed after stabilization of septum morphology. Porous pillar zones that connected chamber liquid with the tissue of the living siphuncle were formed between mineral ends of the organic siphuncular tube within septal necks.

Key words: Perisphinctida (*Quenstedtoceras*), Nautiloidea (*Nautilus*), siphuncular tube, septum, skeleton, aragonite, organic microstructure.

Zusammenfassung: Bei der Neubildung einer Gehäusekammer schied *Quenstedtoceras* das Siphonalrohr ab, bevor sich ein neues Septum bildete. Das Rohr wurde der ventralen, inneren Schalenoberfläche und dem vorherigen Septum mit organischen Lamellen verheftet. Letztere setzen sich in sphärolithisch-prismatische Aragonitwülste fort, die auf der mineralischen Schalenoberfläche aufgewachsen sind. Das Septum mit seiner komplex verfalteten, randlichen Sutura entstand rasch aus mineralischen und organischen Ausscheidungen im Schleim der vom Mantelgewebe ausgeschiedenen, extrapallialen Flüssigkeit. Hierbei wurde die Oberfläche des unter Zug stehenden Mantelepithels in seiner Form nachgeprägt nicht aber selbst mineralisiert, wobei der Aufwuchs sphärolithisch-prismatischer Aragonit-Kristall-rasen nach hinten erfolgte. Nach der mineralischen Versteifung des Septums und der vollständigen Abscheidung des organischen Siphonalrohres löste sich der rückwärtige Mantel von den geregelt verteilten Muskelanheftungspunkten und -linien an der Schaleninnenseite ab, und erst danach erfolgte die Ausscheidung des Perlmutterseptums. Nach Beendigung der Perlmutter-Abscheidung wurde die neue Kammer funktionell. Der neue Abschnitt des Siphonalrohres greift in den nach

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vorne gebogenen Septenkragen des vorhergehenden Septums hinein. Hierbei liegt zwischen sphärolithisch-prismatischer Anheftung des hinteren Rohrsegments und der gleichartig strukturierten Anheftung des vorderen Rohrsegmentes eine ausgedehnte, poröse Pfeilerzone, in der eine von der Kammerflüssigkeit abgetrennte kleine Flüssigkeitsmenge Platz fand, und die das Gewebe des Siphostranges mit dem Innenraum der abgeschlossenen Kammer in Verbindung brachte. Die Kammerbildung bei Ammoniten wird mit der von *Nautilus* verglichen und die Struktur, Bildung und Funktion des Septalapparats diskutiert.

Introduction

The siphuncular tube is the most characteristic feature of shell bearing cephalopods. It differentiates them from all other members of the phylum Mollusca. In regard to all other shell features, such as planispiral coiling, shell of aragonitic nacreous and prismatic structure, septation of apical shell portions, other mollusc groups may show one or more of these characters, but none are known that have a tube connecting sealed off portions of the shell with the living tissue as is present in the chambered cephalopods. This very ancient acquisition of a septate, benthic limpet-like mollusc that lived in Cambrian times (YOCHELSON et al., 1973) enabled the cephalopod branch of the molluscs to conquer the water above its original benthic habitat and adopt a free swimming mode of life. The tube connecting the soft body situated in the anterior portion of the shell (living chamber) with the sealed off apical portion of the shell and its chambers is filled with living tissue. The sealed off chambers themselves no longer contain living tissue and after formation are filled with water. DENTON (1974), DENTON & GILPIN-BROWN (1961, 1966, 1971) and DENTON, GILPIN-BROWN & HOWARTH (1961, 1967) have shown conclusively that living cephalopods with chambered shell can pump water in and out of the chambers quite easily and can thus adapt their weight to the desired depth of water. They attain neutral buoyancy by changing the amount of liquid held within the chambers by interaction of the cells of the living siphuncle with the liquid held within the chambers.

The siphuncular tube of *Nautilus* is permeable to sea water, impermeable to air and able to withstand pressures equivalent to well above 450 m of water depth (COLLINS & MINTON, 1967). According to these authors a *Nautilus* shell would fill in about 2 hours if the living siphuncle did not prevent it, since the siphuncular tube acts as a permeable membrane. Gas can enter the chambers by diffusion only. CHAMBERLAIN (1978) estimated the permeability of the siphuncular tube of *Nautilus* and fossil ectocochleate cephalopods using previously published data on the siphuncle composition for his calculations. Thus he used the assumption that liquid must move through the horny tube of the *Nautilus* siphuncle only. He therefore came to results which were controversial to COLLINS & MINTON's experiments. CHAMBERLAIN concluded that the rate of fluid removal from the chambers

is low, lower than suggested by COLLINS & MINTON (1967) and DENTON & GILPIN-BROWN (1966).

The living siphuncle and the chambered portion of the shell that has been sealed off from the living tissue in *Sepia* and *Spirula* remains throughout life the most important apparatus for buoyancy control. The contact between living tissue and the liquid held in the chambers thus lies within the siphuncular tube. This tube is not permeable throughout, but only at certain places, as BANDEL & BOLETZKY (1979) have shown conclusively for the living members of chambered, shell-bearing cephalopods (*Sepia*, *Spirula*, *Nautilus*). According to these authors the function of the siphuncular system in general has most probably never changed in the chambered shells of recent and fossil cephalopods. BANDEL & BOLETZKY (1979, Figs. 25, 26) also demonstrated that the siphuncular tube of the Ammonoidea and its attachment to the septum differs in several respects from that of recent *Nautilus* and *Spirula*. The data for their reconstruction of the siphuncular tube of ammonites had been extracted from the available literature. Thanks to Prof. Dr. A. ZEISS (Inst. für Paläontologie, Erlangen) it was now possible to study extremely well-preserved Jurassic material of the ammonite *Quenstedtoceras* from the Polish locality Lukow, and to verify and correct this reconstruction.

Quenstedtoceras

Previous data: BANDEL & BOLETZKY (1979, Figs. 23, 24, 25, 26) combining literature data of GRANDJEAN (1910), MILLER & UNKLESBAY (1943), MUTVEI (1967), ERBEN & REID (1971), BAYER (1975) and others came to the following reconstruction of the relationship of siphuncular tube and septum in ammonoids. The septal neck of semi-adult and adult ammonoids always points towards the living chamber (apertural). The walls of the siphuncular tube are not continuous with this septal neck, but are made of organic material similar to the horny tube of the *Nautilus* siphuncle. The siphuncular tube consists of portions, each of which has the same length as the corresponding chamber. These individual portions are not fused with one another so as to form one continuous organic tube; instead they are connected to each other by calcareous material. The apical part of each tube segment is narrower than the apertural part in the segment formed before. The siphuncular tube of the ammonoids is covered by an organic pellicle that separates from the tube near its ends. With these organic sheets the siphuncular tube is attached to the ventral shell wall.

The siphuncular tube in most ammonoids becomes independent from the septum during ontogenesis and MUTVEI (1975) suggested that it formed after the septum is completed. KULICKI (1979), in contrast, presented convincing evidence that a new tube section forms before the septum

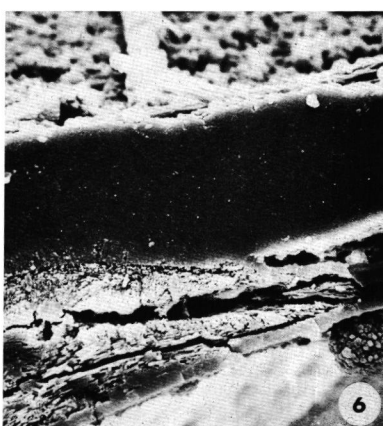
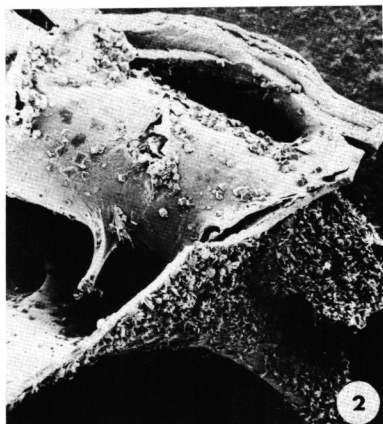


Fig. 1—6 (Legend see p. 157)

is completed. The siphuncular tube is attached to the septal neck by surrounding calcareous deposits. In the course of their ontogeny the ammonoids develop a new porous zone in their siphuncular tube, when the septal necks changed from a retro- to prosiphonate arrangement. BANDEL & BOLETZKY thought that it might be possible that chamber liquid could be drained on both ends of the tube segment crossing the chamber.

New data: The septum of *Quenstedtoceras* in construction is mainly nacreous. At the place where the siphuncle penetrates through the septum, a round aperture is bent towards the living chamber forming the so-called prochoanitic septal neck. The position of the siphuncular tube is close to the outside of each whorl (ventral) in the individuals that have grown after hatching from the egg case. Thus the siphuncular tube runs marginally, almost in contact with the inner side of the outer shell (Fig. 1).

The nacreous layer composing most of the outer shell is overlain by a thin inner prismatic layer throughout. Along the insertion of the nacreous septum onto the inner side of the outer shell this prismatic layer increases in thickness, attaining greatest thickness just posterior of the attachment of the septum (Fig. 4). This increased thickness is due to the fact that a prismatic ramp attaches a thick organic pellicle here, which further backwards (apically) merges with the organic siphuncular tube (Fig. 1), forming its outermost layer. There may be not only one such sheet, but several, in which case each of these pellicles shows an individual attachment to the inner prismatic layer of the mineral shell. The organic pellicle enters this prismatic structure. If the aragonitic material of the prismatic ramp is

Fig. 1. The septal neck of *Quenstedtoceras* with the most ventral portion of the septum and the attachment of the siphuncular tube coming from the apical chamber (left) and the apertural chamber (right). x 200.

Fig. 2. The siphuncular tube (left) with its outer layers is attached to the outside of the septal neck of the previously formed septum. Special pellicles attach it also to the ventral side of the inner shell surface (upper portion of picture). x 50.

Fig. 3. Detail from Fig. 1 showing the siphuncular tube (upper portion of the picture) attached to the septal neck by spherulitic-prismatic cushion-like growths. The continuation of the pellicle of the siphuncular tube visible in the lower left of the picture is seen in Fig. 4. x 900.

Fig. 4. The primary siphuncular tube finds its attachment to the ventral wall in a prismatic ridge (lower right). The first septum formations consist of spherulitic prismatic layers overlain later by the nacreous septum (center of picture). At the upper right the prismatic cushion attaching the following section of the siphuncular tube to the outer side of the septal neck is visible. x 900.

Fig. 5. A porous pillar zone is developed between the attachment of the apertural section of the siphuncular tube to the septal neck (upper side) and the first formed spherulitic prismatic layer of the septal neck (lower side). x 1800.

Fig. 6. The apertural end of the pillar zone with its contact to the chamber shows the horny siphuncle above and the end of the nacreous septal neck in the lower left. x 4500.

etched slightly with acidic acid, the thin organic sheets which are continuous into the mineral layer can be detected. Within the prismatic ramp the pellicle is split into a number of thin discontinuous sheets and lamellas. Thus formation of this prismatic ramp at the posterior side of the septum attachment to the inner wall and formation of the organic pellicle joining the siphuncular tube further backwards (Fig. 1) must have been simultaneous.

The prismatic aragonite crystal needles have mineralized and attached the organic sheet to the inner prismatic layer before a septum could form, because it underlies it. This one or these few pellicles join the siphuncular tube apically and remain part of it until its approach to the septal neck of the previous septum (Fig. 2). Here the pellicle is split from the organic tube and covers the outer side of the septal neck. It finds its attachment to the base of the septal neck in a crystalline ridge composed of prismatic needle-like aragonite crystals (Fig. 7). Only a thin fraction of the organic sheet is continuous across this prismatic ridge, attaching the bulk of it, and overlies the upper (apertural) side of the septum.

In the formation of the new septum before the next stage of mineralization the exact shape of the septum with all its complications of saddles and lobes must have been held in place by the soft outer epithelium of the mantle of the apical portion of the soft body. Evidence for this is found in the fact that crystals have grown in an apical direction. Crystal growth started in spherulitic form (Figs. 3, 4). These spherulites and crystal aggregates formed in a mucus excreted from the epithelium of the mantle. Within this special CaCO_3 enriched extrapallial liquid rapid growth of spherulitic, prismatic needle mounds and thickets pushed organic materials outwards into posterior position or inwards into the newly forming septal neck (Fig. 3). At the same time the new siphuncular tube in its final shape was secreted from the differentiated tissue of the living siphuncle. Near the CaCO_3 rich zone of the mineralizing septum crystals and crystal aggregates became included into the organic pellicles forming the tube (Fig. 3). Further away from the septum the tube contains no CaCO_3 crystals (Figs. 1, 6). But as it approaches the septal neck of the old septum, a loosely arranged crystal growth with thin organic membranes between widely spaced groups of vertically arranged aragonite needles is secreted. Here a pillow zone forms with plenty of free space between mineral components, a space differentiated into many minute cavities by thin discontinuous organic sheets. This pillar zone now lies within the septal neck (Figs. 5, 6, 7). It covers most of the inner surface of the neck and opens towards the tube interior on the apical side of the neck.

Above the pillar zone formed within the septal neck of the old septum, crystal growth of spherulitic prismatic type is present. It is the most apical continuation of the organic siphuncular tube. On its anterior end the tube terminates in just the same type of prismatic spherulitic attachment ridge

as present on the apical side of the newly formed septum. Due to slight diagenetic solution, the border between organic siphuncle and spherulitic prismatic aragonite growths seems to be more pronounced (Fig. 3) than it had originally been. The siphuncle attachment coming from the chamber before (Fig. 5) shows a normal transition from the organic tube into its mineralized attachment to the septal neck. Thus growth of crystals and polymerization of organic sheets and fibres forming the tube occurred at the same time and from similar organic liquid substances, but extruded by the siphuncular tissue and the apical portion of the mantle respectively. This extrapallial liquid varied only in the amount of CaCO_3 present in it from place to place.

When the siphuncle was completed and the septum fixed in its final shape by rapid mineralization of spherulitic-prismatic structure, the mantle could relax its tension. Now the folded margin of the septum could hold its shape without supporting tissue. The time required for fixing the septum into its complicated lobe and saddle shape does not have to exceed the time in which *Helix* can repair a shell damage or the larval shell of an archaeogastropod becomes mineralized (BANDEL, 1979). This would be a few hours to a

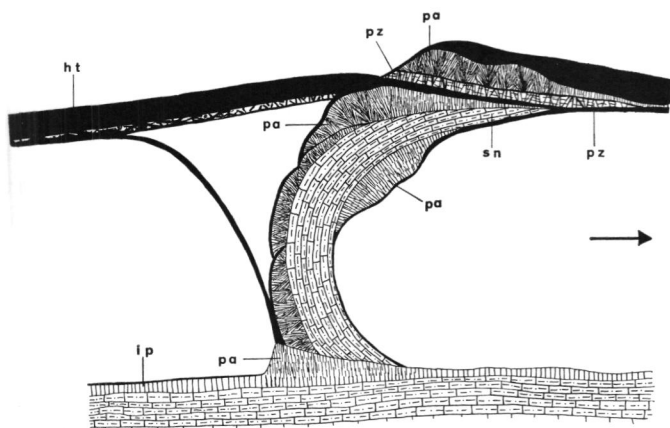


Fig. 7. Longitudinal section through the ventral half of the siphuncular tube of *Quenstedtoceras*. The arrow points towards the aperture. The horny tube (ht) is attached to the first septal layers, with spherulitic-prismatic structure (pa) in its first pellicles, directly onto the inner prismatic layer (ip) and with its whole width to the first mineral deposits of the septum. The septal neck (sn) and the nacreous septum strengthen this first deposit. A new chamber forms with the growth of first organic pellicles and their attachment to the inner side of the septal neck (pa) followed by the formation of the pillar zone (pz), and after that the attachment of the new section of the siphuncular tube to the inner side of the septal neck (right).

maximum of a day. The mineralized septum is brittle and weak, yet unable to withstand stress nor to be used for buoyancy control. But now the formation of the nacreous septum is started on top of all these layers and after the siphuncular tube is completely formed. During the formation of nacre the mantle must have filled all depressions and have been in close contact to the shell surface throughout, contouring the complicated morphology of the septum, but it need not be attached to the shell any more.

Nautilus

The septum in *Nautilus* is composed of nacre mainly and is pierced by the siphuncle in an almost central position. Around the foramen formed by the siphuncle, the septum bends away from the living chamber, thus forming a retrochoanitic septal neck. The siphuncular tube maintains this central position within the chambers from the first chamber onwards.

The nacreous layer on the inner side of the outer shell wall is covered throughout by a thin prismatic layer, which at the insertion of the nacreous septum to the outer wall is thicker than normal (BLIND, 1976, Pl. 5, Fig. 2). Here a thin organic pellicle is mineralized and attached to the prismatic inner layer of the outer shell in a conspicuous additional ridge on top of the mural ridge ("Prismenkissen", BLIND, 1976, Pl. 12, Fig. 1a; Pl. 13, Fig. 1). This sheet or thin pellicle is continuous into the outermost layer of the siphuncular tube and forms the organic pellicle on which the chalky layer of the siphuncular tube is deposited (Fig. 8). Further backwards on the entrance to the septal neck of the previous septum the pellicle bends sideways, finding attachment to the shell surface of this septum with prismatic needle-like aragonite crystals and crystal groups distributed on the surface (Fig. 8, BLIND, 1976, Pl. 15, Figs. 4, 5, 6).

The primary organic shell forming the base for the mineral septum at first must be held under pressure by the mantle epithelium in a fairly stable way and for some time. Evidence for this is found in the solid attachment of the pellicle to the shell wall by a prismatic ring-like ridge, while the outermost pellicle of the siphuncular tube that is not under stress during the mineralization phase is fixed to the old septum only by single aragonite needles and needle groups. The organic and flexible shell of the newly forming septum is only overlain by a loose needle-like mineral layer held together by organic sheets similar to the chalky layer that covers the organic siphuncular tube in a much greater thickness, but was formed simultaneously.

This basal layer is covered by nacre, which represents a mineralization with a highly organized structure (BANDEL, 1977) which can not be secreted very rapidly. Before the deposition of nacre starts, the so called chalky layer of the siphuncular tube is secreted and, at the inner side of

the septal neck, a prismatic pillar zone forms (BANDEL & BOLETZKY, Figs. 21, 81, 93, 94). The nacreous septum and the horny tube form simultaneously. The horny tube is split into thin organic sheets before it reaches the non-porous calcareous ridge composed of prismatic needles of aragonite that fuses it to the inner side of the septal neck (BANDEL & BOLETZKY, Fig. 21, 92). These discontinuous and irregular organic sheets are held apart from each other by interspersed irregular prismatic crystals of aragonite just like those found in the chalky layer. The siphuncular tube, shortly before finding its attachment to the inner side of the septal neck of the old septum is thus of spongy structure (BANDEL & BOLETZKY, Fig. 90).

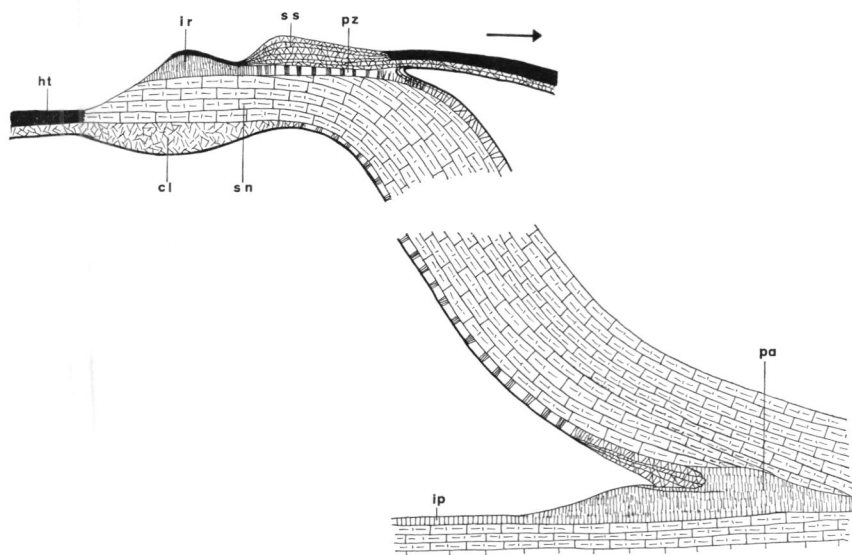


Fig. 8. Longitudinal section of the siphuncular tube and half the septum of *Nautilus*. The arrow points towards the aperture. The nacreous layers of the septum continue into the septal neck (sn), the organic parts of which are continuous with the horny tube (ht). The septal neck and the horny tube are covered with the chalky layer (cl). The apical end of each section of the siphuncular 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) consisting of many discontinuous organic membranes interspersed with aragonite crystals. This spongy structure brings the liquid contained in the pillar zone (pz) in contact with the siphuncular tissue. The first formed pellicle of a septum is attached to the inner prismatic layer (ip) by a prismatic attachment ridge (pa) situated on top of muscle deposits.

A comparison of septal and siphuncular features of *Nautilus* and *Quenstedtoceras*

1. The first organic pellicle attached to the surface of the old septum and forming the outermost layer of the siphuncular tube in *Nautilus* is very thin, while it is quite thick in *Quenstedtoceras*.

2. The attachment of first organic sheets in *Nautilus* as well as in *Quenstedtoceras* lies on the apical surface of the old septum, but differs in magnitude. In *Nautilus* low, loosely arranged needle growths, spread in a thin layer over the septum, attach the thin pellicle. In *Quenstedtoceras*, the thick pellicles are anchored by ridges of spherulitic prismatic structure.

3. In *Nautilus*, the first formed organic pellicle is thin and elastic and forms the base for final crystal growth of the septum. It is attached to the inner side of the outer shell with a ring-like prismatic ridge. In *Quenstedtoceras*, in contrast, the attachment of the first organic pellicle (pellicles) in apertural direction is independent of the septum. The first siphuncular tube is attached to the ventral shell only with one or more solid ridges, just apical of the later insertion of the septum, as mineral connections of the pellicle or pellicles holding the tube in its place.

4. In *Nautilus*, septal mineralization is slow and build-up of mineral deposits proceeds in apertural direction (forwards). It is nacreous practically from the beginning. In *Quenstedtoceras* a rapid mineralization occurs, which is characterized by a prismatic-spherulitic aragonite crystallization proceeding from the tissue of the mantle into apical direction (backwards).

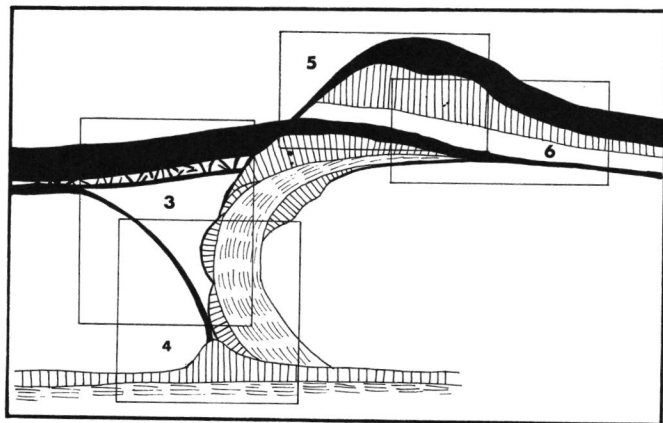


Fig. 9. Sketch of Fig. 7 showing the exact position of Figs. 3 to 6.

5. In *Nautilus*, the mantle attachment to the inner side of the outer shell is along a continuous ribbon that during septum secretion slowly migrates forward, keeping pace with the growth of the nacre until the septum is solid. In *Quenstedtoceras*, the muscle epithelium, which held the mantle in its complicated folded shape, was attached with many tie points separated from each other by areas of non-attachment.

6. The base for mineral deposition in *Nautilus* is the first organic elastic septum that has to be held in place by mantle pressure for a fairly long time and is solidly attached to the inner shell wall. In *Quenstedtoceras* the septum formation started within a liquid secreted by the mantle epithelium and mineralization and polymerization took only a short time.

7. The formation of the nacreous septum and of the organic siphuncular tube in *Nautilus* are synchronous. Thus the mineral septal neck is continuous into the organic tube of the siphuncle. In *Quenstedtoceras* the siphuncular tube was completed before the nacreous septum could form. Thus nacre deposited on the septal neck is not continuous into the organic tube of the siphuncle.

8. The porous zones of the siphuncular tubes in *Nautilus* and *Quenstedtoceras* lie where the newly formed tube section enters the inner side of the septal neck of the former septum. In *Nautilus* the cameral liquid comes in contact with the living siphuncle through the porous apical portion of the organic tube itself, near its attachment within the septal neck. In *Quenstedtoceras* liquid could leave the chamber along the porous zone present below the attachment of the new tube.

9. The horny tube of *Nautilus* is thinner than that of *Quenstedtoceras* and has a weak and porous apical end. The siphuncular tube of *Quenstedtoceras* is thicker than that of *Nautilus* and being solid and practically impermeable along its whole length.

10. In *Nautilus* the pillar zone (the zone which can hold a small amount of water decoupled from the bulk of the cameral liquid) is restricted to a narrow ring between the entrance into the septal neck and the prismatic ridge attaching the siphuncular tube to the inner side of the neck. In *Quenstedtoceras* this zone is extended and covers almost the whole inner surface of the septal neck.

Discussion

a) Structure of siphuncular tube

BANDEL & BOLETZKY (1979, Fig. 26), using literature data only, suggested that there might be two porous zones present on the septal necks of ammonoids. This is not the case, as the extremely well-preserved septal

necks of *Quenstedtoceras* show in several septa (Fig. 7). A porous zone is present only on the inner surface of the septal neck. It is situated between prismatic spherulitic mineral attachment of the siphuncular tube posterior of the septum and the prismatic spherulitic mineral attachment of the siphuncular portion anterior of this septum (Fig. 7).

The primary attachment of the newly forming siphuncle to the outer side of the septal neck is also present in the Maastrichtian ammonite *Sghalinites*, as can be gathered from BIRKELUND & HANSEN (1974, Pl. 5, Figs. 1, 5). A prismatic ridge at the attachment of this organic sheet was figured by KULICKI (Pl. 35, Figs. 5, 6) in *Kosmoceras*. KULICKI (Pl. 35, Figs. 5, 6) also figured the thick prismatic layer composing the base for the nacreous septum, which serves as attachment for the first siphuncle pellicles in an anterior direction. Such prismatic structures near the apical base of a *Quenstedtoceras* septum to the outer wall were interpreted by BLIND (1975, Pl. 20, Fig. 2) as "mural ridges", supposedly deposited by muscular epithelium. In the *Quenstedtoceras* studied here, such angular, step like ridges are connected with the attachment of organic pellicles branching off from the siphuncular tube (Fig. 2). This indicates that these prismatic ridges are attachments of organic sheets to mineral walls rather than mineral deposits of muscular epithelium. Even though it is quite reasonable to assume that muscular epithelium did produce prismatic structure where it was attached to the shell, it can not be stated that all prismatic deposits have been produced by muscle epithelium exclusively. In bivalves and gastropods with a nacreous shell structure comparable to that of the cephalopods, very commonly prismatic layers are not secreted by myoadhesive epithelium (BANDEL, 1977, 1979).

Rapid transition from purely organic to mineral shell occurs fairly commonly within the shells of molluscs in general and in cephalopods in particular. Thus in *Nautilus*, the nacreous septum is continuous into the purely organic siphuncular tube (MUTVEI, 1972). In *Sepia* organic layers mineralize rapidly to form the spine (BANDEL & BOLETZKY, 1979, Figs. 14, 41, 84); in *Spirula* the mineral siphuncular tube continues in organic sheets (BANDEL & BOLETZKY, 1979, Fig. 7).

b) Formation of the siphuncular tube

MUTVEI (1975) expressed the opinion that the horny tube of the ammonoids is of secondary origin in that it is not continuous with the septal neck. He thought that the horny tube was secreted after the new septum and after the septal neck had reached its full thickness. From the data presented here it is obvious that it is just the other way around. The nacreous septum formed only after the siphuncular tube was completed.

KULICKI (1979, Pl. 40, Fig. 1) had actually found and figured in a Jurassic ammonite a siphuncular tube as it is forming before the septum is present. The stage figured by this author is that in which the siphuncular tube in its full length is already present, attached only with the apertural pellicles to the inner wall of the ventral shell side.

BLIND (1975) suggested that the mural ridge was deposited by the muscle epithelium at the same time as the septum directly apical to it, at a time when the soft body was still in connection with the septal wall. It is quite possible, that ammonites attached the early siphuncular pellicles on top of these formations of muscle epithelium, as is the case in *Nautilus* (Fig. 8); but they then enlarged them to their present step-like shape at a time, when the body had already withdrawn in an anterior direction to be able to secrete this sheet to the outside.

WARD & WESTERMANN (1976) have shown that the mantle of an ammonite, after having withdrawn from the space of a newly forming chamber into the position for septum mineralization, is attached to the shell not along a continuous circular ribbon as *Nautilus* (BLIND, 1976) but by single tie points. If the pressure of the liquid held behind the mantle tissue in the place of the newly forming chamber is less than that within the mantle, the tissue between tie points, which are points of muscular shell attachment, is bent in evenly rounded shape backwards. Normally the pressure of the liquid is higher than that within the animal tissue, so that the epithelium between attached areas of the mantle is evenly bent forwards. WARD & WESTERMANN (1976, Figs. 2, 3) showed that an inversion from low to high pressure had occurred between formation of successive septa within one individual of an ammonoid. Thus lobules and folioles change from convexity to concavity between points of attachment of the mantle to the shell from one septum to the next. These attachments or tie points of the mantle could lie within the zone of the attachment of the apical portion of the body, the so called zone of subepithelial muscle attachment as suggested by BLIND (1975). If in contrast to *Nautilus*, where this muscle ring remains totally fixed with slight forward displacement during septum formation, in ammonoids this muscle only remains fixed at certain points or discontinuous zones and resorbed between these, then SEILACHER's (1975) pull-off model can explain the morphology of the septum. The septum of ammonites in its morphology thus represents the mineralized elastic membrane of a stretched mantle epithelium. If this model is correct, the specific shape of the suture represents the genetically controlled arrangement of the fix points of the mantle to the shell when the septum forms. The subepithelial mantle attachment in the case of *Nautilus* remains stable and the muscle withdraws very slowly into its new forward position, while in ammonites the muscle is resorbed except in some places. Here the somewhat instable situation of stretched mantle membranes is lessened

by secretion of extrapallial liquid from which a rapidly mineralized organic-mineral septum wall forms posterior to the epithelium and fixes the shape of the soft tissue mould. At this stage the muscle attachment and the tense mantle can relax and withdraw into a more stable situation, allowing ordered deposition of nacre to strengthen the septum against pressure.

WESTERMANN's (1975) model of septum formation in ammonoids includes several steps. After withdrawal of the mantle from the space of chamber formation the soft body is fixed to the outside shell wall in tie point position, but then WESTERMANN suggests that the margins of the mantle attach a conchioline septal membrane along the whole suture before mineral deposition begins. This is not the case in *Quenstedtoceras*, where no membrane could have been present when the first mineral shell formed. SEILACHER's (1975) conclusion that the septum of ammonoids reflects the shape of the withdrawing mantle sack, which forms a rigid replica by secretion and mineralization can be confirmed, if "withdrawing" is replaced by "withdrawn", because mineralization fixed a momentary stable situation, which did not change until the wall was solidified by mineral deposits.

BAYER (1978) strongly opposed the possibility of inversion of suture lines in ammonoids based on four assumptions. The first is that an organic membrane formed before the nacreous septum could form on it. The second is that this membrane was fixed to the shell along a closed line and the suture was thus completed in its final course on the shell before the septum formed and inversion of lobules and folioles could, therefore, not form. The third assumption is that a closed membrane must be present "so that aragonitic material could not be lost into this fluid (cameral) during secretion of the nacreous layer". In the fourth assumption BAYER thought that the mantle, filled with visceral mass with its own stability "cannot be inverted like an empty sac".

The first two assumptions are not valid, as has been shown below. In ammonoids, in contrast to *Nautilus*, an organic membrane as base for mineral deposits is not present when septum secretion starts. Organic lining of the apical portion of the septum forms at the same time when the prismatic basal layers are secreted from the extrapallial fluid. Such fluid is a mucus substance and a highly ordered gelatinous liquid which will hold the calcium-carbonate needed for mineralization without the aid of membranes, as can be observed at the growing mantle edges of all conchifera. The lobed mantle-edge of the otherwise rounded apical end of the visceral mass, like similarly crenulated mantle edges in other molluscs, most probably, was not filled with viscera and quite elastic. It could very well react to pressure differences in places where it was not attached to the shell wall.

c) Function of the siphuncular tube

During the early ontogenetic stages of ammonites, when the siphuncle is still in a *Nautilus*-like central position, the septal necks are also bent backwards (ERBEN, FLAJS & SIEHL, 1969). As the animal grows, the siphuncle gradually or abruptly approximates the outside of the shell (TANABE, OBATA & FUTAKANI, 1979). Only after the siphuncular tube has moved to the outside of the whorl, the septal neck becomes bent towards the aperture. In *Quenstedtoceras* this outward migration is rapid and occurs within the first chambers (KULICKI, 1979; own observations). Thus there is a connection between the development of a prochoanitic septal neck and the position of the siphuncular tube close to the outside of the whorl. This finds its explanation in the stated differences between *Nautilus* and *Quenstedtoceras* regarding the growth of the siphuncular tube. While a centrally located siphuncular tube has to be held in place by the soft body of the withdrawn animal until the mineral septum is secreted, a marginal siphuncular tube can be attached to the outer wall (as is the case in *Quenstedtoceras*) and thus form independently from the septum.

During this shift, the porous zone of the siphuncular tube, being situated at the apical end of each tube section, did not change its position but only its formation. The pillar zone could now be extended in width, since it lies below the tube attachment between the inner side of the septal neck and the prismatic attachment ridge of the apical end of the tube. In a retrochoanitic septal neck of the *Nautilus* type attachment ridge and pillar zone lie side by side, crowding each other. Thus more liquid can be held in the pillar zone in ammonites than in *Nautilus*. Since liquid decoupled from the chamber liquid is a prerequisite for rapid liquid pumping (DENTON, 1974) this difference is functionally significant.

In contrast to the situation in *Nautilus*, the organic siphuncular tube in ammonoids is not porous, not even within the septal neck. This may have added to its strenght, supporting MUTVER's (1975) assumption that ammonoid shells were adapted to withstand considerably higher hydrostatic pressures than *Nautilus* shells. TANABE et al. (1979) noted that the septal necks are characteristically longer in Upper Cretaceous ammonites with a narrow siphuncular tube, which would also mean an extended pillar zone to make up for the reduction of decoupled liquid in a narrower tube.

Independent formation of siphuncular tube versus septum may have also aided the ammonites to construct a more complicated septum with corrugated and fluted margins. Thus many small indentations are formed on each side of the septum between the inner face of the outer shell wall and the septum proper. In chambers only partially filled with liquid this differentiation of the septal margins may have assisted in the de-coupling

of the chamber liquid from the liquid contained within the pillar zone of the siphuncular tube (BANDEL & BOLETZKY, 1979; KULICKI, 1979). The effect would be similar to that described by BANDEL & BOLETZKY (1979) in the cuttlebone of *Sepia*, where chamber liquid is also held in many small and isolated locations within the chamber. After de-coupling of chamber liquid from the liquid held in the pillar zone close to the living siphuncle, water could be rapidly pumped out or in by several such pillar zones, which could have been active contemporaneously. De-coupling was also aided by the absence of a blotting paper effect as it is provided by the chalky layer on the outside of the siphuncular tube in living *Nautilus*.

The cameral liquid removal system in *Nautilus* is designed to maintain neutral buoyancy but not to produce rapid changes in the overall density that could aid in ascent and descent (WARD, 1979). According to WARD et al. (1977) *Nautilus* possesses slightly negative buoyancy at all growth stages. Positive uplift from gas filled chambers is offset by the weight of the shell, soft parts and cameral liquid. But these authors showed that cameral liquid is largely removed from the shell of *Nautilus*, in fact the liquid used for buoyancy control is essentially restricted to the last chamber, or to the last three as a maximum. *Nautilus* usually travels slowly with pendulum-like motions corresponding to the jets of water expelled from the funnel (HAMADA et al. 1980, Fig. 3.3). When the animal travels forward it turns the funnel posteriorly, when it ascends vertically it turns the funnel downwards propelling itself with jets of water that can be quite powerful. The shells of dead *Nautilus* washed to the shores usually show empty chambers and the siphuncular tube preserved from the first to the last gas filled chamber. This is different in ammonoids. In the chambers of the last whorl of *Quenstedtoceras* and other genera, no siphuncular tube is preserved (KULICKI, 1979). This author found that specimens with the body chamber preserved very rarely have organic siphuncular tubes preserved in the last chambers of the phragmocone, although the prismatic connecting structures in and on the septal necks are present. This difference indicates that the last chambers of adult ammonoids, in contrast to *Nautilus*, were largely filled with water. Here the wet organic siphuncle could be utilized as food by aquatic microorganisms, while it remained undamaged further back in the phragmocone where the chambers were gas filled. Sufficient time for bacterial or fungal decomposition of the organic siphuncular tube in the liquid-filled chambers was available if we accept MUTVEI's (1975) assumption that ammonoid shells without soft body may have drifted several months on the surface of the sea before they sank to the bottom or became stranded.

The amount of cameral liquid in ammonoids has probably been much greater than in adult *Nautilus*. According to HEPTONSTALL (1970) and MUTVEI & REYMENT (1973) between 20 and 50 % of the chamber space

was filled with fluid. MUTVEI & REYMENT got this result from experiments with plastic shell models. Ammonoids often had a narrow living chamber, in many cases narrower than the living chamber of *Nautilus*. According to LEHMANN (1975, 1976) the worm-like soft body of individuals with narrow living chambers had little place to produce powerful jet propulsion. According to MUTVEI (1975), the unstable and highly variable position of the shell during motion made swimming by jet propulsion also impossible. MUTVEI concluded that ammonoids essentially floated in the upper 1000 m of the water column, but undertook considerable daily vertical migrations, similar to the recent *Spirula*, mainly by changing their buoyancy.

Summary

In the process of formation of a new chamber the organic siphuncular tube of the ammonite *Quenstedtoceras* was secreted before the septum. It was attached to the ventral inner shell wall and the apertural surface of the old septum by organic pellicles that are continuous into solid ridges of spherulitic prismatic structure secreted onto the mineral shell wall. The septum with its complicated marginal suture was fixed in shape rapidly by spherulitic-prismatic aragonite mineralization within the extrapallial liquid secreted by the epithelium of the mantle. Within this mucus substance crystal growth proceeded in apical (backward) direction together with polymerization and arrangement of organic sheets and fibres of the septum and the thickening siphuncular tube. This mineralization followed the morphology of the stretched mantle epithelium without including it, by spherulitic-prismatic overgrowth in an apical direction. Afterwards the complicated pattern of the myo adhesive epithelium attached in tie points and lines to the shell wall was released. After total completion of the new section of the siphuncular tube and mineral fixation of the marginal septal shape the nacreous septum was deposited and the chamber could become functional. The sections of the siphuncular tube are connected to each other within the septal neck in such a way that between spherulitic-prismatic deposits an extended pillar zone is formed that could be utilized to decouple some liquid from the bulk of chamber liquid and connect the closed-off chamber with the living siphuncle. The mode of septum-siphuncular tube construction in ammonites is compared with that of *Nautilus* and structure; formation and function of these features are discussed.

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Anschrift des Verfassers:

Dr. KLAUS BANDEL, Institut für Paläontologie, Loewenichstr. 28, D-8520 Erlangen.

