

Organic components in phragmocones of Boreal Triassic ammonoids: implications for ammonoid biology

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With 23 figures

Kurzfassung: Aus der borealen Trias von Svalbard und NE-Sibirien werden Ammonoideen-Faunen beschrieben, bei denen die ursprünglich aragonitischen Schalenbestandteile früdiagenetisch in Apatit umgewandelt worden sind. Durch den Umstand, daß die Gehäuse später mit Kalzit ausgefüllt wurden, läßt sich der Kammerinhalt chemisch herauslösen. Damit wird eine außergewöhnliche räumliche Betrachtungsweise des Septenbaues und des Siphonal-Apparates ermöglicht. Das Besondere an diesem Ammonoideen-Material besteht jedoch darin, daß durch den frühen Zeitpunkt der Phosphatisierung auch ehemals organische Gehäusebestandteile in Apatit umgewandelt und damit erhalten geblieben sind. So zeigen fast alle untersuchten Gehäuse ehemals organische Membranen, die die Septen und die Gehäuseinnenwände auskleiden. Diese Membranen können mit dünnen Protein-Lagen im Phragmokon des rezenten *Nautilus* homologisiert werden, die eine besondere Rolle beim Pumpvorgang spielen, wenn die Kammerflüssigkeit nicht mehr im direkten Kontakt mit dem Siphonalrohr steht. In einer Anzahl von Exemplaren sind im Phragmokon phosphatisierte, flächenhaft ausgedehnte Lamellen erhalten, die in einem z.T. komplizierten System Teile des Kammerlumens von dem übrigen Raum abriegeln. Nach ihrer Form und Lage innerhalb der Kammer werden drei Typen unterschieden: 1. Siphonal-Lamellen, 2. Transversal-Lamellen, 3. Horizontal-Lamellen. Aus der Interpretation dieser intrakamerale organischen Strukturen ergeben sich neue Erkenntnisse bezüglich der Funktions-Morphologie von Ammonoideen-Gehäusen besonders im Zusammenhang mit Schwimmfähigkeit, Lokomotion und Lebensweise. Die Beschreibungen ähnlicher Strukturen bei phosphatisierten Ammonoiden aus dem Perm und dem Volgium der UdSSR belegen, daß das Vorkommen derartiger Lamellen nicht auf triassische Arten beschränkt ist, sondern vielmehr ein allgemeines Phänomen darstellt, dessen Erhaltung jedoch besonderer Fossilisations-Bedingungen bedarf.

Abstract: Extraordinarily well-preserved ammonoids from the Boreal Triassic of Svalbard and NE-Siberia are described, in which the original aragonite of the shell had been replaced by apatite during very early stages of diagenesis. Because of subsequent calcite cementation of the phragmocones, it is possible to dissolve the chamber contents. This allows three-dimensional observations at different ontogenetic stages. The most remarkable features, however, are preserved organic sheets in the ammonoid phragmocones which are normally readily destroyed. Nearly all specimens examined show phosphatized membranes lining the septal surfaces and the inner shell wall. These membranes are most probably homologous to thin protein layers in the phragmocone of the recent *Nautilus*, where they are termed the pellicle. They play an important part in the buoyancy control when the chamber liquid is no longer in direct contact with the siphuncular tube. In a number of specimens, a complicated system of formerly organic sheets which close off single compartments from the main chamber volume are preserved within the phragmocone. Depending on type and position of these layers in an ammonoid chamber, three different groups may be distinguished: 1. siphuncular sheets, 2. transverse sheets, and 3. horizontal sheets. The interpretation of the presence of these sheets leads to new conclusions concerning the functional morphology of the shell, especially related to questions of buoyancy, locomotion, and mode of life. Descriptions of similar structures within Permian goniatitids and Volgian ammonites indicate, that cameral sheets are not restricted to our Triassic species, but are a more general feature. They were probably present in most ammonoids, but have rarely been preserved.

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Introduction

Studies on the preservation of soft integument by secondary phosphatization have received increasing attention during the last few years and are a most important source of detailed morphological information. Recently, one of us (WEITSCHAT 1986) described an extraordinarily well-preserved ammonoid fauna from the Middle Triassic of Spitsbergen in which the original calcium carbonate of the ammonoid shells had been replaced by apatite during very early stages of diagenesis. Because of subsequent calcite infilling of the ammonoid phragmocones, it was possible to dissolve the chamber contents by acetic acid. This permitted three-dimensional observations of various morphological elements at different ontogenetic stages.

The most remarkable features, however, are preserved organic sheets in the ammonoid phragmocones which are normally readily destroyed.

In addition to the phosphatized ammonoids from Spitsbergen material from the Upper Ladinian of East Siberia (Kolyma Basin) has been investigated which shows similar structures.

Discussion of the function of the former organic sheets in phragmocones of different ammonoid genera leads to some new inferences regarding Triassic ammonoid biology, especially buoyancy.

Material and localities

Svalbard Archipelago

Phosphatized ammonoids were mainly collected within the Botneheia-Member, Barentsøya-Formation which is typically well-developed on Central and East-Spitsbergen, on Barents- and Edgeøya. This unit consists of dark grey to black organic-rich shales and siltstones with carbonate and phosphate nodule layers throughout the sequence. Its maximum thickness in Central Spitsbergen is about 160 m, and it thins towards the east. The base of the unit is marked by the Lower Anisian transgression, and deposition continued under marine shelf conditions throughout the Lower Carnian.

Phosphatized ammonoids were discovered in several levels from the Lower Anisian to the base of the Lower Carnian. The majority of the faunas investigated here comes from the Middle Anisian and from the Ladinian/Carnian transition. The Middle Anisian ammonoids were collected at the top of a thin carbonate layer enriched in phosphate. It was first discovered at Wallenbergfjellet (WEITSCHAT 1986), and has later been traced nearly all over Central- and East-Spitsbergen.

The fauna is composed of different species of the genera *Anagymnotoceras*, *Hollandites*, *Amphipopanoceras*, *Czekanowskites* and *Leiophyllites*. While several hundred specimens of the three first mentioned genera were collected, leiophyllitids and czekanowskitids are extremely rare. Biostratigraphically this fauna indicates the upper part of the *Anagymnotoceras varium* zone (subzone of *Czekanowskites hayesi*).

A second Middle Anisian phosphatized ammonoid fauna was discovered by KULLING (1931) at Kapp Torell (Nordauslandet) and was later described by TOZER (1973). Additional material from this outcrop was collected during the work of the Palaeontological Institute of the University of Oslo (A. MORK, D. WORSLEY). Both collections have been studied for the current investigation. Ammonoids from Kapp Torell occur in small phosphate nodules. They have been collected in moraine deposits so that their exact stratigraphical position is unknown. While the presence of Beyrichitidae (*Anagymnotoceras*, *Hollandites*) leaves no doubt that the Middle Anisian (*varium*-zone) is represented, other ammonoids such as *Stenopopanoceras* and *Japonites* indicate a Lower Anisian age. It is possible that they are from a condensed sequence or two different nodule layers mixed by glacier activity.

Ladinian phosphatized ammonoids have also been discovered in the Upper Ptychitid-Layer (WEITSCHAT & LEHMANN 1983). This fauna occurs in limestone concretions and consists of *Aristoptychites kolymensis*, *Indigrites tozeri*, and *Ussurites spetsbergensis*. Biostratigraphically it is from the Upper Ladinian (*tozeri*-zone). Phosphatized samples of this horizon are restricted to the eastern outcrop areas.

First examples of Carnian phosphatized ammonoids were discovered during the last field season (1988) on the east coast of Spitsbergen (Wiche Bukta). They occur in small phosphate nodules about 2 m above the Ladinian/Carnian boundary. The fauna belongs to the Lower Carnian (*tennis*-zone) and is composed of *Stolleites tennis*, *Stolleites* n. sp. and *Paracladiscites* cf. *diurturnus*.

East Siberia

Material from Siberia has been placed at our disposal through the courtesy of A.S. DAGYS (Ecological Institute, Lithuanian Academy of Sciences, Vilnius). The Siberian ammonoids were collected in the Kolyma Basin from the banks of the Korkodon river and Dschugajak creek. The fauna occurs in dark grey phosphate nodules in a sequence of black shales enriched with organic material. It is composed of *Aristoptychites kolymensis*, *Indigirites* sp., *Sphaerocladiscites omolonensis* and *Nathorstites* sp. This assemblage indicates an Upper Ladinian age and may be correlated with the *tozeri*-zone of the Svalbard Archipelago.

Systematic position

The investigated phosphatized ammonoids belong to 6 superfamilies with the following different families and genera:

Ceratitidae	(<i>Anagymmotoceras</i> , <i>Hollandites</i>)
Japonitidae	(<i>Japonites</i>)
Ptychitidae	(<i>Arctoptychites</i> , <i>Aristoptychites</i>)
Danubitidae	(<i>Czekanowskites</i>)
Longobarditidae	(<i>Lenotropites</i> , <i>Groenlandites</i>)
Aplococeratidae	(<i>Karangatites</i>)
Nathorstitidae	(<i>Indigirites</i> , <i>Stolleites</i> , <i>Nathorstites</i>)
Cladiscitidae	(<i>Sphaerocladiscites</i> , <i>Paracladiscites</i>)
Parapopanoceratidae	(<i>Amphipopanoceras</i> , <i>Stenopopanoceras</i>)
Ussuritidae	(<i>Ussurites</i> , <i>Leiophyllites</i>)

Mode of preservation and preparation techniques

The ammonoid faunas investigated from different localities and levels within the Boreal Triassic sequences generally show a quite unusual but uniform state of preservation. A common feature of all the material is phosphatization which took place during a very early stage of diagenesis, followed by calcite filling of the phragmocones and sediment filling of the body chamber.

The preparation techniques which have been described in detail by WEITSCHAT (1986) are based on the chemical differences between apatitic and calcitic material. By etching with acetic acid the phragmocone filling (calcium-carbonate) can be completely dissolved, making visible the former cavities of the phragmocone and all organic structures. As well as allowing three dimensional observations of nearly all skeletal elements within the ammonoid phragmocone, phosphatized formerly organic layers can be studied in detail.

The degree of phosphatization depends on the amount of phosphate which was available during diagenesis. Thus we can distinguish between two fundamentally different types of preservation. In the first, enough phosphorus was available for all originally aragonitic shell material and also formerly organic tissue to be replaced by carbonate apatite. In the second type with less phosphorus only formerly organic tissue has been phosphatized and preserved.

The first type of preservation is restricted to phosphate nodules or phosphatic limestones while the second occurs in phosphatic limestones or limestone concretions. The state of preservation of organic tissue is normally better in the second type. On the other hand dissolved specimens of this type are very fragile and difficult to handle. It has proven useful to fix the specimens onto SCAN-stubs before the etching process is begun. During the

etching process it is also important to keep the production of gas bubbles to a minimum. Very delicate phosphatized sheets can easily be destroyed by large bubbles.

Formerly organic structures found within the ammonoid phragmocone are pellicles which line the septal surfaces and different kinds of sheets stretching across parts of the whorls. In the preservation of such details a considerable variation can be observed not only between different localities and levels, but also from the same outcrop and even within a single specimen. This phenomenon can be explained by phosphatization taking place during the initial phase of decomposition of ammonoid soft tissue. Thus, the differences in preservation reflect different stages of decomposition at the time of phosphatization.

Phosphatization and diagenesis

Recent studies on preservation of soft integument by secondary phosphatization have shown that this phenomenon is more widespread geographically and stratigraphically than hitherto realized. The best known examples of phosphatized fossils are Upper Cambrian arthropods from the »Orsten« of Sweden. Their study has led to new and exciting findings concerning the phylogeny of arthropods (MÜLLER 1979a, b, c, 1982, 1985a, b, MÜLLER & WALOSSEK 1985a, b, 1986, 1987). A second example of phosphatization of organisms from the Paleozoic was recently discovered by ANDRES (1985, 1988) who described phosphatized parasitic worms from the Tremadocian of the Island of Öland (Sweden).

For the Mesozoic the most productive samples investigated so far have come from the famous fish-bearing limestone concretions of the Lower Cretaceous (Aptian) Santana Formation of NE Brazil. From these nodules phosphatized ostracods with preserved appendages (BATE 1972, 1973), copepodes (CRESSEY & PATTERSON 1973, CRESSEY & BOXSHALL 1989) and phosphatized soft tissues of teleost fishes (MARTILL 1988) have been described.

Other examples from the Mesozoic are phosphatized ostracods with preserved appendages from the Jurassic of the USSR (DZIK 1978) and from the Lower Triassic (Spathian) of Spitsbergen (WEITSCHAT 1983a, b).

Comparing all these records of secondary phosphatization of soft tissue within different fossil groups several similarities are evident which have been pointed out by MÜLLER (1985) and WEITSCHAT (1986):

1. Limestone nodules with a phosphate content occurring in still water sediments are the most promising lithology for such preservation.
2. Chitinous organisms are especially prone to replacement and coating by phosphate.
3. Phosphatization seems to be restricted to objects less than about 3 mm in size.
4. Phosphatized specimens are rare even in beds yielding productive samples.
5. Phosphatization must have occurred very early (at the time of the death or immediately afterwards).

Concerning the phosphatized ammonoid faunas described in the current paper only some of these assumptions turn out to be true.

1. Most productive samples are phosphate nodules or phosphatic limestone.
2. Soft tissue seems to play the important role. The phosphorus is probably liberated by microbial grazers.
3. No restriction in size has been observed.
4. All ammonoids are phosphatized in productive samples.

A main difference between the example represented here and others mentioned above seems to be the amount of phosphorus which was available during early diagenesis. This is normally quite low in limestone concretions, leading to phosphatization of only small

chitinous organisms or to an apatite coating of soft tissue of larger ones. In phosphate nodules or phosphatic limestones where the content of phosphorus is fairly high (up to 30% apatite) not only soft tissue but also aragonitic shell material is replaced by apatite.

Phosphate-rich sediments associated with high organic content are common especially in the Middle Triassic of the Svalbard Archipelago. Similar settings in Middle Triassic sediments have also been reported from the Sverdrup Basin (EMBRY 1984), the North Slope of Alaska (PARRISH 1986), and NE Siberia. These occurrences indicate uniform conditions over large areas which point to a major mechanism controlling sedimentation. From this point of view the phosphate-rich sediments of the Boreal Triassic Realm can be compared with main phosphate events which are widely distributed in the geological column, particularly in strata of Cambrian, Permian, Cretaceous/Lower Tertiary and Miocene/Pliocene age. The problems of the source of the phosphorus and the environmental conditions under which phosphatic sediments are deposited are still under discussion (BERNER 1968, BENMORE et al. 1983).

Following the discovery of modern phosphorite concretions in diatomaceous mud on the continental shelf regions of SW-Africa (Namibia) and South America (Chile, Peru), a substantial amount of work has been done towards understanding modern phosphogenetic events (BURNETT 1977, MACONELL 1973).

There is a common consensus that carbonate-apatite can form either by direct precipitation from sea water, at or close to the sediment/water interface, or alternatively during diagenesis by interstitial replacement or replacement of pre-existing sediments. Phosphatic facies seem to be restricted to a marine environment in areas with access to the open sea which are neither too shallow nor too deep (stable shelves or platforms).

Concerning the source of the phosphorus, the present consensus is that most of it became concentrated by phytoplankton (particularly diatoms) which occur abundantly in cold nutrient-rich waters associated with current or upwelling systems. Dead organisms sinking to the sea floor became remineralized by bacteria thus liberating phosphorus from the organic matter. The phosphorus is prevented from escaping in the water column by being rapidly adsorbed onto clay minerals, and organic particles like fecal pellets (BANDEL & MIKBEL 1985).

Eventually a fluid mud layer develops at the sediment/water interface which is composed of loosely aggregated material. Benthic and microbial communities utilize the complex organic matter to release nitrogen and phosphorus, thereby raising the levels of N and P species in the interstitial fluids. Thus, the phosphorus concentration of the interstitial fluids is raised to supersaturation. An increase in pH produced by the vast amount of ammonia may accelerate the precipitation of carbonate-apatite or initiate phosphatization of CaCO_3 and organic tissues.

Reconstruction of diagenetic processes which affected the Triassic ammonoids should be viewed in relation to those phosphatic events.

Following the death of the ammonoids their shells sank to the sea-floor and became enveloped in a phosphatic mud. Normally soft tissues of ammonoids would decompose within a few hours to days. In these examples, however, the dissolved phosphate in the fluid mud seeped into the ammonoid phragmocones and instead of staying in solution was rapidly precipitated as carbonate-apatite. This process seems to have been mediated by the soft tissue of the ammonoid phragmocones (e.g. siphuncular tube, organic sheets, septal lining) where additional phosphorus became liberated by microbial grazers. Thus, tissue phosphatization took place during a very early stage of diagenesis, probably within a few hours or days of the animals' sinking to the seabed. This supposition is supported by the fact that organic sheets have usually started to decompose prior to phosphatization. In contrast, phosphatization of the aragonitic components of the ammonoid shells must have occurred at a later stage.

Descriptions of morphological features

Muscle scars

The hollow interiors of our extremely well-preserved ammonoid phragmocones allow a thorough investigation of the inner shell and septal surfaces at different stages of ontogeny. Of particular interest is the search for muscle scars, especially scars of the main retractor muscle, which might be impressed on the inner shell walls in these well-preserved specimens.

While there are no impressions on the lateral or ventral sides of the inner shell wall, we discovered, in nearly all investigated specimens of the different genera, scars situated on the dorsal part at the surface of the previous whorl adoral of each septum, immediately inside the internal lobe. All of these scars are unpaired and have a characteristically long slender outline and a rugose surface structure. They usually extend for 2/3 of a chamber length. Because of the excellent preservation their outline and position can be demonstrated through all ontogenetic stages (WEITSCHAT 1986).

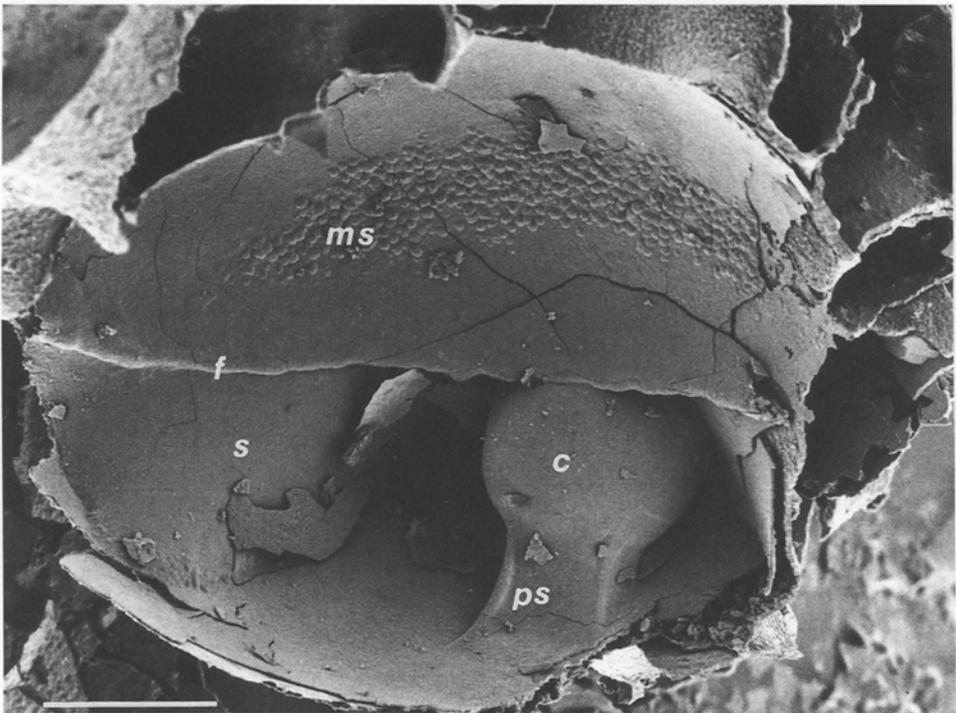
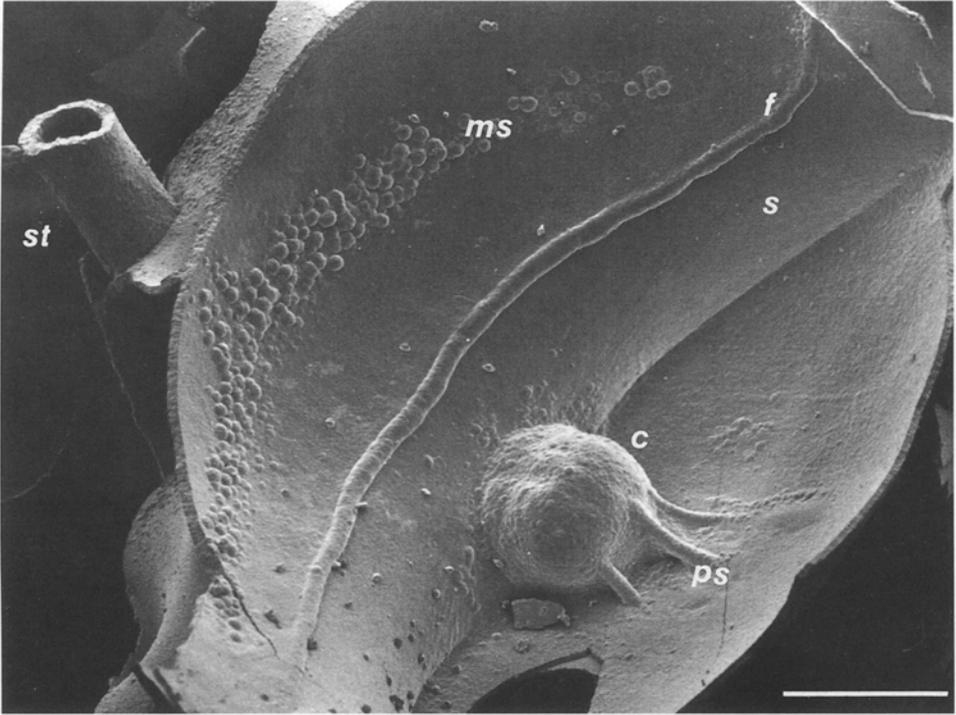
Differences in the outline and position of muscle scars are only evident in embryonic stages of the ammonoids. The first scar within the protoconch looks totally different from all of the following scars. It is situated opposite to the flange and extends almost the entire breadth of the protoconch. While its aboral limitation is quite straight the oral edge shows a more undulating structure (Figs. 1, 2). Like the first scar, the second scar is developed during the embryonic stage of the ammonoid. This is the only paired scar and is situated on the dorsal part of the first septum (proseptum) on each side of the first siphuncular segment. The outlines of the two scars are nearly spherical. Both move together and fuse with each other in the third scar which is situated on the previous whorl in the position of the internal lobe. The single third scar differs from later scars only in its broader and less elongated outline (Figs. 3, 4).

In our material muscle imprints with identical ontogenetic development have been observed in the following genera: *Amphipopanoceras*, *Anagymnotoceras*, *Czekanowskites*, *Nathorstites*, *Arctoptychites*, *Aristoptychites*, *Sphaerocladiscites*, *Paracladiscites*, *Stolleites*, *Indigirites*.

Information concerning muscle attachment impressions is extremely rare in the ammonoid literature. The first detailed studies were made by CRICK (1898) who described as muscle attachment small paired, oval-shaped scars on the dorsal side of the body chamber of some Mesozoic ammonoids. Because many of CRICK's illustrations are rather vague, usually depicting impressions on internal moulds, many subsequent authors have doubted the validity of his findings (SPATH 1919, ARKELL et al. 1957). However, more recent results of MUTVEI (1957, 1964), JORDAN (1968), PALFRAMAN (1969), MUTVEI & REYMENT (1973) seem to confirm the early observations by CRICK.

Fig. 1. *Aristoptychites kolymensis* KIP., Upper Ladinian, Barentsøya Formation, Bertylryggen (Central Spitsbergen). – View into the hollow interior of the protoconch, showing the first septum (s), the caecum (c) with the siphon attachment (prosiphon) (ps), the flunch (f), and the broad scar of the body attachment (ms). SGPIMH no. 3585. Scale 100 µm.

Fig. 2. *Sphaerocladiscites* cf. *diurturnus* (MOJ.), Lower Carnian, Tschermafjellet Formation, Hahnfjella, East Spitsbergen. – View into the hollow interior of the protoconch, showing the first septum (s), the caecum (c) with the prosiphon (ps), the flunch (f) and the scar of the body attachment (ms). SGPIMH no. 3586. Scale 100 µm.



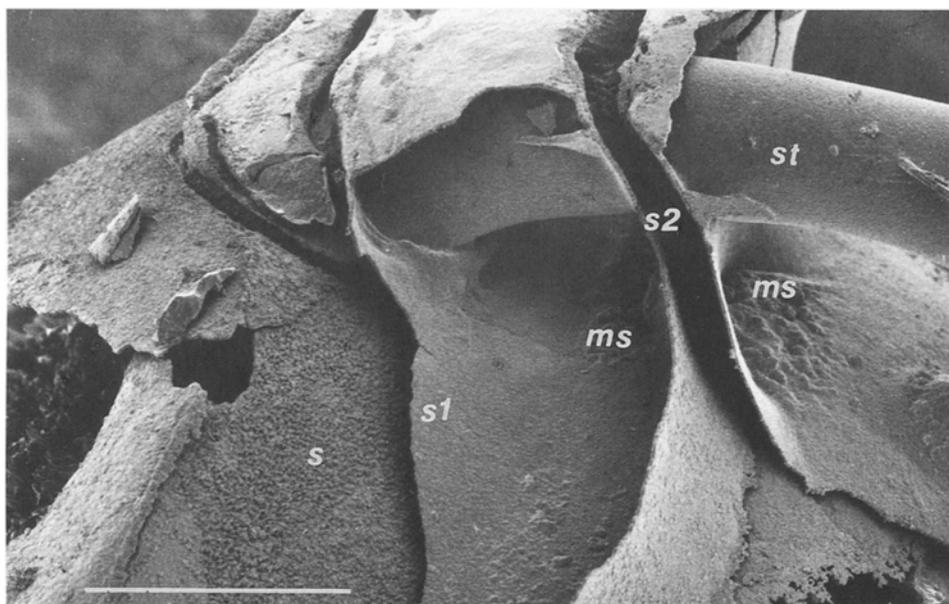


Fig. 3. *Stolleites* cf. *lindstroemi* BÖHM, Lower Carnian, Tschermakfjellet Formation, Hahnfjella, East Spitsbergen. – Lateral view, showing the first septa (s, s1, s2), the respective scars of the retractor muscles (ms), and the siphuncular tube (st). SGPIMH no. 3587. Scale 100 μ m.



Fig. 4. *Aristoptychites* *kolymensis* КИР., Upper Ladinian, Barentsøya Formation, Bertylryggen, Central Spitsbergen. – 3rd and 4th septa (s) with muscle scars (ms) situated within the internal lobe. SGPIMH no. 3588. Scale 100 μ m.

All of the authors described paired muscle scars typically situated on the dorsal face of the body chamber. An additional unpaired ventral muscle scar observed by MUTVEI in MUTVEI & REYMENT (1973), and KENNEDY & COBBAN (1976), was interpreted as »some kind of gill retractor muscle« (KENNEDY & COBBAN 1976). JONES (1961) also described three muscle attachment impressions on the internal mould of a heteromorph (*Diplomoceras*) from the Upper Cretaceous.

A novel suggestion by HENDERSON (1984) was that the fluted septal periphery of Mesozoic ammonoids functioned as an attachment for the muscle. Nearly all of the observations mentioned above are based upon insufficiently preserved ammonoid material, usually on imprints on internal moulds.

More recently BANDEL (1982), and LANDMANN & BANDEL (1985), have studied the internal structures of some extraordinarily well-preserved ammonoids from the Callovian of Lukov (Poland) and from Lower and upper Cretaceous of N-America. Because the investigated phragmocones are free of matrix detailed investigations of all internal structures have been done. Muscle attachment scars were described from the genera *Quenstedtoceras*, *Kosmoceras*, *Euhoplites*, and *Hypacanthoplites*. They are situated at the dorsal side of the phragmocone just adoral of each septum, and have a rounded to oval outline with a typically rugose surface structure. Only the impressions on the first septum are paired, later impressions are clearly unpaired. Comparison of these scars with our Triassic material shows only a few differences in the outline of the single impressions which are more elongate in the Triassic ammonoids than in Jurassic and Cretaceous ammonoids (Fig. 5). In

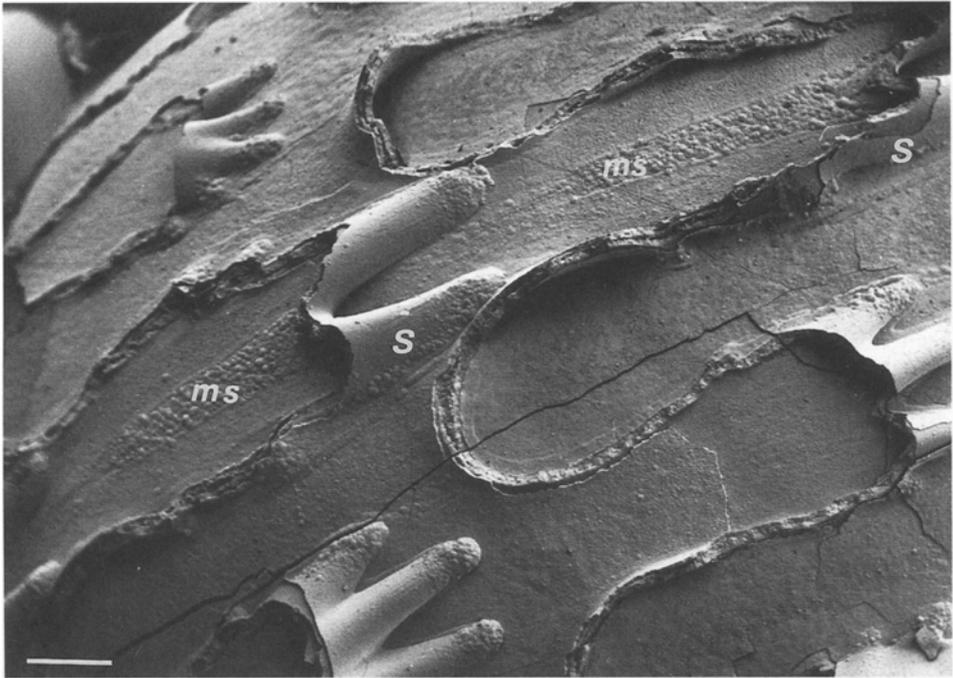


Fig. 5. *Amphipopanoceras* cf. *medium* (MCLEARN), Middle Anisian, Barentsøya Formation, Wallenbergfjellet, Central Spitsbergen. – 5th whorl with characteristically elongate muscle scars (ms) within the internal lobe; (s) septum. SGPIMH no. 3187. Scale 300µm.

all this Mesozoic material there is no evidence for the existence of ventral unpaired muscle impressions.

If our interpretation of the unpaired dorsal scars as the main retractor muscle impression is correct, distinct differences in muscle patterns between ammonoids and recent *Nautilus* are apparent. In *Nautilus* the muscles are attached on either side at the rear of the living chamber and the scars are much larger. This difference suggests that the volume of muscle tissue and presumed power of contraction must be far greater in *Nautilus* than in ammonoids. Because the main function of the retractor muscle is for swimming (WARD 1987), it is suggested that *Nautilus* may be a much better swimmer than any ammonoids of equivalent size.

A further difference between both seems to be the manner in which the muscle attachment is translocated during growth. In *Nautilus* this is accomplished by a slow periodic forward movement of the animal in its shell (WARD 1985, 1987). For ammonoids we suggest that the retractor muscles were episodically detached, withdrew into their new position and were rapidly reattached.

Organic linings of the phragmocone

Nearly all of the investigated specimens show phosphatized, formerly organic membranes lining the surfaces of the septal faces and the inner shell wall. They are connected with the siphuncular tube by broad sheets, thus forming a closed system in each chamber. Due to diagenetic processes the membranes show a granular surface structure and may become as thick as a septum itself.

The most impressive specimens for demonstrating the membrane system are those where only formerly organic tissue is phosphatized. When the calcitic shell material is dissolved, the complicated septal structures remain supported only by the phosphatic membranes.

Due to their former organic composition the fossil record of such membranes is quite poor. BAYER (1975) observed and described black layers lining the septal surfaces of some well-preserved ammonoids from the Pliensbachian of SW-Germany. He also mentioned their typical rugose surface structure. A further record comes from the famous extraordinarily well-preserved Callovian ammonoid fauna of Lukow (Poland) where KULICKI (1979) discovered conchiolin films with a granular structure coating the septal faces of the ammonoid phragmocones.

The question of the function of these organic membrane systems may possibly be answered by reference to the experimental investigations by DENTON & GILPIN-BROWN (1966) on Recent *Nautilus*. They described a thin protein membrane, termed the pellicle, lining the septal faces and the inner shell walls. The pellicle remains wet in all chambers of the conch. DENTON & GILPIN-BROWN demonstrated that this pellicle system plays an important role in the buoyancy control of *Nautilus* when the chamber liquid is no longer in direct contact with the siphuncle ("decoupled cameral liquid"). During this phase, chambers continue to be emptied via the pellicle, which draws liquid onto the siphuncle according to the "blotting paper principle". In addition to this transportation function, the pellicle also seems to have a liquid storage function (WARD 1987). In Recent *Nautilus* it thickens at the low angle intersection of shell wall and septum (suture zone), causing liquid to be trapped by surface tension in these areas. Although the amount of liquid within any single chamber is quite low, the sum total of all liquid in 30–32 chambers was estimated to be about 3–5 ml. WARD (1987) assumed that *Nautilus* uses this volume of liquid for rapid short-time buoyancy changes, moving liquid into and out of the pellicle layer within the chambers.

The presence of such pellicles with a similar function in ammonoid phragmocones also has been suggested by several authors (MUTVEI 1967, BAYER 1975, KULICKI 1979, BANDEL

1981, 1982) while others have doubted it (WESTERMANN 1971, ERBEN & REID 1971, KENNEDY & COBBAN 1976). This discussion was revived by WARD (1987), who reflected on the functional importance of the complexly fluted ammonoid septa in contrast to the much simpler folded septa of nautiloids. He pointed out two major advantages for the fluted ammonoid septa:

1. An increase in the pellicle system surface area, leading to a far greater amount of liquid which can be stored in it;
2. an enormous increase in the length of the sutural zones, where in small pockets much more liquid can be trapped by surface tension.

Both will be enlarged still further when the total number of septa, usually more than 3 times as many in ammonoids as in *Nautilus*, is taken into account. With regard to the decoupled transport of liquid, the presence of an increased pellicle system may have accelerated the pumping procedure considerably. Therefore the volume of decoupled liquid which might have been of use to the animal for rapid buoyancy regulation could have been far greater in ammonoids than in *Nautilus*. The total amount is estimated to be about 30 to 50 ml within an ammonoid phragmocone of comparable size to that of Recent *Nautilus*. Thus, the typical ammonoid phragmocone may have maintained significant fluid reserves available for movement out of the chamber on demand.

The functional importance of the fluted ammonoid septa cannot be related solely to a mechanical strengthening but must be considered as an important factor in buoyancy control.

Intracamerar conchiolin layers

Perhaps the most remarkable feature of the investigated material is that, due to the very early time of phosphatization, organic layers, which normally are readily destroyed, are well-preserved within the phragmocone of some specimens. A great variation is observed in the preservation of such sheets even within a single phragmocone. The state of preservation obviously reflects the state of decomposition of the animal rather than the presence or absence of such formerly organic structures within the ammonoid phragmocone as a whole. According to the type and the position of these layers in a chamber three different groups may be distinguished: a) siphuncular sheets, b) transverse sheets, and c) horizontal sheets.

Siphuncular sheets

The most common structures, observed in nearly all of the investigated ammonoid genera, are siphuncular sheets. They have been recognized from early ontogenetic stages (usually at the beginning of the 3rd whorl) up to the adult conch. Siphuncular sheets consist of two membranes which originate from the outer organic layers at each side of the siphuncular tube. The membranes are attached to the internal surface of the ventral wall. They are also connected to the septa where they merge into the pellicle layer of the septal faces at the lateral saddles (abapertural) and the ventral lobes (apertural). The course of these sheets towards the ventral wall is not vertical but rather oblique. Thus, relatively large compartments are produced along each side of the siphuncular tube (Figs. 6, 7).

In a number of specimens a very special and unusual development of siphuncular sheets can be seen. In this type the spaces which are formed by the sheets on each side of the siphuncle are again divided by small organic membranes directed vertically and curved slightly forward. Thus, a row of up to ten separate compartments is formed in a single chamber on each side of the siphuncular tube (Figs. 8, 9, 11). These small compartments vary in size. The largest ones occur at the apical side of each chamber where the two main sheets are in direct contact with the septal walls, thus forming quite deep and broad

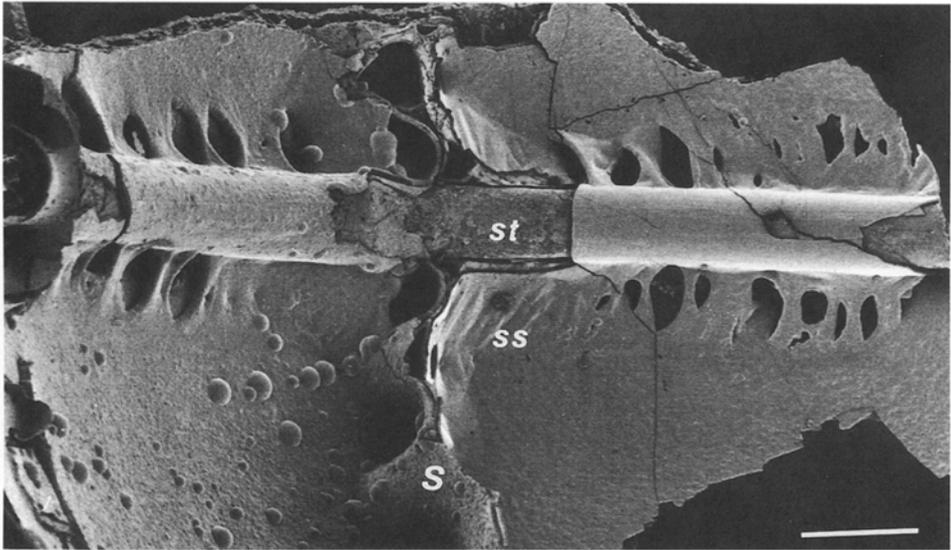


Fig. 6. *Aristoptychites kolymensis* KIP., Upper Ladinian, Barentsøya Formation, Roslagenfjellet, East Spitsbergen. – View into the interior of two consecutive chambers with siphuncular sheets (ss) preserved on the siphuncular tube (st); (s) septum. SGPIMH no. 3589. Scale 300 μ m.



Fig. 7. *Anagymnotoceras varium* (MCLEARN), Middle Anisian, Barentsøya Formation, Wallenbergfjellet, Central Spitsbergen. – Lateral view into a hollow chamber showing well-preserved siphuncular sheets (ss); (s) septum, (st) siphuncular tube. SGPIMH no. 3590. Scale 300 μ m.

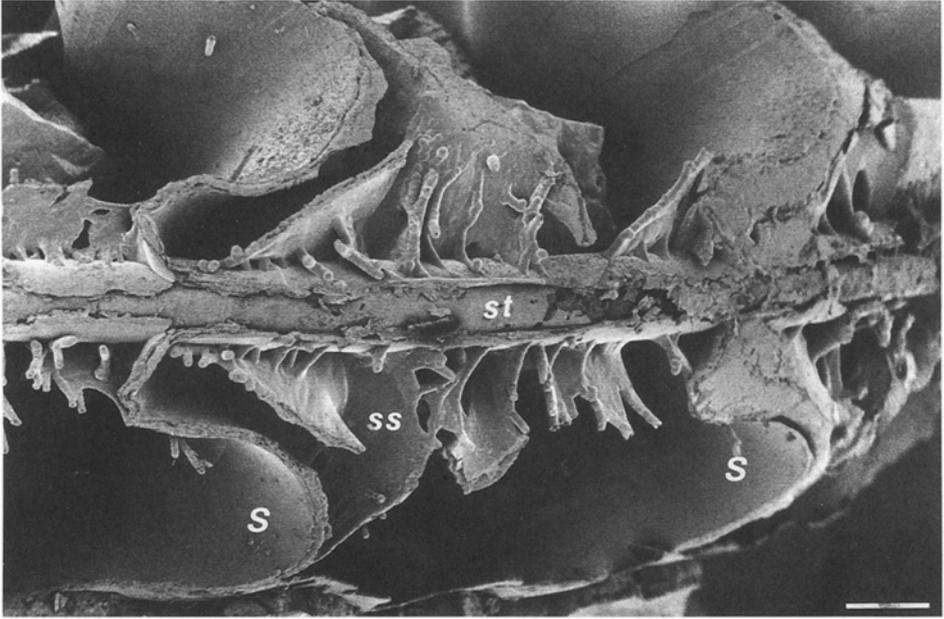


Fig. 8. *Anagymnoceras varium* (MCLEARN), Middle Anisian, Barentsøya Formation, Wallenbergfjellet, Central Spitsbergen. – View into a hollow chamber with siphuncular sheets (ss) connected to additional vertically directed membranes; (s) septum, (st) siphuncular tube. SGPIMH no. 3591. Scale 300 μ m.

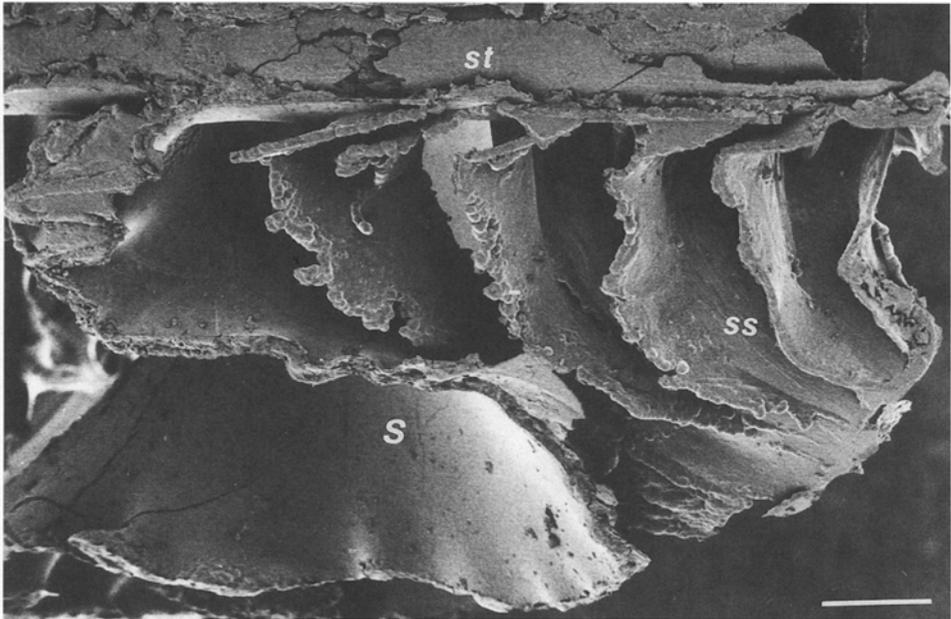


Fig. 9. *Czekanowskites hayesi* (MCLEARN), Middle Anisian, Barentsøya Formation, Wallenbergfjellet, Central Spitsbergen. – Detail of siphuncular sheets (ss) with additional vertically directed, short membranes; (s) septum, (st) siphuncular tube. SGPIMH no. 3592. Scale 300 μ m.

individually closed compartments. The individual compartments become gradually smaller and narrower in apertural direction (Fig. 11a, b). This special type of siphuncular sheet appears to be restricted to platycone ammonoid conchs. In our material they have been observed in the genera *Anagymnotoceras*, *Hollandites*, *Czekanowskites*, *Pearylandites*, and *Stolleites*.

Siphuncular membranes were first described by GRANDJEAN (1910) from longitudinal and transverse sections of some Jurassic and Cretaceous ammonoids, and were also observed by SHULGA-NESTERENKO (1926) in phosphatized Permian goniatids from the USSR. They were neglected by most subsequent authors until SCHINDEWOLF (1968) described intracameral conchiolin layers in some well-preserved specimens from the Volgian of the Russian Platform. Later WESTERMANN (1971), ERBEN & REID (1971), KULICKI (1979) and BANDEL (1982) mentioned similar structures, mainly in hollow phragmocones of single specimens of well-preserved ammonoids from the Jurassic and Cretaceous. The first record of siphuncular sheets in Triassic ammonoids was made by WEITSCHAT (1986).

While earlier authors supposed that the siphuncular tube and sheets were originally composed of calcium-phosphate (GRAND-JEAN 1910, ANDALIB 1972, BAYER 1975), it was later pointed out that they were most probably composed of conchiolin. The fact that both structures are locally wrinkled through shrinkage indicates that they were originally soft and flexible and purely organic in composition (ERBEN & REID 1971, BANDEL 1982, WEITSCHAT 1986).

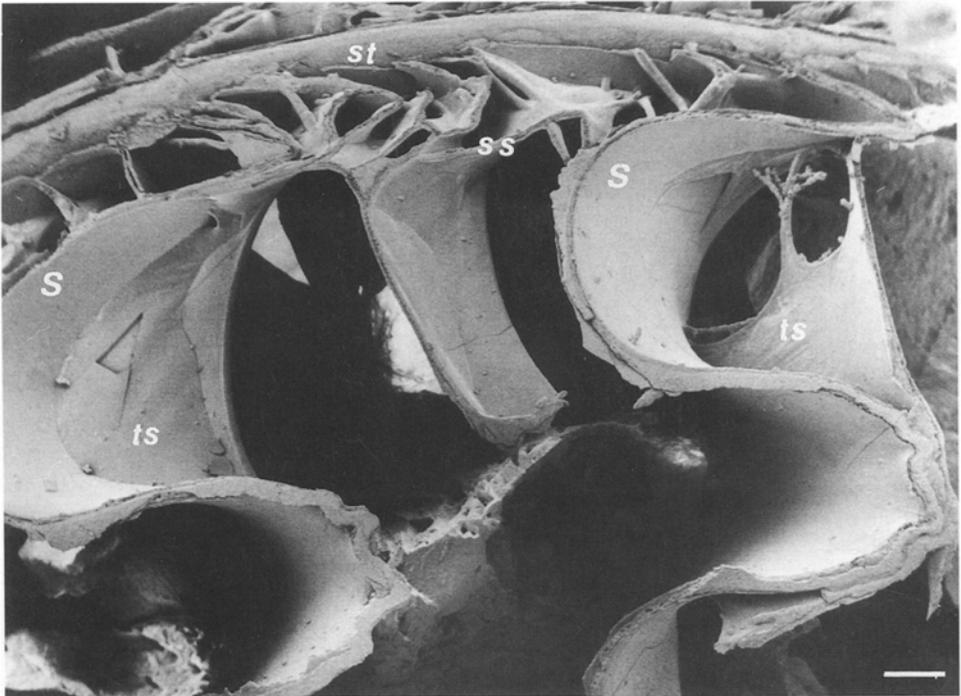


Fig. 10. *Czekanowskites hayesi* (MCLEARN), Middle Anisian, Barentosøya Formation, Wallenbergfjellet, Central Spitsbergen. – View into a hollow chamber with well-preserved siphuncular sheets (ss) and additional transverse sheets (ts); (s) septum, (st) siphuncular tube. ŠGPIMH no. 3593. Scale 300 μ m.

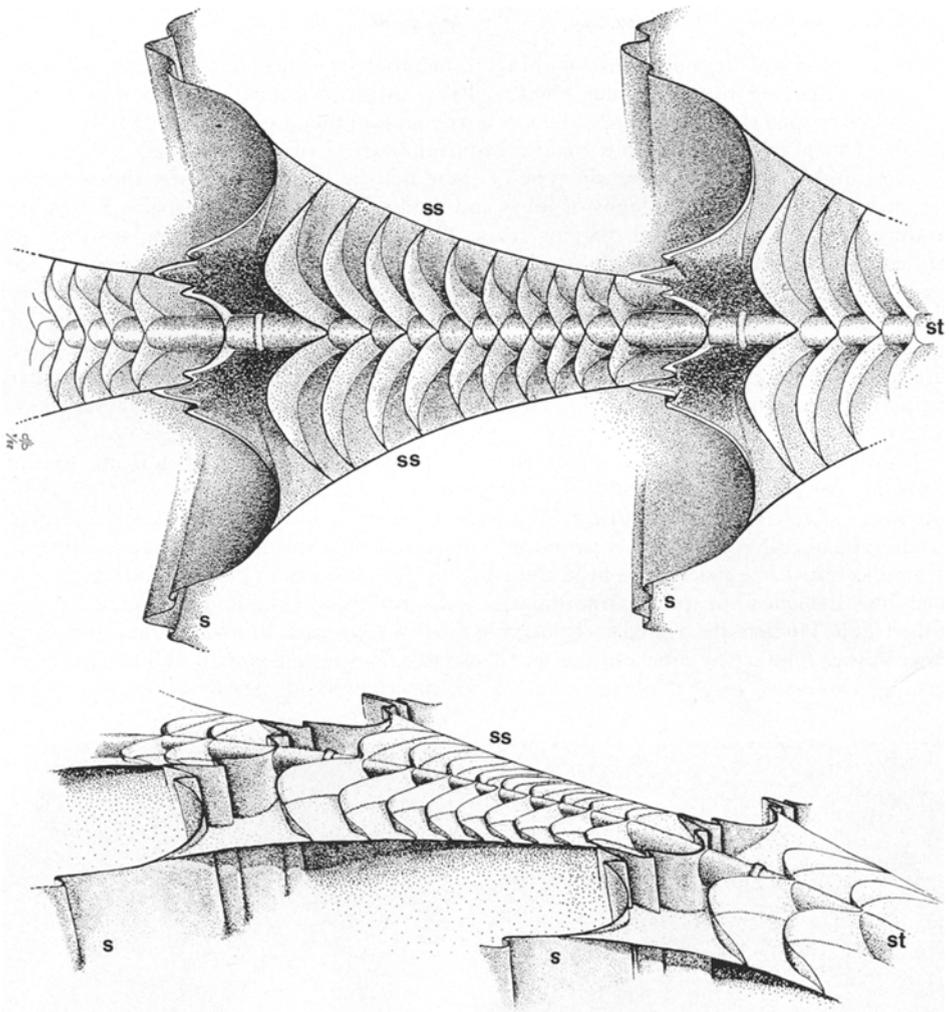


Fig. 11. The reconstruction of siphuncular sheets (ss) within one chamber of *Anagymnotoceras*, demonstrating the two main sheets connected to vertically directed sheets. – a: Frontal view; b: Lateral view. (s) septum, (st) siphuncular tube.

Comparing siphuncular sheets of the Triassic ammonoids with similar structures from Jurassic and Cretaceous ammonoids, an important difference is evident in the orientation of the sheets. They are rather obliquely orientated in the Triassic material but are usually short and straight in Jurassic and Cretaceous ammonoids where they most probably function only to attach the tube to the inner shell wall.

Transverse sheets

All intracameral organic layers within the material investigated which stretch in an ammonoid chamber from the inner shell wall in a direction subparallel to a mineralized septum are termed transverse sheets. Unlike a true septum they never reach the floor of the chamber (the previous whorl), but are attached to the surface of a true septum.

The simplest and most common type of these pellicle structure are flat sheets which stretch between topographic highs of lobes and saddles, thus closing off spaces which are produced by the fluted septal margins (Figs. 12–15). The size of the compartments so formed depends on the angle with which the sheets meet the mineralized septum; i. e. the steeper the angle the larger the compartment. Other transverse sheets are suspended from the siphuncular tube into the free space of the chamber, twisting at about half the height of the chamber into a forward direction to attach ultimately to the next septum. Some of these structures lay quite close to a septum and are stretched obliquely to this. Thus, triangular compartments are formed which are separated from the main volume of the chamber (Figs. 14, 15).

Transverse sheets have been observed in a number of specimens belonging to the following genera: *Czekanowskites*, *Amphipopanoceras*, *Lenotropites*, *Aristoptychites*, *Arctoptychites*, *Paracladiscites*, *Stolleites*. This type of sheet is obviously not restricted to a certain type of coiling. They often co-occur with siphuncular sheets in the same specimen.

Similar transverse sheets have been described by SCHINDEWOLF (1968) as "intrakamerale Cochiolin-Lamellen" in some extraordinarily well-preserved ammonoids from the Volgian of the USSR. He first discovered such sheets in median sections as thin black lines stretching between the siphuncular tube and the septal surfaces. In specimens with hollow chambers enabling three-dimensional observations, SCHINDEWOLF could clearly demonstrate that

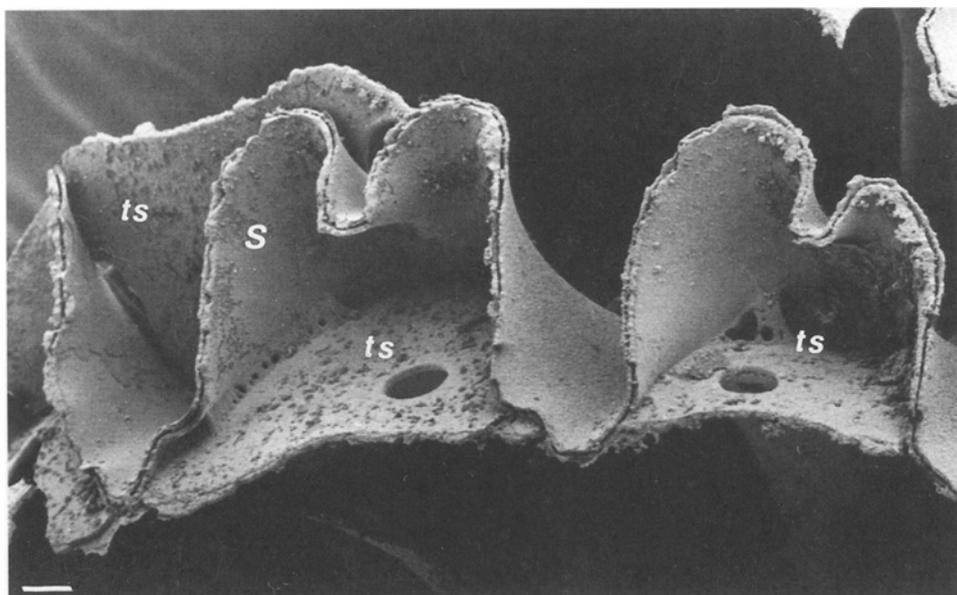


Fig. 14. *Arctoptychites* sp., Upper Ladinian, Barentsøya Formation, Hahnfjella, East Spitsbergen. – Transverse sheets (ts) produce separated small compartments on both sides of the septum (s). SGPIMH no. 3595. Scale 300 μ m.

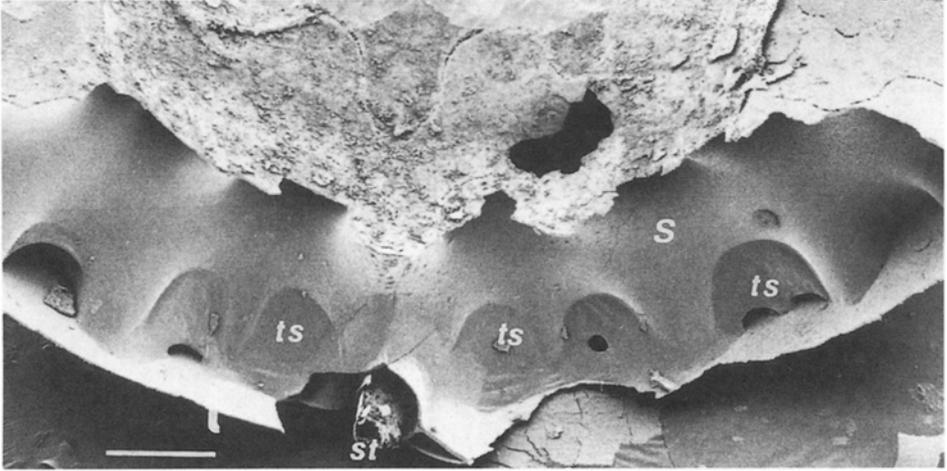


Fig. 12. *Arctoptychites* sp., Upper Ladinian Barentsøya Formation, Hahnfjella, East Spitsbergen. – Frontal view of one septum with well-preserved transverse sheets (ts), closing off the spaces which are produced by the fluted septal margins; (s) septum, (st) siphuncular tube. SGPIMH no. 3594. Scale 300 μ m.

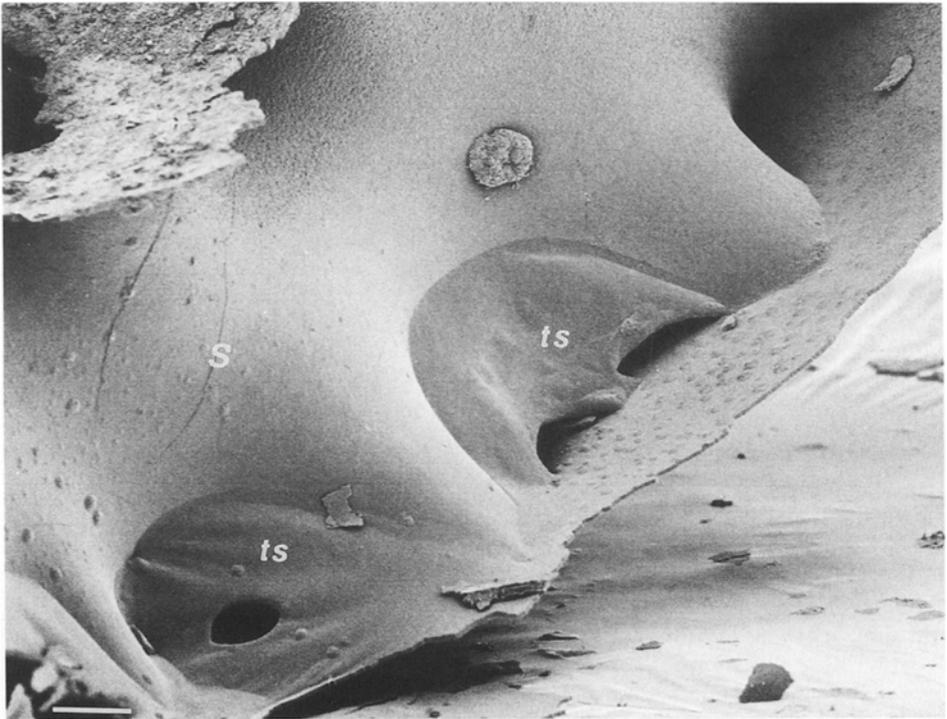


Fig. 13. *Arctoptychites* sp., enlarged detail of Fig. 12, with transverse sheets (ts) that stretch from the inner shell wall to the septum (s). SGPIMH no. 3594. Scale 100 μ m.

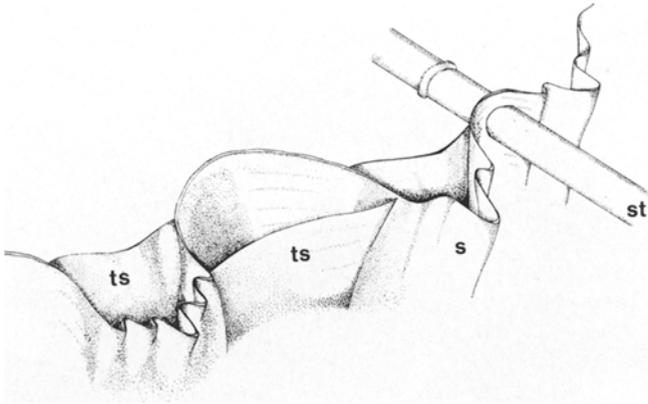


Fig. 15. Reconstruction of the transverse sheets (ts) in *Arctoptychites* sp. that are expanded between septum (s) and inner shell wall thus closing off spaces produced by the fluted septal margins; (st) siphuncular tube.

such lines were not single pillars supporting the siphuncular tube but were septum-like organic sheets separating off small compartments from the main volume of the chamber. Reinvestigation of SCHINDELWOLF's material has shown that the Volgian specimens were phosphatized in a very early stage of diagenesis, as in our Triassic ammonoids.

Horizontal sheets

Horizontal sheets are organic membranes which stretch in a longitudinal direction across the ammonoid chamber thus dividing it into two main compartments of nearly equal size, a ventral and a dorsal compartment. Originating at the siphuncle, the sheets stretch in a curved plain to the flanks of the chamber where they are attached at approximately half the whorl height. Longitudinally they extend from septum to septum where they are attached nearly at the midline (Figs. 16–22).

Horizontal sheets have been observed within our material only in the genera *Aristoptychites*, *Arctoptychites*, and *Paracladiscites*. All of these genera are characterized by nearly spherical conchs. Thus, we infer that horizontal sheets are restricted to this type of coiling. Genera with horizontal sheets often also possess transverse sheets (Fig. 16).

Horizontal sheets are most completely preserved where only the organic layers are phosphatized. The best samples come from carbonate concretions of the *Ptychites* layer in Svalbard and from apatite-rich limestone from the Kolyma Basin. Since these specimens usually also have the innermost whorls preserved, it is possible to give detailed information about the ontogenetic development of such sheets from the very beginning of phragmocone formation. It can be shown that these specimens contain only relatively broad siphuncular sheets during the first 4 whorls. From the beginning of the 5th whorl they start to develop horizontal sheets. This does not happen abruptly but occurs over several transitional steps, the line on which the sheets are fixed migrating slowly from the ventral part of the whorl to the flanks (Fig. 22). This is the first observation of horizontal sheets within ammonoid phragmocones.

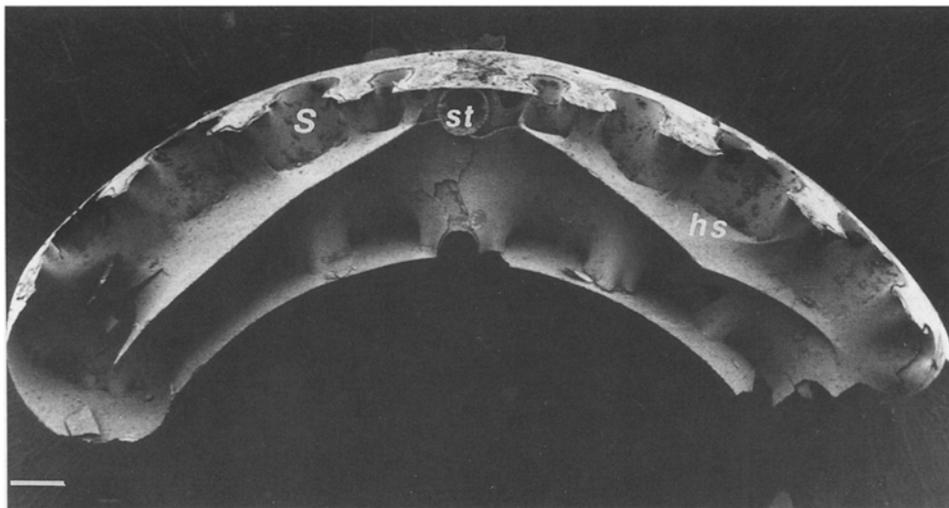


Fig. 16. *Aristoptychites kolymensis* KIP., Upper Ladinian, Barentsøya Formation, Bertylryggen, Central Spitsbergen. – View into the chamber with well-preserved horizontal sheets (hs) attached to the septal surface (s) and the siphuncular tube (st). The sheets divide the chamber in two main compartments. SGPIMH no. 3596. Scale 300 μ m.

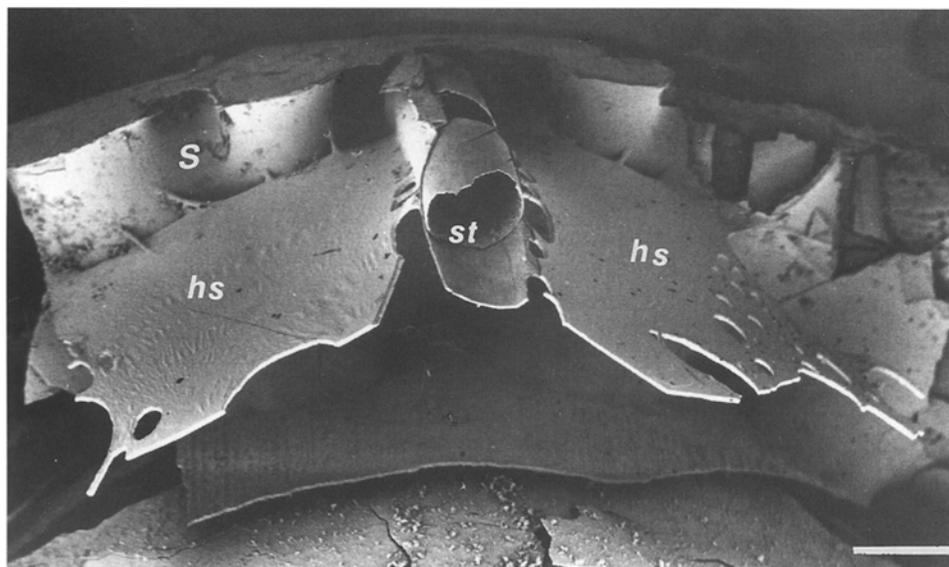


Fig. 17. *Aristoptychites kolymensis* KIP., Upper Ladinian, Barentsøya Formation, Bertylryggen, Central Spitsbergen. – Well-preserved horizontal sheets (hs) with wrinkled surface structure demonstrate their formerly organic composition; (s) septum, (st) siphuncular tube. SGPIMH no. 3597. Scale 300 μ m.

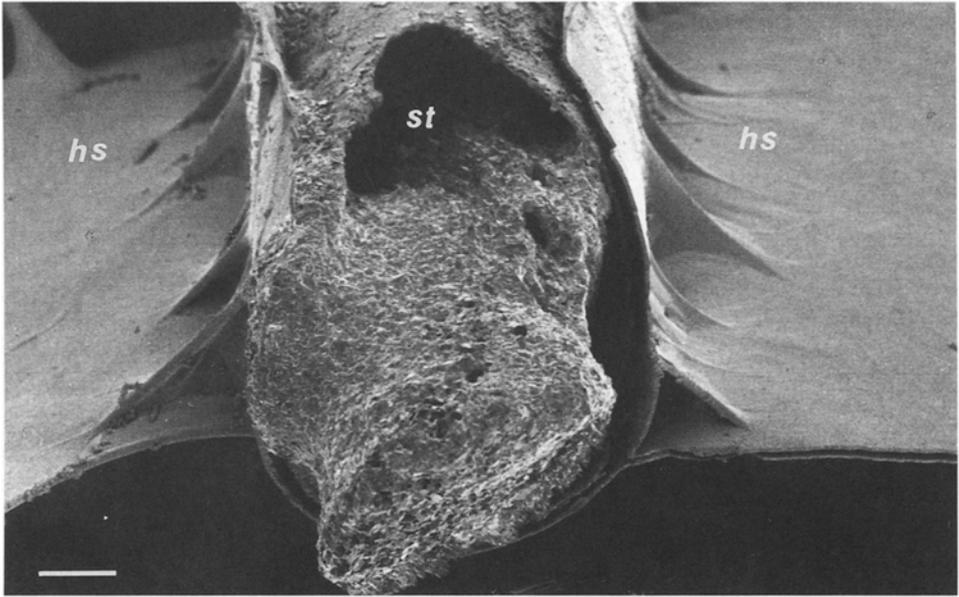


Fig. 18. *Aristoptychites kolymensis* KIP., Upper Ladinian, Barentsøya Formation, Draschedalen, Central-Spitsbergen. – Enlarged detail of horizontal sheets (hs) with their attachments to the siphuncular tube (st). SGPIMH no. 3598. Scale 300 μ m.

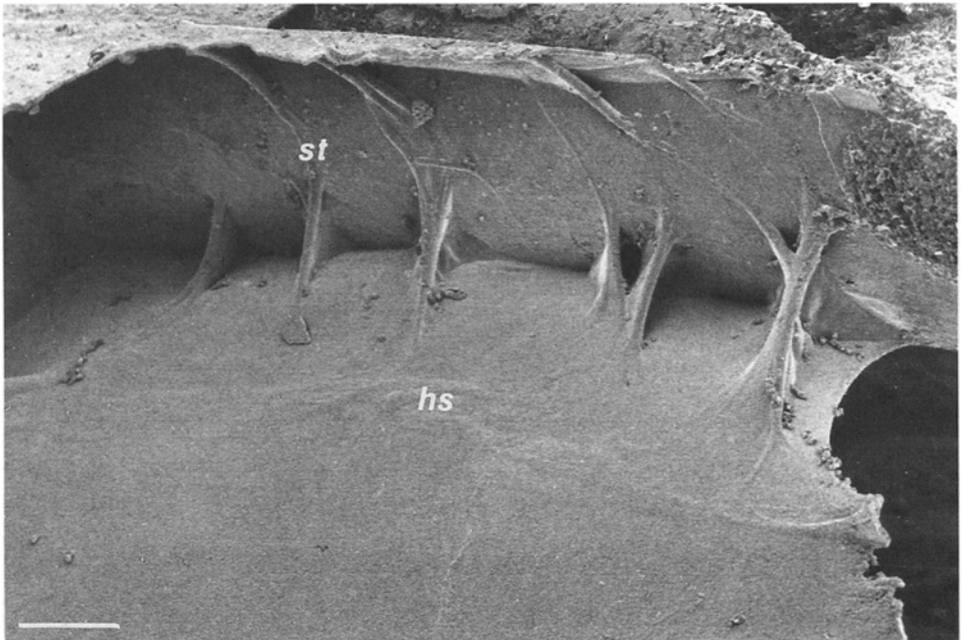


Fig. 19. *Aristoptychites kolymensis* KIP., Upper Ladinian, Barentsøya Formation, Draschedalen, Spitsbergen. – Enlarged detail of horizontal sheets (hs) showing their lateral attachments to the siphuncular tube (st). SGPIMH no. 3598. Scale 300 μ m.

Formation of the sheets

Organic sheets within the ammonoid phragmocone can only be secreted by the mantle epithelium when in direct contact with it. Therefore, such sheets have to be produced during the process of chamber formation. Before discussing details of the secretion of the different types of organic sheets some comments concerning the structure and the function of the molluscan mantle should be made based on studies of Recent cephalopods (BANDEL & BOLETZKY 1979).

1. The mantle is a muscular epithelium and can thus change its shape.
2. The epithelium cells of the mantle can attach themselves to any part of the shell by way of organic fibres. Such attachment can be rather permanent (muscular scars) or only temporary (BANDEL 1982).
3. Mantle cells can secrete shell which may be purely organic, mineralized or a mixture of both.
4. Mantle cells can secrete liquids with different amounts of mucus and different chemical compositions. Some mantle cells are also able to absorb salt ions.
5. Different parts of the molluscan mantle may serve different functions.

Concerning the secretion of the organic sheets in the ammonoid chamber, they can be attached to any wall within the posterior portion of the living chamber (e.g. shell wall, septa, siphuncular tube, organic sheet). Some parts of the sheets evidently remained anchored to the epithelium of the mantle, and could be enlarged and further manipulated. In the simplest case where sheets are anchored to a mineralized septum and the shell wall



Fig. 20. *Aristoptychites kolymensis* KIP., Upper Ladinian, Korkodon River, Kolyma Basin, East Siberia. – Horizontal sheets (hs) which are severed, enroled and wrinkled, indicating clearly their former organic nature; (s) septum, (st) siphuncular tube. SGPIMH no. 3599. Scale 300 μ m.

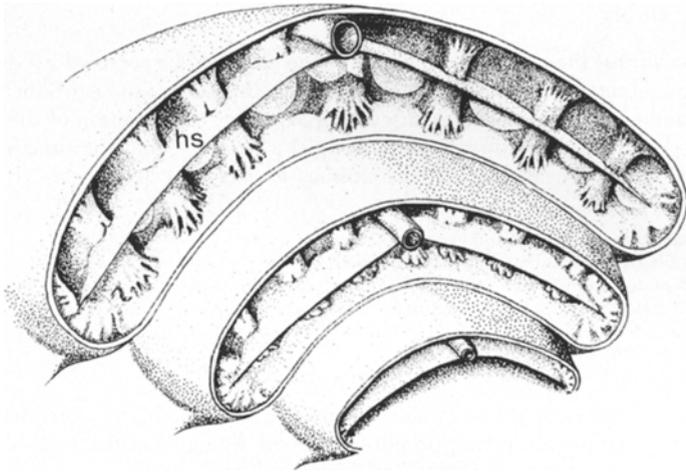


Fig. 21. Reconstruction of horizontal sheets (hs) stretched out in the phragmocone of *Aristoptychites*. There they divide each chamber in two main compartments.

(transverse sheets), they will have been detached from the mantle tissue after secretion. The interpretation of all sheets which are attached to the newly formed septum (siphuncular sheets, horizontal sheets) is more difficult (SCHINDEWOLF 1968: 153).

In the case of the complex siphuncular sheets (Figs. 9–11), the mantle had to remain in contact with the anterior portion of the two main sheets during the whole process of chamber formation until the organic base of the new septum was produced and formed a new anchor. The small vertical sheets which separated the tent-like room into several compartments were secreted in the same way as the transverse sheets. However, unlike these they are attached partly to solid walls (siphuncular tube, shell wall) and partly to the soft and flexible main sheets which were still held by the mantle. Thus the secretion of the two different types of sheets must have occurred by a series of steps, similar to the way in which the vertical sheets follow the formation of small segments of the main sheets. The successive compartments reflect the progressive withdrawal of the visceral mass from this area. The siphuncular tube must be present already before sheet formation can commence.

Horizontal sheets which separated the chamber into two main compartments start from the siphuncular tube, follow the approximate midline of the septum, and end at the lateral whorl sides. The broad attachment of the sheets to the mineralized septum demonstrates that the visceral mass occupied the whole posterior part of the living chamber at this time. During continuous secretion of the horizontal sheet the visceral mass withdrew from the ventral part of the posterior living chamber until it reached the position of the new septum. There it was anchored when the first organic layers were formed.

The formation of these sheets also gives evidence of the rapid construction of a new chamber, probably at a rate (one to two days) similar to the new chamber of a Recent *Sepia*. The only place where no sheets are produced and which therefore remains free of suspended organic walls is the dorsal portion of the future chamber where the visceral mass is stretched out into the attached retractor muscle.

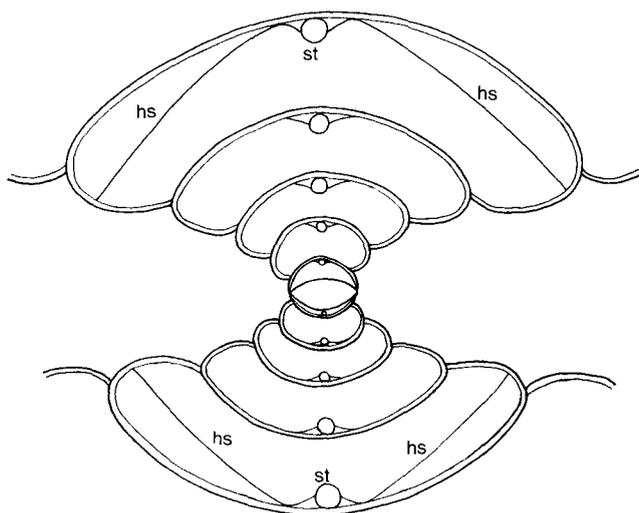


Fig. 22. Ontogenetic development of horizontal sheets (hs) in the phragmocone of *Aristoptychites*; (st) siphuncular tube.

Function of the sheets

Because no comparable organic wall-like structures exist within the phragmocone of Recent *Nautilus*, the discussion of their function in ammonoids remains somewhat speculative. Nevertheless, investigations on the biology of *Nautilus* (DENTON & GILPIN-BROWN 1961, 1966; WARD 1985, 1987), especially those concerning buoyancy regulation, give some useful hints for understanding the function of the complicated system of sheets within ammonoid phragmocones. The only sensible reason for secreting organic sheets and suspending them within the chambers can be to subdivide chamber liquid into several separate portions. What may be the advantage for the animal?

Sheets suspended in ammonoid chambers may serve three main functions:

1. decoupling and transport of cameral liquid;
2. storage of cameral liquid;
3. trimming of buoyancy.

1. DENTON & GILPIN-BROWN (1966) introduced the concept of decoupled cameral liquid in Recent *Nautilus*. With this system the bulk of the chamber liquid is decoupled from the liquid which is in direct contact with the porous siphuncular tube. Thus the cameral liquid stays in contact with the connecting ring only through the wettable properties of the pellicle system which lines the chamber walls and septal faces. The advantage of decoupling for *Nautilus* is that only a small fraction of cameral liquid is involved in the pumping process. Therefore when the animal changes depth, only a small amount of liquid is in contact with the pumping epithelium and very few salt ions and little liquid have to be exchanged across the siphuncular tube. Little work and energy are required for this process in contrast to the work that is needed to tackle the entire volume of a chamber or of several chambers. Experiments with Recent *Nautilus* have shown that emptying of liquid at depths in excess of 250 m can only occur in decoupled chambers (WARD 1985). It seems likely that the

decoupling process was also important for ammonoids. Organic sheets within the ammonoid chamber would have decoupled chamber liquid considerably.

Sheets in our Triassic ammonoids served as devices to separate chamber liquid into different portions that became smaller closer to the siphuncular tube (siphuncular sheets). Therefore these ammonoids should have been able to maintain buoyancy control even in depths greater than 250 m where *Nautilus* can no longer empty its chambers because osmotic pressure can no longer overcome depth pressure (DENTON & GILPIN-BROWN 1973, WARD 1985). The decoupling of significant amounts of liquid from the main volume of the ammonoid chamber may also serve another function. As shown in Recent *Nautilus*, new chambers cannot be constructed if previous chambers are not emptied, and thus, the emptying rate of cameral liquid becomes a limiting factor of growth (WARD 1987). If, however, significant amounts of cameral liquid are decoupled from the siphuncular tube and stored in small pockets formed by the presence of a system of organic sheets, emptying of a chamber might be accomplished more rapidly. Thus, ammonoids might have been able to build new septa in a much shorter time than Recent *Nautilus*.

2. Some of the most interesting investigations done on Recent *Nautilus* concern experiments on buoyancy questions (WARD & MARTIN 1978, WARD & GREENWALD 1982, WARD 1986). In all these experiments compensatory buoyancy was provoked by adding or subtracting weight to captured nautilids with almost neutral buoyancy. An unexpected result was that a significant percentage of the compensatory change could not be related to measurable changes in cameral liquid volume. This problem was solved by using high-resolution radiographs. These show that a considerable amount of cameral liquid is trapped in the pellicle system covering the septal surfaces and the inner shell wall. Especially at the septa/wall contact where the pellicle layers thicken, wedges of liquid are stored due to surface tension. These areas obviously play a significant role in water storage in Recent *Nautilus*.

The presence of a pellicle system for ammonoids, as demonstrated in our Triassic material, suggests an analogous function in liquid movement. As mentioned above, ammonoid phragmocones may maintain significant fluid reserves available for movement out of the chamber on demand. Due to the fluted septal margins of ammonoids this amount of liquid may be about 10 times greater than in Recent *Nautilus*. Transverse sheets enlarge this amount even more; they close off spaces which are produced by the fluted septal margins (lobes and saddles) where pockets of liquid can be stored. If this liquid remains there during the entire development of the ammonoid phragmocone, the amount of fluid reserve which is decoupled from the siphuncular tube is extremely high when compared with Recent *Nautilus*. It may be estimated that an ammonoid has more than 100 ml of liquid that would be at the animals disposal for compensatory buoyancy change, compared with 3–5 ml for a Recent *Nautilus* of similar size.

3. Due to the presence of the complicated system of wall-like sheets in the ammonoid phragmocone, the animal was able to separate small pockets of cameral liquid from the main volume and store it in certain areas of the chamber. This may have served for a finer trimming of the buoyancy, and in stabilization of the conch during locomotion. This assumption is supported by the fact that different kind of sheets are developed in ammonoid conchs with different types of coiling. Horizontal sheets, for example, which are restricted to more-or-less spherical conchs, may serve a similar function to bulkheads in a ship's hull. If the animal was able to fill or empty these liquid pockets when required in different parts of the phragmocone, this would be an ideal method for fine trimming of buoyancy.

Paleobiological implications

The presence of a complicated system of organic sheets suspended in the ammonoid phragmocone leads to some new conclusions concerning the functional morphology of the shell, especially relating to questions of buoyancy.

Descriptions of similar structures within Permian goniatids by SHULGA-NESTERENKO (1926) and Volgian ammonites by SCHINDEWOLF (1968) indicate that cameral sheets are not restricted to our Triassic species but are a more general feature. They were probably present in most ammonoids, but have rarely been preserved during fossilisation.

Chamber formation

As in Jurassic ammonites, the Triassic forms discussed here secreted an organic siphuncular tube before the visceral mass started to withdraw from the space of the new chamber. Evidence for this sequence of events is found in the attachment of several sheets onto the completed tube. The tube is formed in a fold of the mantle that migrates forward until the full segment is finished. Afterwards it lay in a fold of the visceral mass that opened ventrally (backwards). Siphuncular tube length coincides with and determines the width of the next chamber which is thus fixed before a chamber is actually built.

The new segment of the siphuncle is usually firmly attached by organic sheets in its ventral position close to the shell wall. It encloses mantle tissue (living siphuncle) which, after secretion of the tube, changes its function to become a salt pumping apparatus, possibly active some time before the actual chamber is built. When the visceral mass begins to withdraw from the area of the new chamber it secretes organic sheets which are attached to the mantle tissue and thus are pulled and stretched until they are finally 'glued' into place of the walls and to each other. The succession of sheets reflects the sequence of withdrawal of the visceral mass from the new chamber. It also gives evidence for the rapid construction of a new chamber which is probably comparable to that of the similarly complex new chamber of Recent *Sepia* (one to two days). The sheets in ammonoids are of similar thickness to those of Recent *Sepia*. Their position is stable within the chamber because of the liquid in the space behind them. The only place where no sheets are produced and which therefore remains free of organic walls, is the dorsal portion of the future chamber where the visceral mass is stretched out into the attached retractor muscle.

After all of the sheets have been formed the epithelium of the visceral mass attaches itself along the inner shell wall at the position of the new septum. Attachment occurs at a position anterior to the attachment ramp (mural ridge) which at this stage of chamber formation is yet to be secreted. From this stage on the cameral sheets and the liquid filling of the chamber are complete. They are no longer influenced by the visceral mass directly, but only by way of the salt and liquid pump of the living tissue within the siphuncular tube. As soon as the new attachment of the mantle tissue is completed the retractor musculature is detached, withdraws into the new position, and reattaches. Detachment and reattachment may occur quite rapidly. This has also been observed in a number of extant molluscs; for example in bivalves during the change from larval to benthic life, and in gastropods during shell reconstruction and deformation (BANDEL 1982). Dissolution of organic fibres attaching the mantle cells to the shell and reattachment by the secretion of new fibres by the same cells can occur within a few minutes. The cells of the mantle become transformed into shell secreting and attachment cells.

Secretion of the new septum starts when the retractor muscle is loosened and becomes reattached at its new position. In the first phase a mineral ramp of prismatic aragonitic needles (mural ridge) is produced which defines exactly the shape of the new septal edge

where it intersects with the shell wall (sutural zone). This ramp will serve as a mineral anchor and a foundation for organic sheets which in turn are the base to the mineral layers of the septa. Thus, on the septum itself only organic shell grows at first; mineral growth is restricted to the attachment of this organic septum to the outer wall and the siphuncular tube.

The visceral mass detaches from the walls as soon as the organic septum is formed entirely and is anchored firmly to the outer walls and the siphuncular tube by continuous mineral deposits and ramps. Attachment of soft body to the shell now occurs only within the internal lobe at the dorsal end of the living chamber and thus at the fixation of the retractor muscle to the shell. Similar septum formation can also be observed in gastropods and bivalves (BANDEL 1975, 1979). Transitional fixation of mantle tissue to the shell occurs rather commonly during embryogenesis of gastropods and bivalves with yolk-rich development, but also occurs in shell transformation of pelagic pteropods (BANDEL 1982).

After detachment from the walls the visceral mass acquires a slightly different shape that exerts pressure on the elastic organic septum and causes the formation of wrinkles and stretch folds. Mineralization over the entire surface of the septum means that these features become permanently fixed in shape. Cephalopod septa are, in a morphogenetic sense, 'instant skeletons', their pneu modelling can be straightforward (SEILACHER 1988).

As soon as the visceral mass has become detached from the shell walls a new segment of the siphuncular tube starts to form. In a rare case it is observed that two segments of the siphuncle were formed prior to the formation of a septum (DRUSHCHITS & DOGUZHAYEVA 1974). These authors described a tube of about the width of two chambers which extended beyond the last mineral septum into the body chamber. At its very end the tube widened, indicating a former elastic composition and flexibility. The ammonoid apparently died and was preserved immediately after it had completed the organic closure of a new chamber and formed a new siphuncular segment.

Siphuncular tube and pumping process

The composition of the siphuncular tube of ammonoids in general is purely organic outside the mineral attachment rings (septal necks) of the septum (Fig. 23). The tube remained flexible throughout life. Its permeability was probably higher than that of the siphuncular tube of Recent *Nautilus* and liquid could have passed through it more rapidly.

As in chambers of the phragmocone of Recent cephalopods, the cameral liquid in ammonoids was first made hyposmotic to body fluids, and consequently removed by osmosis (DENTON & GILPIN-BROWN 1961, 1966, 1973). Emptying of a chamber only occurs if osmotic pressure is greater than the pressure difference between ambient and chamber pressure. At 200 m depth cameral liquid concentration has to be less than 20% seawater concentration if emptying is to occur (WARD 1985). The salt pump of the new segment of the siphuncular tube could begin to function by lowering the salt concentration of the cameral liquid before producing an osmotic gradient. Once the septum had become mineralized, which could, by comparison with Recent *Sepia*, be accomplished within a day (BANDEL & BOLETZKY 1979), the pressure in the chamber could have been lowered so much that gas was liberated from the liquid and formed bubbles. Since the next siphuncular segment was already preformed at this time, the formation of the next chamber could commence immediately and thus much more rapidly than in Recent *Nautilus*.

DENTON & GILPIN-BROWN (1966) noted that it is far more efficient to have chambers with volumes of liquid which are decoupled from contact with the siphuncle or from the bulk of the cameral liquid if depth changes of the animal are to occur. The advantage of this decoupling for *Nautilus* is that only a small fraction of cameral liquid is concerned in the



Fig. 23. *Stolleites* cf. *lindstroemi* BÖHM, Lower Carnian, Tschermakfjellet Formation, Hahnfjella, East Spitsbergen. – The view into the hollow interior of several chambers shows the siphuncular tube (st) in different kinds of preservation. This indicates the originally organic nature of the siphuncular tube; (s) septum. SGPIMH no. 3600. Scale 1 mm.

pumping process. If the animal dives it will have to remove salt ions actively. Little work is required when only a very small amount of cameral liquid is in contact with the pumping epithelium. If, however, the entire volume of a chamber or of several chambers is in contact, then much more work must be done by the living siphuncle, resulting in a slower diving rate.

In our Triassic ammonoids the system of cameral sheets together with the fluted septa increase decoupling considerably by separating the siphuncle from the bulk of chamber liquid of the dorsal compartment of the chamber. We therefore infer that, when compared with Recent *Nautilus*, ammonoids would have had a much better control of buoyancy regulation.

Septal morphology

The significance of the complexly folded septa of ammonoids when compared with nautiloids has been discussed repeatedly. Many hypotheses have been advanced, some proposing a chiefly mechanical function, others a physiological function. That the complex ammonite sutures were primarily for strengthening the shell is clearly the most attractive and common explanation and was first proposed by PFAFF (1911). Ammonite shells are thinner than those of nautiloids and fluted septa clearly represent a close approach to an ideal form of vaulting. Other hypotheses include increasing overall weight for buoyancy control (REYMENT 1958, TEICHERT 1964), serving for better body attachment (SPATH 1919),

and increasing the efficiency of respiration (NEWELL 1949). HENDERSON (1984) suggested that fluted septa served for better muscle attachment for the posterior mantle, and MUTVEI (1967) thought that the increased surface area of the septa would have provided a faster transport of fluid to the siphuncle via the wettable conchiolin layer of the chambers.

Interesting new ideas were expressed by KULICKI (1979) who suggested that the edge zone between septa and shell wall served as water reserve for cameral liquid. If, as in Recent *Nautilus*, wedges of liquid, held in place by surface tension, were stored in this area, the complexly folded ammonoid septa would produce over the whole length of the sutural zone in significant reserve of liquid decoupled from the siphuncle. This amount of cameral liquid would increase with the complexity of the suture zone and would be at the animal's disposal when needed for compensatory buoyancy change.

The evolution of ammonoids shows that sutural complexity increased progressively from Paleozoic goniatites to Triassic ceratites to Jurassic and Cretaceous ammonites. If sutural complexity was chiefly related to mechanical strengthening of the shell it would suggest that ammonoids could inhabit increasingly greater depths of water during their evolutionary history. Moreover ammonoids should have been able to inhabit far deeper water than nautiloids. This is clearly not true. Siphuncular studies by WARD (1985) have shown that nautiloids lived as deep or deeper than any of the ammonoids. Secondly, the facies from which both groups are collected does not usually indicate deeper water for ammonoids than for nautiloids; in fact in many areas just the opposite is the case. The strength model for the complex ammonoid septal suture also does not fit with the fact that the angle of contact between septa and shell is usually quite low in ammonoids (BAYER 1975, 1977b). Explanations other than shell strength alone must be used to explain the fluted ammonoid septa. The presence of a formerly organic layer covering the septal surfaces comparable with the wettable pellicle layer of Recent *Nautilus*, combined with the complicated system of wall like cameral sheets, indicates that the most likely interpretation of the fluted ammonoid septa could be the model presented by KULICKI & MUTVEI (1988).

Fluted septa increase the surface of the pellicle system, allowing a far greater amount of liquid to be stored in it. In addition the enormous increase of the length of the sutural zone greatly enlarged the area where small pockets of liquid could be trapped by surface tension.

This amount of fluid reserve, decoupled from the bulk of the chamber liquid, is available for movement out of the chamber on demand. It is considerably enlarged still further by organic sheets which close off spaces produced by the fluted septal margins. Therefore the total amount of fluid which can be used for buoyancy regulation is far greater than that of Recent *Nautilus*. In addition, the separation of cameral liquid into different portions decoupled from the siphuncular tube may accelerate the pumping process many times over.

Thus, an additional explanation for the fluted septal margins is to produce spaces which can be closed off easily by short organic sheets which stretch between the septal surface and the inner shell wall. The more complicated is the folding in a sutural zone, the greater is the possibility of producing such compartments which can be filled with liquid decoupled from the main chamber liquid. When comparing, for example, a simple goniatitic suture line with a complexly folded suture of a Jurassic ammonite the latter one may maintain significantly more fluid reserve which can be stored and is available for rapid buoyancy regulations.

Following these ideas, the evolutionary record of progressively increasing sutural complexity in ammonoid history can be interpreted as reflecting improvement in buoyancy regulation combined with an acceleration of the pumping process.

Functional morphology of the shell

A basic feature of cephalopods is the chambered shell. Aided by this shell they evolved from benthic ancestors to become free swimmers able to move to new feeding grounds regardless of the consistency of the sediment on the sea bed beneath. Buoyancy control is the major reason for retaining the chambered shell throughout their evolution.

In order to regulate buoyancy, the tissue of the visceral mass extends into the chambered portion of the shell protected by the outermost layer of the siphuncular tube. This tube is permeable to water and dissolved salts and the living tissues are able to pump.

From studies of Recent cephalopods (DENTON & GILPIN-BROWN 1961) we know that cells of the mantle tissue are able to excrete and absorb salt ions and thus to change the concentration of ions within the liquid covering the mantle (extrapallial liquid). Due to the ability to pump salt, the living tube is able to build up an osmotic pressure which, when high enough, starts first to extract salt ions, and later to pull liquid across the barrier of the siphuncular tube.

Extraction of salt in connection with pumping liquid from a chamber, consumes energy. This is of importance when the cameral liquid has to be extracted slowly, or when it has to be repeatedly extracted and refilled. Recent *Nautilus*, for example, covers its pumping tissue with a rather thick organic tube which is non-porous except for a narrow zone near the attachment of one tube segment to the next (BANDEL & BOLETZKY 1979, BANDEL & SPAETH 1983). This results in a very slow emptying of the chambers which proceeds at about the same speed as the living tissue of the growing animal increases in weight (WARD 1987).

Nautilus practically uses its chambers only to compensate for body weight and to keep its relative weight in the seawater very low. Daily movements are not aided by the buoyancy of the phragmocone but are carried out by jet propulsion using the mantle cavity funnel pump.

The same does not apply to Recent *Spirula*, in which extensive daily vertical migrations occur. Here the siphuncular tissue and the cameral liquid are rather effectively decoupled from each other because the tube consists of an outer shelly and an inner porous layer. Similarly constructed double tubes have also been described in some fossil cephalopods (MUTVEI 1975, BANDEL 1985). Unfortunately, the biology of *Spirula* is not yet well-known; however, daily migrations of several hundreds of meters up and down in the water column could be assisted by the pumping of small amounts of chamber liquid.

It has frequently been assumed that the cameral apparatus of ammonoids functioned in a way similar to that of Recent *Nautilus*. However, the presence of complexly folded septa, the morphology and construction of the siphuncular tube, and the significant differences in position and size of the retractor muscle suggests otherwise. The complicated system of cameral sheets within the ammonoid phragmocone also supports a different interpretation.

As mentioned above, septal fluting increases the surface area of the wettable pellicle layer in the chambers for faster decoupled fluid transport, thereby aiding more rapid buoyancy regulation. Wall-like sheets separating chamber liquid into different portions amplify this tendency. Also the timing of the formation of the siphuncular tube in ammonoids contrasts with that of *Nautilus* and points to a much more rapid utilization of the new chambers. The capacity for rapid buoyancy regulations, together with the very small retractor muscle of ammonoids when compared with Recent *Nautilus*, indicates that locomotion in the ammonoids was different.

Nautilus accomplishes its daily movements by expulsion of water from the mantle cavity as a result of a contraction of the funnel, without changing the buoyancy of the phragmocone. The large paired retractor muscles play a major role in this process.

For ammonoids we suggest just the opposite. By pumping small amounts of liquid in and out of the chamber, they mainly used the buoyancy of the phragmocone for their vertical migrations. The small unpaired retractor muscle located dorsally within the internal lobe could not have supplemented locomotion significantly. Thus, most ammonoids were probably adapted for slow vertical movements closer to passive floating than active swimming. Therefore, we suggest that the role of hydrodynamic efficiency in ammonoid shell shape, discussed by several authors (CHAMBERLAIN 1980, CHAMBERLAIN & WESTERMANN 1976), has been greatly overestimated.

Mode of life of ammonoids

A number of generalizations about the mode of life of ammonoids can be drawn from our observations and interpretations on anatomy, shell production, and functional morphology as outlined above.

Embryonic development

Hatching ammonoids were equipped with a functional chambered shell – the ammonitella. This shell measured about 1 mm in size and may well have served a planktotrophic way of life. Among cephalopods, ammonoids belonged to those forms which produce a large number of relatively small offspring. They have been defined as a group which had developed a more r-selected evolutionary strategy in contrast to the k-strategy of the Recent *Nautilus* which produces only a few very large, well developed young (LANDMANN 1988, HEWITT 1985). Consequently the hatching time of ammonoids must have been much shorter than in *Nautilus*. Nearshore spawning Recent coleoids (*Loligo opalescens*) with an egg capsule diameter of about 1.4 mm hatch within 20–40 days depending on temperature. For ammonoids we suggest a similar time. In contrast, the time of the large yolk-rich eggs of Recent *Nautilus* is usually more than one year (pers. comm. K. TANABE, Univ. Tokyo, T. MORI, Toba Aquarium).

The egg size of ammonoids can be considered as small only as far as cephalopods are concerned; eggs of about 1 mm would be extremely large in the case of gastropods or bivalves. Young ammonoids hatched with a basically adult retractor musculature. It has been confirmed that the embryo was attached over much of the width of its protoconch just behind the inner lip (flanch). After formation of the first septum (proseptum), the musculature moved forward and was attached on the apertural face of this septum on each side of the first siphuncular segment (BANDEL 1982). Only at this stage was the retractor muscle split into two bundles.

From the formation of the first nacroseptum (= 2nd septum) onward and throughout life the retractor muscle consisted of a single bundle attached on the surface of the previous whorl within the internal lobe. From our observations we suggest that in Triassic ammonoids hatching occurred with only one septum, the proseptum. Evidence for this is the absence of irregularities of the spacing of nacrosepta (septum 2 to n) within the ammonitella. In Jurassic and Cretaceous ammonites hatching is usually marked by differences in the distances between nacrosepta formed prior to and after hatching (LANDMANN & BANDEL 1985).

A prerequisite of hatching was the presence of the first segment of the siphuncular tube, the caecum. From this stage on, buoyancy regulation was possible. After removal of cameral liquid from the protoconch the young ammonoid may have floated passively or was capable of weak swimming as part of the plankton. This mode of life is common among many modern coleoids with small eggs.

Postembryonic growth

The planktic stage of the young ammonoid which could have lasted some weeks was usually followed by a nektic stage. With growth of several whorls a better up and down movement within the water column was achieved. Complication of the suture line and construction of decoupled chamber spaces enabled a more differential pumping of liquids from the chambers. Compared with the Recent *Nautilus*, the retractor musculature of ammonoids was quite thin, unpaired and situated at the very end of the living chamber. The size of the attachment scar of the retractor muscle provides direct evidence of the maximum width and length of this muscle. The attachment scars in our Triassic ammonoids are slender and narrow but may be stretched out to about half of a chamber length, thus resembling the retractor muscle of gastropods that can withdraw deeply into their shell.

Recent *Nautilus* uses its two large and short bundles of muscles mainly for locomotion and breathing. The comparatively thin and slender retractor muscle of ammonoids may also have served another function. Situated at the end of the living chamber, the muscle could have withdrawn the soft body deeply into the latter when contracted. Such postulations are supported by "in situ" findings of ammonoid jaw apparatus which usually are found quite deep within the living chamber.

We suggest that jet propulsion by way of a funnel-system should have been less powerful in ammonoids than it is in *Nautilus*. The pallial cavity was probably much larger in ammonoids and could therefore also be more contracted when the animal withdrew into its shell. The relative weight of the soft tissue present within the living chamber of ammonoids was thus lower than that of *Nautilus*. This should be taken into consideration when buoyancy of ammonoids is discussed (EBEL 1983, 1990)

Since locomotion of ammonoids was probably not aided by such powerful jet propulsion as in *Nautilus* a better buoyancy control of the chambered shell would have been an aid during up and down movements within the water column. The complexity of the chamber apparatus in ammonoids compared with that of *Nautilus* supports our assumption.

Septal fluting increases the surface area of the pellicle system in the ammonoid chamber, leading to a far greater amount of liquid which can be stored in this system. Further increase is due to the different types of organic cameral sheets described here. Thus, an ammonoid chamber which has been pumped dry still contained considerably more liquid than an emptied chamber of *Nautilus*. The organic sheets divided the bulk of the chamber liquid into several smaller units which were more or less accessible to the epithelium pump of the siphuncle. The purely organic composition of the siphuncular tube of ammonoids increased the direct influence of the siphuncle onto the chamber liquid.

With this chamber apparatus ammonoids should have been able to utilize their buoyancy control much more efficiently than *Nautilus*. We thus suggest that in contrast to *Nautilus* ammonoids used their phragmocone for their diurnal movements. The construction of such a complex chamber apparatus for crawling around on the sea-floor as suggested by EBEL (1990), does not make sense from a biological and constructional point of view.

The chamber apparatus of ammonoids, in principle, is much more similar to that of Recent *Sepia*, in that organic sheets are closely interlinked with the complex mineral walls. As a result both *Sepia* and the ammonoids discussed here, have chambers which are divided into many small compartments.

Sepia constructs each of its chambers very rapidly (within about two days). We suggest that ammonoids also could have been much more rapid in the construction of a new chamber than *Nautilus*, which requires several weeks or months to form an individual chamber.

Our observations regarding the construction of cameral sheets and their attachment to the septa and the siphuncular tube also indicate a rather rapid secretion. This could also

explain the fact that ammonoids formed the new siphuncular segment prior to a new chamber. Even before the septum is fully mineralized the new siphuncule segment is present (DRUSHCHITS & DOGUZHAYEVA 1974). Thus, most ammonoids represented nekctic animals which spent some time of their early life in the plankton. Rapid swimming probably was limited to short bursts, while locomotion in the water column was aided by using the sensitive buoyancy system of the phragmocone.

The position of the slender long retractor muscle indicates that ammonoids were able to withdraw their soft parts deeply into the shelter of the shell. Each new chamber was probably formed within a few days and, thus, the life span of ammonoids may have lasted only one or two years, as is the case in modern coleoids.

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