

THE SIPHONAL TUBE IN JURASSIC BELEMNITIDA AND AULACOCERIDA
(CEPHALOPODA: COLEOIDEA)

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Abstract. The microscopic structure of the wall of the siphonal tube in a belemnite, *Megateuthis gigantea* (Schloth.), and in an aulacocerid, *Mojsisovicsteuthis?* sp., both Jurassic, are described and compared with that in recent *Nautilus* and *Spirula*. In both of these coleoids each connecting ring extends upwards through two shell chambers. It is composed of an outer conchiolin layer and an inner semi-prismatic layer.

INTRODUCTION

Cephalopod shells are composed mainly of aragonite which during fossilization is usually recrystallized into calcite. Owing to this fact it is only in exceptional cases that the shells of fossil cephalopods are preserved well enough to allow a detailed study of their original structures. This is also valid for the material of the fossil coleoids dealt with below.

In the summer 1967 I had an opportunity of studying large collections of Jurassic coleoid cephalopods from W. Germany in Tübingen, Hamburg, Hannover and Braunschweig. Five well preserved phragmocones of a belemnite, *Megateuthis gigantea* (Schloth.), and a single well preserved phragmocone of an aulacocerid, *Mojsisovicsteuthis?* sp., were found in these collections. The present paper deals with the description of the microscopic structure of the wall of the siphonal tube in these phragmocones.

The anatomical orientation of the cephalopod body has been discussed by me in several papers (Mutvei, 1956, 1964 *a, b*, 1967). According to this orientation, which is also here used, the shell

aperture is directed downwards and the shell apex upwards. Such an orientation of the cephalopods is necessary for anatomical comparisons with other molluscan groups, e.g. the system of retractor muscles between cephalopods and monoplacophorids (Mutvei, 1964 *b*). In the afore-mentioned papers, a new terminology for the structural elements in the wall of the siphonal tube was adopted. However, in the present paper the usual terms, septal necks and connecting rings, are retained. The structural relationships between the septal necks and connecting rings in the recent *Nautilus* and *Spirula* were dealt with in detail in an earlier paper (Mutvei, 1964 *a*). These relationships are diagrammatically shown below in Figs. 2 *B* and 2 *C*.

The classification of the coleoid cephalopods adopted here is that proposed by Jeletzky (1966), who also gave a detailed account on the structural elements in the shells of these cephalopods.

DESCRIPTION

ORDER BELEMNITIDA

FAMILY BELEMNITIDAE

Megateuthis gigantea (Schloth.)

Material. I had access to numerous specimens of *M. gigantea* from the collections of the Paläontologisches Institut, Tübingen; Geologisches Staatsinstitut, Hamburg; Niedersächsisches Landesamt für Bodenforschung, Hannover; and Geologisch-Paläontologisches Institut, Technische Hochschule, Braunschweig. The structure of the wall of the siphonal tube in these specimens was at first

studied in dorso-ventral polished sections. The five best-preserved specimens were then chosen for thin-sectioning. None of them includes the early growth stages of the siphonal tube. The studied specimens were collected from the following Dogger localities in W. Germany: Goslar; Gerzen bei Alfeld; Osterfeld.

Description. In a single, slightly pyritized specimen (Pls. 1, 2; Pl. 3, Figs. 1, 2) both the septal necks and the connecting rings in the wall of the siphonal tube are well preserved between about the 35th and 50th shell chambers, counted from the protoconch. In dorso-ventral thin-sections, the lateral sides of the wall of the siphonal tube are distinctly constricted at the septa but expanded between them, giving the siphonal tube a nummuloidal outline (Fig. 1 A; Pl. 1, Figs. 1, 2; Pl. 2; see also Pugaczewska, 1961, p. 139, Pl. 7, Fig. 3).

Each septum proper in the specimen under discussion is composed of a nacreous layer ("Hauptschicht", Christensen, "central calcareous layer", Jeletzky) of the same structural type as that in the recent *Spirula*. As in *Spirula* (Mutvei, 1964 a, *nac*₁, Pls. 16, 17), this layer in *M. gigantea* exhibits, in thin-sections, a fine striation at right angles to the dorsal and ventral faces of the septum, in places also an indistinct growth lamellation parallel to these faces (Pl. 1, Fig. 3). This type of nacreous layer, designated by me the nacreous Type 2, has been recently studied in *Spirula* and in a Jurassic belemnite, *Pachyteuthis russiensis* Orb. (Mutvei, 1970, Text-fig. 3) with the aid of transmission and scanning electron microscopic techniques. It differs considerably from the ordinary nacreous type, Type 1, and is characterized by parallel aragonitic rods which in the consecutive mineral lamellae have a different orientation.

In addition to the nacreous layer, just dealt with, a thin layer could be indistinctly observed in places on the dorsal and on the ventral septal face, respectively. The latter layer, which occasionally shows a granular structure, may correspond to the "Randschicht" of Christensen and "outer layer" of Jeletzky.

Each septal neck (*s.n.*, Figs. 1 B, 2 A; Pl. 2; Pl. 3, Fig. 1) consists of two principal calcareous layers: an outer nacreous layer (*nac*, Figs. 1 B, 2 A;

Pl. 2, *gr*, *l.l.*, Pl. 3, Fig. 1) and an inner porous semi-prismatic layer (*s.pr.*, Figs. 1 B, 2 A; Pl. 2; Pl. 3, Fig. 1). The nacreous layer of the septal neck is a continuation of that layer in the septum proper. In the proximal portion of the septal neck it is composed of three sub-layers: an outer and an inner, thin lamellated sub-layer, separated by a median thick, granular sub-layer (*gr*, Pl. 3, Fig. 1). The lamellated sub-layers are richer in conchiolin than the granular sub-layer. It could not be determined whether the granular structure in the median sub-layer was originally present or has arisen during recrystallization. However, it must be pointed out that also in *Nautilus* the nacreous layer of the septal neck is granular in places (Mutvei, 1964 a, Pl. 13, Fig. 1). Towards the distal end of the septal neck, the outer and inner lamellated sub-layers increase in thickness and ultimately fuse so as to form a single lamellated layer (*l.l.*, Pl. 3, Figs. 1, 2). Since the median sub-layer is here absent, the distal portion of the septal neck contains more conchiolin than the proximal portion. A similar increase of conchiolin content takes place in the nacreous layer of the septal neck in *Nautilus* (unpublished observations). The second principal layer of the septal neck, the porous semi-prismatic layer, invests the inner face of the nacreous layer just dealt with (*s.pr.*, Figs. 1 B, 2 A; Pl. 2; Pl. 3, Fig. 1), but it does not extend upon the ventral face of the septum proper. The prisms in this layer are separated by interspaces and oriented at right angles to the inner face of the septal neck, or approximately so. However, they seem to have been post-mortally dissolved in many places, leaving an irregular conchiolin meshwork, (*s.pr.*, Pl. 2; Pl. 3, Figs. 1, 2).

In each connecting ring (*conn*, Figs. 1 B, 2 A; Pl. 2; Pl. 3, Figs. 1, 2), the following two layers can be distinguished: an outer conchiolin layer and an inner semi-prismatic layer (*ccb*, *s.pr.*, Figs. 1 B, 2 A; Pl. 2; Pl. 3, Figs. 1, 2). The outer conchiolin layer is composed of numerous thin lamellae which are arranged concentrically in relation to the central axis of the siphonal tube. These lamellae can be seen in thin-sections to be direct continuations of those of the lamellated calcareous layer in the distal portion of the septal neck (*s.n.*, *conn*,

Pl. 3, Fig. 2). In contrast to the lamellated calcareous layer, the main part of the conchiolin layer is more or less extensively pyritized (*conn*, Pl. 1, Fig. 2; Pl. 3, Figs. 1, 2). The pyritization was apparently facilitated by the porous and permeable structure of the conchiolin layer. Particularly characteristic for the conchiolin layer is the fact that it extends upwards through two shell chambers (*conn*₁₋₅, Fig. 1 A; Pl. 1, Figs. 1, 2; Pl. 2). In the proximal half of the connecting ring the outer conchiolin layer is invested by the same semi-prismatic layer that covers the inner face of the septal neck (*s.pr.*, Figs. 1 B, 2 A; Pl. 2; Pl. 3, Figs. 1, 2). As in the septal neck, this layer is here partly dissolved leaving a meshwork of conchiolin membranes. Owing to its extreme upward extension, the conchiolin layer of each connecting ring overlaps that of the preceding connecting ring (*conn*₁₋₅, Fig. 1 A; Pl. 1, Figs. 1, 2; Pl. 2). The interspace between the two overlapping conchiolin layers is occupied by the semi-prismatic layer. Consequently, the permeable portions in the wall of the siphonal tube have a three-layered structure in being composed of two conchiolin layers, separated by the porous semi-prismatic layer (*ccb*, *s.pr.*, Fig. 1 B; Pl. 2; Pl. 3, Fig. 2).

These observations on my best preserved specimen are valid for the lateral parts of the wall of the siphonal tube. The extensions of the connecting rings in the anterior and posterior ("dorsal and ventral") parts are still unknown.

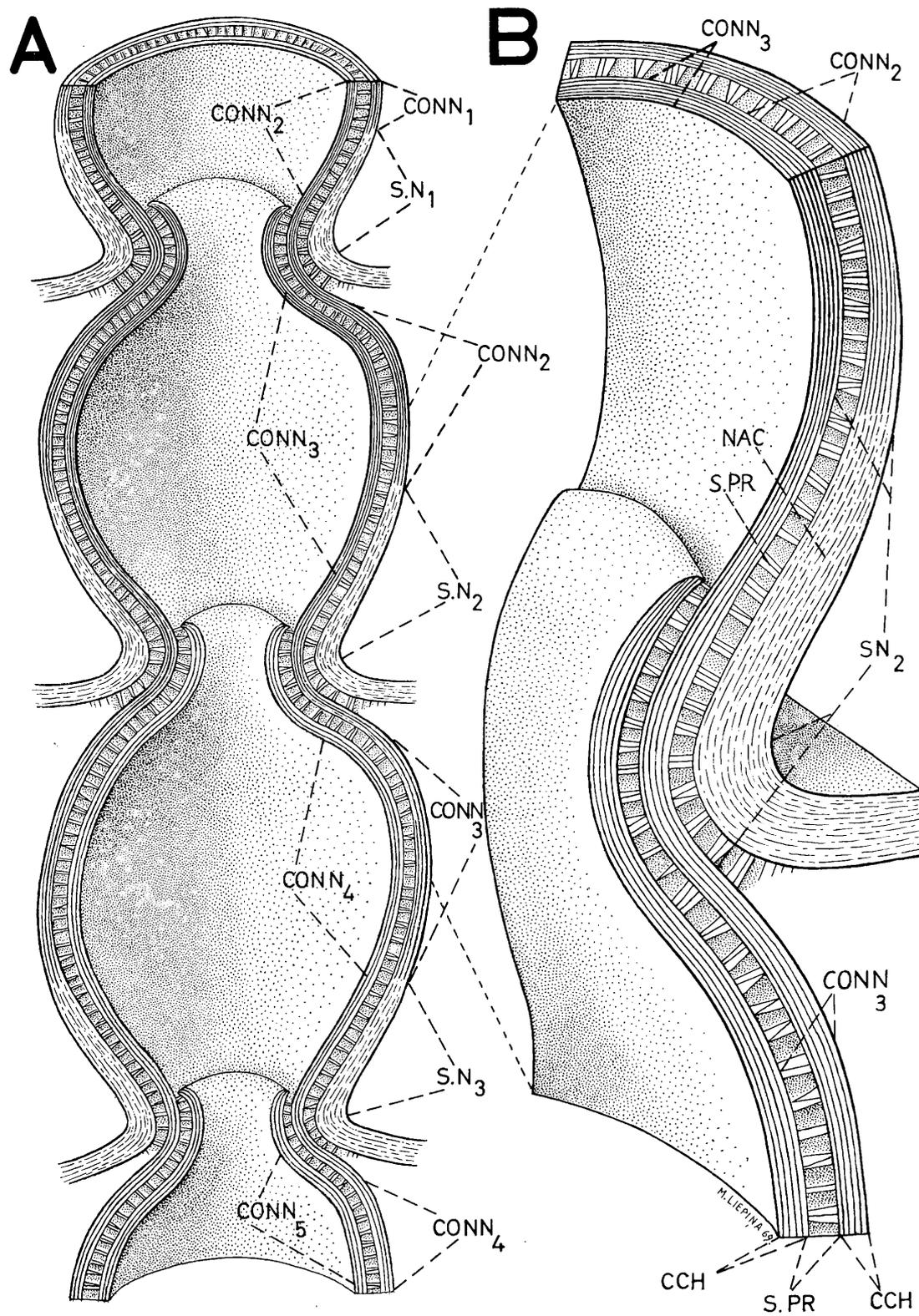
The outer conchiolin layer of the connecting rings (*ccb*, Pl. 4, Fig. 2) is incompletely preserved in the remaining four specimens here studied in thin-sections. The inner porous semi-prismatic layer in the septal necks and connecting rings are on the other hand well preserved. This layer consists of bundles of acicular, calcareous (originally aragonitic) elements which in each bundle diverge slightly in the direction of the central axis of the siphonal tube (*s.pr.*, Pl. 4, Fig. 2). Inasmuch as the bundles of acicular elements are separated by narrow interspaces, the semi-prismatic layer had a porous and permeable structure. The bundles of acicular elements are arranged into dorso-ventral, parallel rows (Pl. 3, Fig. 3) in a manner similar to the aragonite prisms in the corresponding layer

of the septal necks in *Spirula* (Mutvei, 1956, Text-fig. 2 C).

The wall of the siphonal tube in *M. gigantea* differs from that in the recent *Nautilus* with respect to the following features (compare Figs. 2 A and 2 C). (1) The outermost spherulitic-prismatic layer of *Nautilus* (*sph.pr.*, Fig. 2 C) is absent in the septal necks and connecting rings of *M. gigantea* (*s.n.*, *conn*, Fig. 2 A). (2) The outer and the inner conchiolin layers in the connecting rings (*ccb*, Figs. 2 A, C) of *M. gigantea* and *Nautilus*, respectively, are homologues; however, in *M. gigantea* they extend upwards through two shell chambers, but in *Nautilus* only through one shell chamber. (3) The porous semi-prismatic layer coats the inner face of the septal necks and the proximal half of the connecting rings in *M. gigantea* (*s.pr.*, Fig. 2 A), whereas it only coats the inner face of the septal necks in *Nautilus* (*s.pr.*, 2 C).

The septal necks in *M. gigantea* and the recent *Spirula* have a similar structural composition, but they extend higher upwards in *Spirula* than in *M. gigantea* (*s.n.*, Figs. 2 A, B). On the other hand, the connecting rings in *Spirula* differ considerably from those in *M. gigantea*. In *Spirula* they consist solely of a thin spherulitic-prismatic layer (*sph.pr.*, Fig. 2 B), whereas in *M. gigantea* they are composed of the conchiolin and semi-prismatic layers (*ccb*, *s.pr.*, Fig. 2 A). Moreover, the connecting rings extend considerably higher upwards in *M. gigantea* than in *Spirula* (*conn*, Figs. 2 A, B).

Discussion. Christensen (1924, pp. 145—146; Pl. 4, Figs. 16, 17) described well preserved siphonal tubes in *Megateuthis quinquesulcata* and *Hibolites bastatus*. He pointed out that each connecting ring in these two belemnites is continuous with the contiguous septal neck. His observation fully agrees with the conditions in my specimens (Pl. 3, Fig. 2). Judging from Christensen's illustrations, each connecting ring in the posterior ("ventral") side of the siphonal tube in both of his belemnites extends upwards through two shell chambers. Hence it has the same extension as that in the lateral sides of the siphonal tube in *M. gigantea*. On the other hand, it extends upwards only through one shell chamber in the anterior ("dorsal") side of the siphonal tube of *H. bastatus*; in *M. quinquesulcata*



it extends through one and a half shell chambers. It could not be ascertained whether these conditions are due to the imperfect preservation of Christensen's belemnites or whether they represent the actual state of affairs. The "interseptal membranes" ("interseptale Membranen") described by Christensen in his two belemnites (Christensen, 1924, *ism*, Pl. 5, Figs. 16, 17) seem to correspond to the conchiolin meshwork which remains after a post-mortem dissolution of the semi-prismatic layer in one of my specimens (*s.pr*, Pl. 2; Pl. 3, figs. 1, 2).

I have previously described and figured the porous semi-prismatic layer of the septal necks and connecting rings in *M. gigantea* (Mutvei, 1964 *b*, pp. 97—99, Text-fig. 8 C). In the material then available the conchiolin layer of the connecting rings was incompletely preserved.

Jeletzky (1966, p. 127) maintained that each connecting ring in belemnites consists of two laminated layers which were "believed to be predominantly conchiolic". It is not clear from his account whether the two laminated layers belong to a single connecting ring or to two overlapping connecting rings.

ORDER AULACOCERIDA
FAMILY XIPHOEUTHIDIDAE

Mojsisovicsteuthis? sp.

Material. A single specimen of this species was available, kindly placed at my disposal by Prof. U. Lehmann, Geologisches Staatsinstitut, Hamburg. This specimen was collected from glacial drift boulders (= Ahrensburg boulder clan) of Lower Toarcian (Lias ϵ) age, NE of Hamburg (Lehmann, 1968).

Fig. 1. Megateuthis gigantea (Schloth.). A, dorso-ventral section through lateral sides of siphonal tube showing structure and upward extensions of septal necks and connecting rings. Restored after thin-section in Pl. 1, Fig. 1.

B, detail of Fig. A showing a septal neck and contiguous and preceding connecting rings.

cch, outer conchiolin layer of connecting rings; *conn*₁₋₅, connecting rings; *nac*, nacreous layer; *s.n*₁₋₃, septal necks; *s.pr*, semi-prismatic layer.

Description. The genus *Mojsisovicsteuthis* was erected by Jeletzky (1966, pp. 29—30). My specimen agrees with the diagnosis of the genus in the breviconic shape of the phragmocone and in the apparent absence of a guard. Besides, as in the type species, *M. convergens* (Jeletzky, 1966, Pl. 6, Fig. 7), the septal necks proper do not seem to be developed in my specimen (achoanitic condition). Jeletzky also pointed out that the siphonal tube in this genus has a nummuloidal outline in being constricted at the septa but expanded between them. However, in my specimen the outline of the siphonal tube is tubular (Pl. 5, Fig. 1). Also in *Atractites convergens* (Mojsisovics, 1902, Pl. 16, Fig. 1 a), which according to Jeletzky (1966, p. 30) belongs to this genus, the outline of the siphonal tube is almost tubular. The apical angle of the phragmocone in my specimen, estimated in median dorso-ventral thin-section, is about 30 degrees. This angle is considerably greater than the apical angle of 15—20 degrees given by Jeletzky in the generic diagnosis.

In the specimen under discussion, the wall of the siphonal tube is preserved approximately between the 10th—17th shell chambers reckoned from the shell apex. At the anterior ("dorsal") side of the siphonal tube each 10th—15th septum proper turns markedly downwards and then bends with an acute angle into the wall of the siphonal tube (Pl. 5, Figs. 1, 2). The 17th septum proper seems to lack this acute bend.

The septa proper display in places well preserved structures. They consist of a calcareous layer, which shows fine striation at right angles to the dorsal and ventral septal faces, and an indistinct lamellation parallel to these faces (Pl. 5, Fig. 3). Hence, the septa proper have the same microscopic structure as those of *Megateuthis gigantea*. It may therefore be concluded that they consist of a nacreous layer of the Type 2 (Mutvei, 1970; see also in p. 28 of the present paper).

As in the type species, *Mojsisovicsteuthis convergens* (Jeletzky, 1966, Pl. 6, Fig. 7), the septal neck proper seems to be absent in my specimen. Instead, the portion of the septum proper contiguous to the anterior wall of the siphonal tube becomes slightly thickened and forms a so called

choanitic septal neck from which the connecting ring emerges (Pl. 5, Figs. 1, 2). Owing to the imperfect preservation of my specimen, the structural and topographic relationships between the septa proper and the connecting rings could not be studied in detail.

The connecting rings in *Mojsisovicsteuthis?* sp. have essentially the same structure and upwards extensions as those in *Megateuthis gigantea*, described above. Each connecting ring consists of two layers: an outer conchiolin layer, and an inner porous semi-prismatic layer (*cch*, *s.pr*, Pl. 5, Fig. 2). The outer conchiolin layer has lost its lamellated structure and consists of small granules which may be a result of recrystallization. In the anterior ("dorsal") side of the siphonal tube it extends upwards through two shell chambers, or approximately so (*conn*₁₋₃, Pl. 5, Fig. 1). Its upward extension could not be clearly observed in the posterior ("ventral") side of the siphonal tube (Pl. 5, Fig. 1). However, it may be less extensive here than on the anterior side. In the proximal half of the connecting ring the outer conchiolin layer is invested by the porous semi-prismatic layer (Pl. 5, Fig. 1); it is as thick as the conchiolin layer and consists of bundles of acicular calcareous elements (*s.pr*, Pl. 5, Fig. 2). The acicular elements in each bundle diverge slightly towards the central axis of the siphonal tube. The bundles of acicular elements are separated by narrow interspaces. Owing to its extreme upward extension, the conchiolin layer of each connecting ring overlaps that of the preceding connecting ring (*conn*₁₋₃, Pl. 5, Fig. 1). As in *Megateuthis gigantea*, the permeable portions of the wall of the siphonal tube in *Mojsisovicsteuthis?* sp. therefore have a three-layered structure in that they are composed of two conchiolin layers separated by the porous semi-prismatic layer.

Discussion. Fischer (1951) described double walled siphonal tubes in a Triassic aulacocerid, *Choanoteuthis mulleri*. According to his interpretation, the siphonal tube here is holochanitic and "composed of invaginated funnels (septal necks?) each of which extends through slightly more than two chambers". Fischer did not report any porous semi-prismatic layers in his specimen. Jeletzky

(1966, p. 27) restudied the type material of *Choanoteuthis mulleri* and came to the conclusion that its "uniquely long septal necks are actually long, well calcified connecting rings", and that they "extend only through one and one-quarter of the cameral length". Judging from Fischer's photomicrographs (Fischer, 1951, Pl. 2, Figs. 1, 2), it seems likely that the connecting rings actually have an upward extension through somewhat more than two shell chambers, and hence they agree in this respect with *Megateuthis gigantea* and *Mojsisovicsteuthis?* sp., here described.

Jeletzky (1966, pp. 18—22) stressed that in most aulococeroids the septal necks are prochoanitic (directed downwards) and "somewhat similar" to the prochoanitic septal necks in many ammonoids. In one of my previous papers (Mutvei, 1967), I analyzed the microscopic structure of the prochoanitic septal necks in Jurassic ammonoids. I found that the occurrence of this type of septal necks necessarily entails a retardation of the formation of the connecting rings. The main part of such connecting rings is not strictly homologous with that in the normal, retrosiphonate siphonal tubes, and it has no continuation whatever to the septal neck. Contrary to these conditions, the structure and topographic relationships of the connecting rings both in *Megateuthis gigantea* and *Mojsisovicsteuthis?* sp. are typical for the retrosiphonate siphonal tubes.

DISCUSSION

As far as can be judged from the material dealt with here, the structure of the wall of the siphonal tube in Aulacocerida and Belemnitida is essentially the same. It is characterized by the extremely high connecting rings which, in addition to the outer conchiolin layer, also have the inner semi-prismatic layer, but seem to lack the outermost spherulitic-prismatic layer. This extension and structural composition of the connecting rings is found neither in the recent *Nautilus* and *Spirula*, nor in any other group of fossil cephalopods. Due to their extreme height, the connecting rings of every two successive septa overlap. As a consequence the main portion of the wall of the siphonal tube has

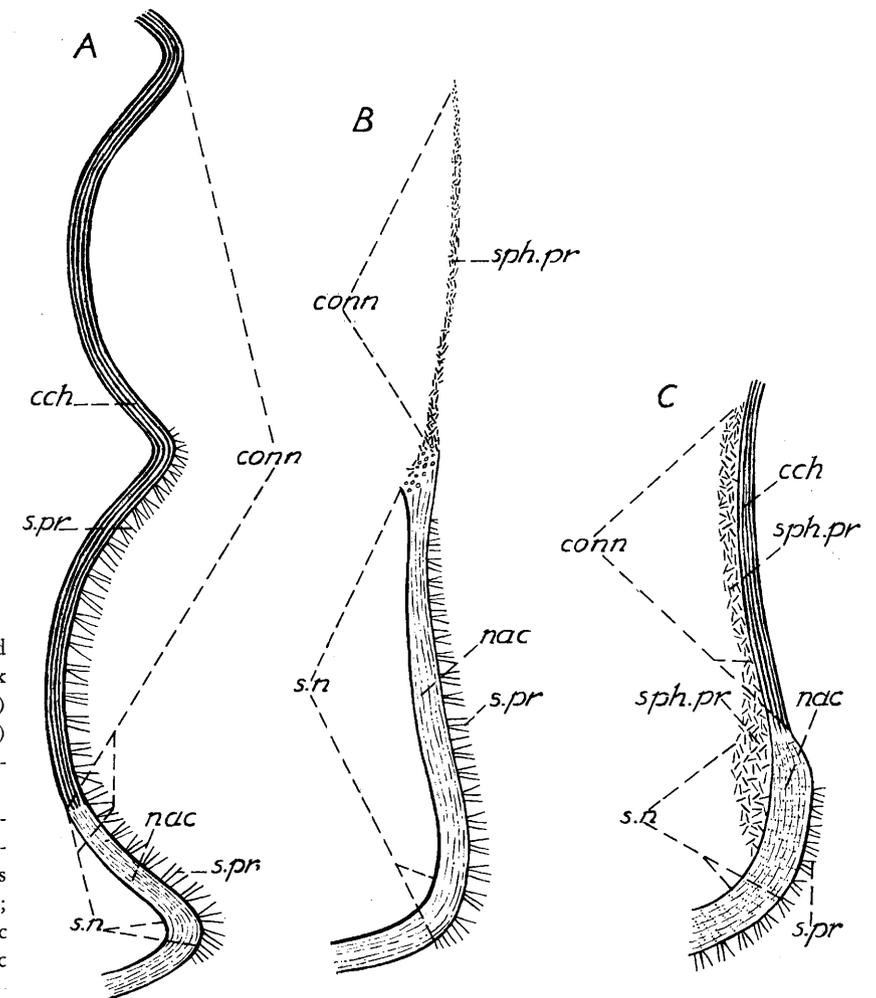


Fig. 2. Structure and upward extension of a septal neck and a connecting ring in (A) belemnite *Megateuthis*, (B) recent *Spirula* and (C) recent *Nautilus*. *cch*, conchiolin layer of connecting ring; *conn*, connecting ring; *nac*, nacreous layer; *s.n*, septal neck; *sph.pr*, spherulitic-prismatic layer; *s.pr*, semi-prismatic layer.

a three-layered structure in that it is composed of two conchiolin layers separated by the semi-prismatic layer. This structure was permeable for the cameral liquid and gave the wall of the siphonal tube great strength.

As shown by Denton and Gilpin-Brown (1966, 1967) and Denton (1961, 1964), the gas space within the shell chambers of the recent *Nautilus*, *Spirula* and *Sepia* brings the animal close to the neutral buoyancy. These two writers also showed that when a new shell chamber is formed, it is initially full of liquid and that this liquid is actively extracted by means of an "osmotic pump mechanism". In *Sepia*, diurnal changes in the density of the animal take place in such a way that the liquid is pumped in and out of the modified

shell chambers and the most dorsal (apical, "posterior") shell chambers are almost always filled with the liquid in order to prevent the apical end of the animal from tipping upwards. On the other hand, in *Nautilus* and *Spirula* only inconspicuous amounts of liquid have been found in the shell chambers older than the most recently formed ones. There is still no evidence that diurnal changes in the volumes of the liquid in the shell chambers of *Nautilus* and *Spirula* take place.

On the basis of the conditions in the recent *Nautilus*, *Spirula* and *Sepia* just referred to, the following conclusions on the buoyancy of the shell in aulacocerids and belemnitids may be made. As already pointed out, the wall of the siphonal tube in the latter cephalopods was permeable and

the liquid filling the last formed shell chamber was pumped out into the siphonal cord through the two conchiolin layers and the semi-prismatic layer by a similar "osmotic mechanism" as reported for the recent cephalopods. Since the siphonal tube was ventral during the life position of the animal, the emptying of liquid from the last-formed shell chambers was facilitated. Therefore, the aulacocerids and belemnitids had no need of the porous layers on the shell septa (semi-prismatic layer) and on the wall of the siphonal tube (spherulitic-prismatic layer), such as occur in *Nautilus* and which act as wick for "sopping up" liquid.

As already mentioned, the three-layered permeable wall of the siphonal tube in aulacocerids and belemnitids seems to have been strong enough to have withstood a high hydrostatic pressure in the sea. On the other hand, as pointed out by Grandjean (1910), Christensen (1924) and Jeletzky (1966), the septa proper of the belemnitids formed during the ontogenetically early stages are only partially calcified and could not have possessed the same strength at those of *Nautilus* and *Spirula*. (According to Bruun (1943, p. 10) the last septum in *Spirula* is the "weak point" which bursts before the shell implodes when tested in a pressure chamber). The latter condition suggests that the belemnitids, at least when still young, could not descend into such deep water as *Nautilus* and *Spirula*, despite the strength of the wall of their siphonal tubes. The presence of a heavy calcareous guard in belemnitids and most aulacocerids prevented the apical end of the animal from tipping upwards. Only in juvenile animals, and in those forms of aulacocerids where the guard was not developed (e.g. *Mojsisovicsteuthis*), the apical shell chambers might have been filled with liquid in the same manner as in *Sepia* (see above).

REFERENCES

- Bruun, A. F. 1943. The biology of *Spirula spirula* (L.). *Dana Rep.* 24, 2—43.
 Christensen, E. 1924. Neue Beiträge zur Bau der Belemniten. *Neues Jb. Miner. Geol. Paläont.* 51, 118—158.

- Denton, E. J. 1961. The buoyancy of fish and cephalopods. *Prog. Biophys. biophys. Chem.* 11, 177—234.
 — 1964. The buoyancy of marine molluscs. *Physiology of Mollusca* 1, 425—434.
 Denton, E. J. and Gilpin-Brown, J. B. 1966. On the buoyancy of the Pearly Nautilus. *J. mar. biol. Ass. U.K.* 46, 723—759.
 Denton, E. J., Gilpin-Brown, J. B. and Howarth, J. V. 1967. On the buoyancy of *Spirula spirula*. *J. mar. biol. Ass. U.K.* 47, 181—191.
 Fischer, A. G. 1951. A new belemnoid from the Triassic of Nevada. *Am. J. Sci.* 249, 385—393.
 Grandjean, F. 1910. Le siphon des ammonites et des belemnites. *Bull. Soc. géol. Fr.* 10, 496—519.
 Jeletzky, J. A. 1966. Comparative morphology, phylogeny, and classification of fossil coleoidea. *Paleont. Contr. Univ. Kans. (Mollusca)* 7, 1—162.
 Lehmann, U. 1968. Stratigraphie und Ammonitenführung der Ahrensburger Glazial-Geschiebe aus dem Lias epsilon (= Unt. Toarcium). *Mitt. geol. StInst. Hamb.* 37, 41—68.
 Mojsisovics, E. 1902. Die Cephalopoden der Hallstätter Kalke. *Abh. geol. Bundesanst. Wien* 6, 175—355.
 Mutvei, H. 1956. A preliminary report on the structure of the siphonal tube and on the precipitation of lime in the shells of fossil nautiloids. *Ark. Miner. Geol.* 2, 179—190.
 — 1964 a. On the shells of *Nautilus* and *Spirula* with notes on the shell secretion in non-cephalopod molluscs. *Ark. Zool.* 16, 221—278.
 — 1964 b. Remarks on the anatomy of recent and fossil Cephalopoda with description of the minute shell structure of belemnoids. *Stockh. Contr. Geol.* 11, 79—102.
 — 1967. On the microscopic shell structure in some Jurassic ammonoids. *Abh. Neues Jb. Geol. Paläont.* 129, 157—166.
 — 1970. Ultrastructure of the mineral and organic components of molluscan nacreous layers. *Biomine-ralization* 2, 48—61.
 Pugaczewska, H. 1961. Belemnoids from the Jurassic of Poland. *Acta paleont. pol.* 6, 105—236.

PLATES

Plate 1

Megateuthis gigantea (Schloth.)

Fig. 1. Dorso-ventral thin-section through lateral parts of wall of siphonal tube at approximately the 43rd—46th shell septa, showing lateral outline of siphonal tube and upward extensions of connecting rings ($\times 20$). Dogger, Goslar.

Fig. 2. Dorso-ventral thin-section through left lateral part of wall of siphonal tube approximately at the 40th—42nd shell septa ($\times 60$). Same specimen as in Fig. 1.

Fig. 3. Dorso-ventral thin-section of shell septum showing structure of nacreous layer ($\times 400$). Note transverse striation at right angles to ventral and dorsal septal faces (indicated by arrow), and indistinct growth lamella parallel to these faces. Same thin-section as in Fig. 2. *conn*₂₋₆, connecting rings; *s.n.*₁₋₄, septal necks; *d*, dorsal face of septum proper.

Plate 2

Megateuthis gigantea (Schloth.)

Detail of thin-section in Pl. 1, Fig. 1 but in higher magnification ($\times 60$). Nacreous layer of septal neck entirely recrystallized and semi-prismatic layer partly post-mortally dissolved.

ccb, outer conchiolin layer of connecting ring; *conn*₁₋₃, connecting rings; *nac*, nacreous layer of septal neck; *s.n.*₁, septal neck; *s.pr.*, semi-prismatic layer.

Plate 3

Megateuthis gigantea (Schloth.)

Fig. 1. Dorso-ventral thin-section of septal neck and parts of contiguous and preceding connecting rings ($\times 150$). Note differences in structure between proximal and distal portions of septal neck. Semi-prismatic layer partially post-mortally dissolved. Same thin-section as in Pl. 1, Fig. 2.

Fig. 2. Distal portion of septal neck and parts of contiguous and preceding connecting rings ($\times 400$). Note continuity in lamellation between septal neck and contiguous connecting ring. Same thin-section as in Fig. 1.

Fig. 3. Tangential thin-section through semi-prismatic layer in wall of siphonal tube showing arrangement of prisms in parallel dorso-ventral rows (indicated by arrow) ($\times 100$). Dogger, Gerzen bei Alfeld.

ccb, outer conchiolin layer of connecting rings; *conn*, connecting rings; *gr*, median granular sub-layer in proximal portion of septal neck; *ll*, lamellated calcareous layer in distal portion of septal neck; *s.n.*, septal neck; *s.pr.*, semi-prismatic layer.

Plate 4

Megateuthis gigantea (Schloth.)

Fig. 1. Dorso-ventral thin-section through lateral parts of wall of siphonal tube ($\times 180$). Note well preserved semi-prismatic layer in septal neck and connecting rings; outer conchiolin layer of connecting rings shrunken and in places destroyed. Dogger, Osterfeld.

Fig. 2. Lower left part of thin-section in Fig. 1 in higher magnification ($\times 400$).

ccb, outer conchiolin layer of connecting ring; *conn*, connecting rings; *s.n.*, septal neck; *s.pr.*, semi-prismatic layer.

Plate 5

Mojsisovicsteuthis? sp.

Fig. 1. Median dorso-ventral thin-section through wall of siphonal tube approximately at 14th shell septum ($\times 60$). Lias, Ahrensburg.

Fig. 2. Detail of same thin-section as in Fig. 1 showing achoanitic septal neck and parts of contiguous and preceding connecting rings ($\times 200$).

Fig. 3. Dorso-ventral thin-section of septum proper showing structure of nacreous layer ($\times 600$). Note transverse striation at right angles to ventral and dorsal septal faces (indicated by arrow) and indistinct growth lamellation parallel to these faces. Same thin-section as in Fig. 1.

ccb, outer conchiolin layer of connecting ring; *conn*₁₋₃, connecting rings; *d*, dorsal face of septum proper; *s.pr.*, semi-prismatic layer.

