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Septal neck-siphuncular complex in *Stolleyites* (Ammonoidea), Triassic, Svalbard

ABSTRACT: Septal neck-siphuncular complex has been redescribed In Triassic (Carnian) Stolleyites tenuis (Stolley). Ammonites whose septal necks change orientation from retro-choanitic through intermediate to prochoanitic may be divided into two categories: dorsoprogressive and ventroprogressive. In the former category, the initial changes in the direction of septal necks orientation occur dorsally; in the latter, the ventral side exhibits more progressive changes. Among forms with siphuncular complex adjacent to the ventral wall, i.e., without a septum between the neck and ventral wall in the medial plane, the changes towards prochoanitic septal neck may begin in the ventrolateral part. The circumsiphonal invagination in those forms did not include the ventral part and their proper interpretation cannot rely on the medial plane only. Primary lamination and primary fibrous structure of the siphuncular tube had been described, as well as the microstructure of the distal tip of cuff and auxiliary deposit.

K e y w o r d s: Arctic, Edgeöya, Triassic, paleontology (Ammonoidea).

Introduction

The trend towards ontogenetic replacement of initially retrochoanitic septal necks by prochoanitic ones, observed in various ammonite groups has been gaining interest from ammonitologists, because of its not fully understood functional significance. Spatial relations between septal necks and siphuncular complex undergo radical changes during this transformation. While in the retrochoanitic condition the wall of the siphuncular tube is formed as a continuation of the interlamellar organic membranes of septal neck, in the prochoanitic condition the tip of septal neck is more or less independent from the siphuncular tube, and the relevant part of the siphuncular tube is connected with the internal surface of the neck by means of a cuff (=auxiliary posterior deposit of Kulicki 1979). Intermediate stages between the retro- and pro-

choanitic septal necks are especially well visible in Triassic ceratites. Differently developed septal neck in the dorsal and ventral parts in the intermediate condition, led Tanabe *et al.* (1993) to classify septal necks at that particular stage into the following three types:

- 1 amphichoanitic necks (Druschits and Khiami 1970) which are entirely projected both adorally and adapically.
- 2 modified retrochoanitic necks type A (Tanabe et al. 1993), which are projected both adorally and adapically on the dorsal side and adapically on the ventral side.
- 3 Modified retrochoanitic necks type B (Tanabe *et al.* 1993), which are projected adorally on the dorsal side and adaptically on the ventral side.

Transformations from retro- to prochoanitic septal necks had been previously studied or illustrated by Branco (1879–1880), Böhmers (1936), Voorthuysen (1940), Miller and Unklesbay (1943), Doguzhaeva (1973), Kulicki (1979), Doguzhaeva and Mutvei (1986), Tanabe et al. (1993), Tanabe et al. (in press).

The specimen discussed herein (ZPAL Am-III/3, housed in the Institute of Paleobiology, Polish Academy of Sciences, Warszawa) is from Lower Carnian (Upper Triassic), Edgeöya Island (Svalbard). It has been already described by Kulicki (1979), but then the size of the specimen allowed only for observations of acetate peels. Recently, direct reexamination of the oryginal specimen with the Philips XL-20 SEM in the Institute of Paleobioloby has been possible, resulting in observing further details. The specimen formerely described as Nathorstites gibbosus Stolley (Kulicki 1979) in the present paper is revised as Stolleyites tenuis (Stolley) (see: Weitschat and Dagys 1989; Dagys et al. 1993). For the SEM studies, the regrinded and polished specimen has been treated with 1% solution of HC1 for about 30 seconds.

Description

The specimen consists of a phragmocone 32.5 mm in diameter, with more than eight complete whorls and 121 septa. A diagram of interseptal angular distances $\Delta \varphi$ (cf. Kulicki 1974) is shown on Fig. 1. There is a clear tendency towards reduction of angular distance between septa in subsequent whorls.

The nacreous and prismatic layers of the septa and shell wall have been diagenetically recrystallized to blocky calcite and the original pattern of laminae in the nacreous layer is only rarely visible; the auxiliary deposits and distal parts of cuff are also only sporadically available for study. Exclusively organic parts of the shell, as the connecting ring, siphuncular membranes and organic linings have been phosphatized (cf. Weitschat 1986, Weitschat and Bandel 1991).

The septal neck-siphuncular complex has extremely ventral position along all whorls. Ventral parts of the septal necks have the same structure in retrochoanitic, intermediate and prochoanitic conditions. They consist of

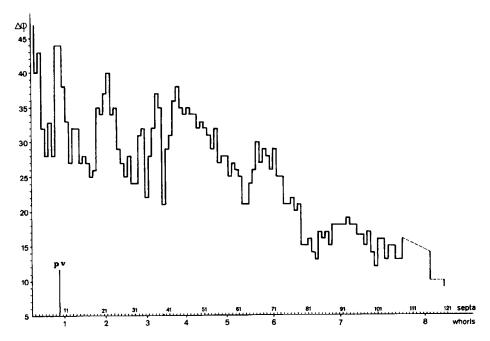


Fig. 1. A diagram of interseptal angular distances in the phragmocon of the investigated specimen. pv — primary varix.

a siphuncular neck or of a cuff, tightly appressed to the internal surface of the shell, and adapically merging into the wall of the previous connecting ring. The next connecting ring is attached to the internal surface of the septal neck or of the cuff, near its adapical tip, with poorly developed auxiliary deposit.

The position of the siphuncular tube results in the fact, that on the median section, changes related to the development of prochoanitic septal necks are visible only in the dorsal part of necks.

Retrochoanitic condition. — In the median section and in the dorsal part of the specimen studied, typical retrochoanitic condition is visible throughout 43 septa (3.72 whorls). Large part of a retrochoanitic septal neck is separated from the rest of the septum by a discontinuity (Fig. 2A; Pl. 1, Fig. 1). Close to the distal tip of the neck, an outline of an auxilliary ridge is visible on the internal surface (Fig. 2A; Pl. 1, Fig. 1). Septa 42 and 43 display some thickening of their walls near the septal neck (Pl. 1, Figs 2-3). Fig. 2A shows the 43th septum in light microscope, with some translucent deeper-lying details and elements. The dorsal part reveals typically retrochoanitic structure in median section. In the distal part of the septal neck, two subparallel lines are visible, that reach the ventral wall and attached to the distal tip of the neck (dn) and the auxiliary ridge (aux). In the anteroventral part of the neck a sharp margin (s.m.) is found, which does not extend up to the dorsal section of the neck, but instead merges

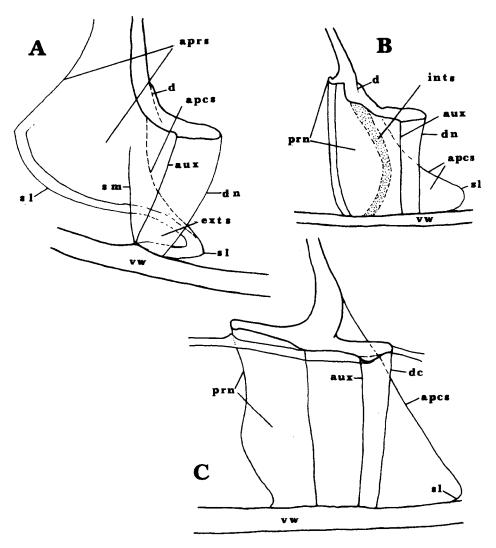


Fig. 2. A diagrammatic drawing of three septal necks of the investigated specimen. A, 43rd septum (3.72 whorls). B, 54th septum (4.74 whorls). C, 64th septum (5.46 whorls). apcs — adapical surface of the septum, aprs — adapertural surface of the septum, aux — auxiliary ridge, d — discontinuity separating distal part of neck from the rest of the neck and septum, dc — distal part of the cuff, dn — distal part of the retrochoanitic septal neck, exts — external secondary sinus, ints — intersection of the septum and the neck (= place of "attachment" of the septum to the neck — cuff structure), prn — prochoanitic septal neck, sl — suture line, sm — sharp margin, vw — ventral wall.

into a smooth, curved surface of the proximal part of the neck. This sharp margin, mentioned by Kulicki (1979, p. 100), results from strong anterior bending of the septum in that part of the neck, due to the deepening of lateral sinuses on both sides of the neck. Actually, the sharp margin represents the anterior margin of the septal fold or even a prochoanitic element of the neck.

Intermediate condition. — The septum 44 (Pl. 1, Fig., 4) is the first one of definitely intermediate character in its dorsal part. The adapertural surface of this septum, above the proximal part of the retrochoanitic septal neck, bears a gentle bulge of its nacreous layer (septal rim of Doguzhaeva and Mutvei 1986) (see Pl. 1, Fig. 4).

Similar structures have been described in *Megaphyllites* and *Leiophyllites* by Doguzhaeva and Mutvei (1986, Text-fig. 1B; 3C; Pl. 3, Fig. 1; Pl. 4, Figs 1-2; Pl. 7, Figs 1-3), and in *Stolleyites tenuis* by Tanabe *et al.* (1993, Fig. 4.3b).

Next four septa (45th to 48th) are of retrochoanitic structure again, and without septal rims. The septal rim reappears from the septum 49 (Pl. 1, Fig. 6), reaching remarkable height on septum 51st (Pl. 2, Fig. 1). Next septa, 52nd, 53rd and 55th (4.58-4.83 whorls), show a diagenetical structure in the axial part of the septal rim, reaching up to the apical part (Pl. 2, Figs 2-3, 5). This structure is probably related to the axial zone, where nacreous lamellae are somewhat distorted (compare Doguzhaeva and Mutvei 1986; Pl. 8, Fig. 1). The adapical surface of the septal neck-septum has a similar outline as in the retrochoanitic condition, showing no adapertural folding, which can be observed in Megaphyllites already at the beginning of the third whorl (Doguzhaeva and Mutvei 1986, Pl. 5, Fig. 1-2) and in Leiophyllites from the beginning of the fifth whorl (op. cit. Pl. 8, Figs 2-4) while in Stolleyites beginning from the 44th septum in the fourth whorl (Tanabe et al. 1993, Fig. 4.3c).

Septum 54th (4.74 whorls) is less progressively developed than the set of several preceding septa, and resembles rather the 44th or 50th septum (3.83 and 4.39 whorls), with its short prochoanitic septal neck above the septal rim (Pl. 2, Fig. 4). The 56th septum (Pl. 2, Fig. 6) can be similarly interpreted.

The discontinuity observed in the retrochoanitic condition, and separating the distal and proximal parts of a retrochoanitic septal neck occurs also in septa 49 to 54, and has similar shape (Pl. 1, Fig. 6; Pl. 2. Figs 1-6). Kulicki (1979) interpreted the discontinuity as a synchronous border between developmental stages of the septal neck, but more probably the discontinuity is of diagenetical origin, and separates modified nacreous layer of the neck from the remaining part of the nacreous layer of the neck and septum: this can be compared to the condition in the appropriate part of the shells of the recent *Nautilus* and orthoconic cephalopods from the Pennsylvanian Buckhorn Asphalt described by Mutvei (1972a, b). Minor elevation on the outer (adapical) surface of the septal neck (Pl. 1, Figs 4-6; P:l. 2, Figs 1-4) accompanying this discontinuity, is found also in both above-mentioned comparative forms (see Mutvei 1972a, Fig. 2; 1972b, Fig. 1; Pl. 7, Fig. 1; Kulicki and Mutvei 1982, Fig. 1).

Beginning from the 57th septum (4.98 whorls), on the adapical surface between the septal neck and septum an adapertural folding forms, pointing to a septal fold formed there, with axis separating the cuff from the proximal part of the septal neck (Pl. 3, Fig. 2). This phenomenon becomes more pronounced in next septa (Pl. 3, Figs 1, 3).

It is difficult to find the border between the prochoanitic and intermediate condition in the material examined, because of the recrystallized nacreous layer. Doguzhaeva and Mutvei (1986 p. 3) assume that the border is at the breakage of the continuity of the nacreous lamellae between both wings of the septal fold. This seems to be a sufficient definition.

Microstructure. — Beginning from the 58th septum (5.06 whorls), the siphuncular tube is preserved, at first within the septal neck, between the distal tip of prochoanitic neck and the cuff, while between farther septa the whole length of the siphuncular tube is completely preserved. On the ventral side, if preserved, it fits closely to the wall, whereas on the dorsal side of outer whorls, it arches towards the axis, between the distal tips of the neck and the cuff of adjacent septa. The siphuncular tube, siphuncular membranes and organic linings covering phragmocone chambers from inside are brownish when observed in light microscope and are phosphatized. The cuff and auxiliary deposit are fully recrystallized or substituted by pyrite in the earliest whorls, but the original microstructure could have been partially preserved, beginning from the 73th septum (6.01 whorls) onwards.

Siphuncular tube. — In median section has multi-layered structure, more or less pronounced depending on position within the specimen (Pl. 3, Fig. 1). The layers are $0.8-1.5~\mu m$ thick, usually about 1 μm . The values are slightly lower than 1-2 μm reported by Obata et al. (1980) for Damesites semicostatus Matsumoto and for Mesopuzosia yubarensis (Jimbo), as well as 2-3 µm reported by Tanabe et al. (1982) for Reesidites minimus (Hayasaka and Fukuda). In the 89th septum (6.94 whorls) see: Pl. 3, Fig. 1; Pl. 4, Fig. 1, the arrangement of siphuncular tube layers is visible near the tip of prochoanitic septal neck and auxiliary deposit. The outermost layers are oriented adaperturally, continuing the orientation of the tip of the prochoanitic neck. More internal layers are fixed to the basal part of the auxiliary deposit and probably merge with the cuff of the next septum. The innermost layers have relatively limited range and vanish on the internal side of the siphuncular tube in mid-length of the septal neck. Individual layers consist of fibres only slightly thinner than the thickness of the layer; the fibre diameter is about $0.75-0.90 \mu m$, more than $0.3-0.4 \mu m$ reported by Obata et al. (1980) for D. semicostatus. The wall of the siphuncular tube between the 88th ant the 89th septa (6.89 – 6.94 whorls), see: Pl. 4, Figs 2 – 4, reveals perpendicular or slightly oblique sections of fibres in median plane. This confirms observations of Obata et al. (1980) that the fibres in D. semicostatus are usually subperpendicular to the axis of the siphuncular tube. The fibres are not very tightly arranged, so that small pores exist between them.

Cuff. — The cuff microstructure in the specimen studied has been preserved only in its distal part, beginning from the 88th septum (6.89 whorls) see: Pl. 3, Fig. 3; Pl. 5, Fig. 2; Pl. 6, Fig. 1. The remaining part is recrystallized, similarly as the nacreous and prismatic layers in the shell wall and septa. There is a sharp border between the cuff and siphuncular tube; it can be seen that the wall of the

siphuncular tube has been somewhat deformed, undergoing moderate shrinkage, contrary to the cuff (Pl. 3, Fig. 1). The cuff itself shows fine granular structure with thin lamination occasionally preserved (Pl. 6, Fig. 1), thus resembling the microstructure of the basal Lamellae in *Quenstedtoceras* (cf. Kulicki and Mutvei 1982, Pls 1, 3, 5-6). No distinct spherulitic arrangement of mineral components has been recognized in preserved portions of the cuff, though such arrangement has been found in *Quenstedtoceras* (Kulicki and Mutvei 1982).

Auxiliary deposit. — In the retrochoanitic condition, the auxiliary deposit is strongly recrystallized, thus its position can be recognized by the presence of a prominent auxiliary ridge (Pl. 1, Figs. 1-3, 5). The deposit is situated dorsally, near the distal tip of a cuff in the intermediate or prochoanitic conditions (Pl. 3, Fig. 1; Pl. 6, Fig. 1) while being farther away on the ventral side (Pl. 5, Figs 1-2). The microstructure of the auxiliary deposit is almost identical as that of the distal tip of the cuff, *i.e.* with fine-granular structure, but no distinct lamination (Pl. 3, Fig. 1; Pl. 6, Fig. 2). The border between the cuff and auxiliary deposit is shown on Pl. 6, Fig. 2, while a sharp border between the siphuncular tube and the auxiliary deposit (Pl. 3, Fig. 1; Pl. 5, Fig. 1; Pl. 6, Fig. 2) seems to have resulted from diagenesis; diagenetic changes are also markedly visible in the inner and outer layers of the siphuncular tube, and in organic linings, which had been not only secondary phosphatized but also thickened (Pl. 5, Figs 1-2; Pl. 6, Figs 1-2).

Discussion and interpretation

Categories of intermediate condition between retro- and prochoanitic septal necks introduced and defined by Tanabe et al. (1993), i.e. amphichoanitic, and modified retrochoanitic necks type A and B, do not represent all known possibilities. Voorthuysen described a specimen of Halorites macer Mojsisovics (Voorthuysen, 1940, Fig. 2). where transformation from retro- to prochoanitic septal necks occurs in the first half of the second whorl; at this stage the siphuncular tube is still in central position. Contrary to the specimens described so far by Kulicki (1979), Doguzhaeva and Mutvei (1986), Tanabe et al. (1993, 1994) and other authors, in the Halorites macer more progressive changes occur on the ventral side: while a typical prochoanitic neck is already developed on the ventral side, an intermediate condition persists on the dorsal side. Halorites macer is quite exceptional among the ammonids, because its siphuncular tube in the first whorl lies on the dorsal wall, like in many clymeniids.

In Stolleyites tenuis, the septal neck-siphuncular complex is so tightly connected with the ventral wall, that it is difficult to tell from SEM median sections what changes occurred in the ventral part of septal necks. The presence of a sharp margin in the ventral part of the retrochoanitic neck (Fig. 2A) may suggest that it was in that part of the septal necks where progressive

changes appeared first in *Stolleyites*, and only later became visible on the dorsal side as the septal rim. Light microscope observations show that in later stages of development of the septal necks in *Stolleyites*, the tip of the prochoanitic element of a septal neck, or the septal fold, extends on the ventral side far before the auxiliary ridge, which is very close to the distal part of the cuff both dorsally and ventrally in all growth stages of the specimen studied (Fig. 2B, C).

Intermediate and prochoanitic condition correlates with the presence of a circumsiphonal invagination, as shown by Mutvei (1967), Kulicki (1979), Kulicki and Mutvei (1982) and Doguzhaeva and Mutvei (1986). In cases of centrally, subdorsally or subventrally situated siphuncular complex, median sections always reveal a fragment of a septum, connecting the septal neck with

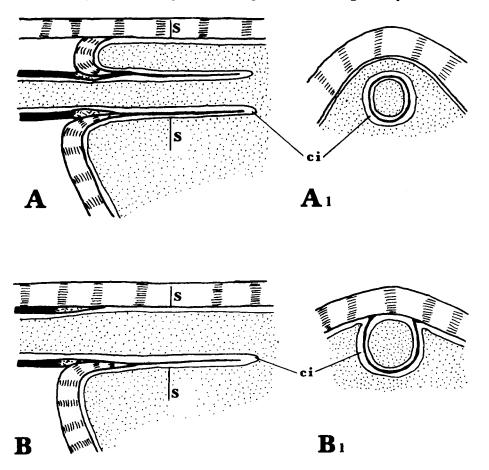


Fig. 3. A diagrammatic drawing, showing relationship between ventral wall, last formed septum and soft body in median and transverse sections in prochoanitic condition. A, A1 - typical relationship as in Ammonitina. B, B1 - telationship as in case of investigated specimen. A, B, median sections. A1, B1, transverse sections. s — the line of the transverse section, ci — circumsiphonal invagination.

the dorsal or ventral walls. The circumsiphonal invagination can be easily reconstructed then (Fig. 3A, Al). For such position of the siphuncular complex as in *Stolleyites*, with no part of a septum connecting the neck with the shell wall, a restoration of the circumsiphonal invagination has to differ from the above mentioned scheme, and look instead rather like in Fig. (3B, B1). The difference between a subventral position of the siphuncular tube and that in *Stolleyites*, is that in the latter case, the epithelium of siphonal cord had directly and tightly to adhere to the ventral wall in the strictly median plane, and the newly formed circumsiphonal invagination did not extend to the ventral side. Thus there was no septum connecting the septal neck with the ventral wall of the shell in the median plane. Such an extremely ventral position of the siphuncular complex occurs in no other Mesozoic ammonoid, but can be found in most Lytoceratina, Phylloceratina and Goniatitina (Druschits *et al.*, 1976).

Diagrams by Schindewolf (1960) show continuous suture lines on the ventral side of the shell in most growth series of Mesozoic Ammonitina, but in Lytoceratina and some Phylloceratina the suture lines are broken at the position of their septal neck. This may indicate lack of the portion of septum connecting the septal neck with the ventral wall in strictly median plane, and consequently, lack of the septum-producing epithelium in that plane in vivo.

Direct growth of the siphuncular tube components to the ventral wall in many specimens of Phylloceratina has been documented by Sharikadze et al. (1991). They have described the siphuncular tube in the living chamber of 50 specimens belonging to the four genera: Euphylloceras, Phyllopachyceras, Holcophylloceras and Salfeldiella. In Euphylloceras sp. (Sharikadze et al. 1991, Fig. 4) the siphuncular tube merges into the ventrall wall so that there is no organic wall of the connecting ring betwen the ventral shell wall and siphuncular lumen. On internal mould the place of attachment is visible as two paraxial lines.

Kulicki (1979) noted that the presence of the circumsiphonal invagination makes possible a simultaneous secretion of both internal and external components of the siphuncular tube. In Stollevites (Pl. 4, Fig. 1; Pl. 3, Fig. 3) connections between the tip of the prochoanitic neck and the external layers of the connecting ring are well visible. Sharikadze et al. (1991) mention that in seldom cases of siphuncular tubes preserved in the living chambers of Phylloceratina, the siphuncular tube has a two-layered wall. The outer layer continues into the tip of the prochoanitic septal neck, while the internal one connects with auxiliary deposit on the internal surface of the septal neck. According to those authors, in many specimens the siphuncular tube in the living chamber consists only of a single, outer layer, being an extension of the tip of the septal neck. Similar structure of a siphuncular tube with outer organic lamellae periaxially attached to the ventral wall has been described in Lytoceras jurense by Grandjean (1910, Figs 4-5). Tanabe et al. (1982) described ultrastructural differentiation of the outer layer of the siphuncular tube (pellicle) with relation to the remainig, internal part. Two-layered structure of the connecting ring, consisting of a thick siphuncular wall and a thin pellicle was described also by Hasenmueller and Hattin (1985) in *Baculites* sp.

Generally speaking, the intermediate condition in the Stolleyites described differs from other known cases, such as Megaphyllites or Leiophyllites, by prolonged phase with no septal fold forming on a septum adapically, with simultaneous development of a prominent septal rim, or even a prochoanitic element of the neck.

As for the reconstruction of the circumsiphonal invagination (Fig. 3), the following should be noted: 1 — in Stollevites a strong bending of the septal edge appears near the siphonal perforation in the ventrolateral part, and gradually extends onto the dorsal part. This is accompanied by simultaneous deepening and development of two secondary paired ventral lobes, separated by a secondary outer saddle, within which the septal neck is situated. 2 — the septal rim, sensu Doguzhaeva and Mutvei (1986), is a structure that indicates origin and deepening of the circumsiphonal invagination during the secretion of a neck and septum. 3 – the presence of a septal fold, sensu Doguzhaeva and Mutvei (1986), implies that the circumsiphonal invagination has been already developed, when the secretion of the adapical surface of the neck and septum started, 4 — breakage of the continuity of the nacreous lamellae in the septal fold is typical for the prochoanitic condition and provides the evidence for a division of the original single secretive zone (septum - septal neck - cuff) into two separate zones: one secreting the septum and septal neck, the other secreting the cuff and siphuncular tube.

Kulicki and Mutvei (1982) had mentioned with, regard to the possible functional significance of the above mentioned spatial separation, that this modification could allow for an accelerated secretion of the siphuncular tube (before the septum). Doguzhaeva and Mutvei (1986) note that it is difficult to envisage any adaptive advantage in forms with the septal neck projected adorally on the dorsal side and adaptically on the ventral. This reasoning has to be rejected, however, as in many cases of final structures with explainable in adaptive categories, the adaptive meaning of particular developmental stages of those structures are difficult to find. Earlier formation of the siphuncular tube than the septum is also observed in the Recent Nautilus pompilius (Tanabe et al. 1982), but there is no detailed data available on the relationships between the soft tissues and the siphuncular tube in this case.

Conclusions

1. Among ammonoids showing transformation of septal necks from retrochoanitic to prochoanitic condition, the changes are much more progressive on one side, dorsal or ventral. Thus, the ammonoids can be divided into dorsoprogressive and ventroprogressive groups.

- 2. The change in orientation of the septal necks is due to the development of so-called circumsiphonal invagination in the soft tissues. This structure presumably appears in soft tissues during formation of septal necks with septal rim only (intermediate condition). It develops gradually during the secretion of the neck and septum. The septa having a distinct septal fold also on the adapical side have been secreted already after the circumsiphonal invagination had formed on one side of the siphuncular cord. Discontinuity of lamellae in the nacreous layer in the axial zone of the septal fold indicates that the circumsiphonal invagination was well developed. This required the original single secretion zone of the septal fold divided into two zones of secretion: for the septal neck and for the cuff. 3. In those ammonids, whose siphuncular complex was very closely appressed to the ventral wall, and with no portion of septum linking the neck and ventral wall, the circumsiphonal invagination did not extend on the ventral side. In intermediate and prochoanitic conditions of such forms, there is no septal neck in the above stages and sections. The initial changes of septal necks' orientation in such form cannot be determined reliably on the basis of median sections
- 4. The Triassic Stolleyites tenuis (Stolley) has multilayered concentric structure of its siphuncular tube. Each layer consists of a single layer of fibres, which are oriented perpendicularly to the axis of the siphuncular tube. The auxiliary deposit and the distal tip of the cuff show microstructural similarities to the relevant elements in Jurassic and Cretaceous ammonites and the Recent Nautilus.

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References

alone.

- BÖHMERS J. C. A. 1936. Bau und Struktur von Schale und Sipho bei Persmischen Ammonoiden.

 Diss. Drukkerij Univ. Amsterdam, Apeldoorn, 125 pp.
- BRANCO W. 1879-80. Beiträge zur Entwicklungsgeschichte der fossilen Cephalopoden. Paläontogr. 27: 17-81.
- DOGUZHAEVA L. A. 1973. Vnutriennoe stroienie rakoviny roda Megaphyllites. Bull. Mosk. Obsh. Isp. Prirody, Otd. Geol. 48 (6): 48 [in Russian]
- DAGYS A., WEITSCHAT W., KONSTANTINOV A. and SOBOLEV E. 1993. Evolution of the boreal marine biota and biostratigraphy at the Middle/Upper Triassic boundary. Mitt. Geol.-Paläont. Inst. Univ. Hamburg, 75: 193-209.
- DOGUZHAEVA L. A. and MUTVEI H. 1986. Retro and prochoanitic septal necks in ammonoids, and transition between them. Palaeontogr., Abt. A, 195: 1-18.
- DRUSCHITS V. V. and KHIAMI N. 1970. Stroienie sept, stenki protokonkha i natchalnykh oborotov rakoviny nekotorykh ranniemelovykh ammonitov. Paleont. Jour. 1970: 35-47, [in Russian].

- DRUSCHITS V. V., BOGOSLAVSKAYA M. F., and DOGUZHAEVA L. A. 1976. Evolution of septal necks in the Ammonoidea. Paleont. Jour. 1976: 37-50.
- GRANDJEAN F. 1910. Le siphon des ammonites et des belémnites. Bull. Soc. Géol. Fr. Ser. 4, (10): 496-519.
- HASENMUELLER W. A. and HATTIN D. E. 1985. Apatitic connecting rings in moulds of *Baculites* sp. from the middle part of the Smoky Hill Member, Niobrara Chalk (Santonian) of Western Kansas. Cretaceous Research, 6: 317-330.
- KULICKI C. 1974. Remarks on the embryogeny and postembryonal development of ammonites.

 --- Acta. Palaeont. Polon. 19(2): 201 224.
- KULICKI C. 1979. The ammonite shell: its structure, development and biological significance.

 Paleontol. Polon. 39: 97-142.
- KULICKI C. and MUTVEI H. 1982. Ultrastructure of the siphonal tube in *Quenstedtoceras* (Ammonitina). Stockholm Contr. Geol. 37: 129-138.
- MILLER A. K. and UNKLESBAY A. G. 1943. The siphuncle of late Paleozoic ammonoids.

 Jour. Paleont. 17: 1-25.
- MUTVEI H. 1967. On the microscopic shell structure in some Jurassic ammonoids. N.Jb. Geol. Paläont. Abh., 129(2): 157-166.
- MUTVEI H. 1972a. Ultrastructural studies on cephalopod shells. Part 1, The septa and siphonal tube in *Nautilus*. Bull. Geol. Inst. Univ. Uppsala, 3: 237 261.
- MUTVEI H. 1972b. Ultrastructural studies on cephalopod shells. Part 2, Orthoconic cephalopod from the Pensylvanian Buckhorn Asfalt. Bull. Geol. Inst. Univ. Uppsala, 3: 263-272.
- OBATA I., TANABE K. and FUKUDA Y. 1980. The ammonite siphuncular wall: its microstructure and functional significance. Bull. Nat. Sci. Mus., Ser. C (Geol. and Paleontol.) 6(2): 59-72.
- SCHINDEWOLF O. H. 1960. Studien zur Stammesgeschichte der Ammoniten. Abh. Math.-Naturwiss. Kl., Akademie der Wissenschaften und Lit. in Mainz, Jg. 1960, Lieferung I, (10): 639-743.
- SHARIKADZE M. Z., LOMINADZE T. A. and KVANTALIANI I. V. 1991. Sifon v zhiloi kamere filoceratid (Ammonoidea): In: Voprosy Geologii i Gidrogeologii Azerbeidzhana, Baku: 69 76 [in Russian].
- TANABE K. and LANDMAN N. H., (in press). Structure, morphogenesis, and evolution of septal necks. In: Landman N.H., Tanabe K. and Davis R.A. (eds), Ammonoid paleobiology, Plenum Press, New York.
- TANABE K., FUKUDA Y. and OBATA I. 1982. Formation and function of the siphuncle-septal neck structures in two Mesozoic ammonites. Trans. Proc. Palaeont. Soc. Japan, New. Ser. 128: 433-443.
- TANABE K., LANDMAN N. and WEITSCHAT W. 1993. Septal necks in Mesozoic Ammonoidea: Structure, ontogenetic development, and evolution. In: House M.R. (ed.), The Ammonoidea: Evolution and Environmental Change, Clarendon Press, Oxford: 57-84.
- VOORTHUYSEN J. H. 1940. Beitrag zur Kenntnis des inneren Baus von Schale und Sipho bei Triadischen Ammoniten. — Van Gorcum and Comp., Assen, 143 pp.
- WEITSCHAT W. 1986. Phosphatisierte Ammonoideen aus der Mittleren Trias von Central-Spitzbergen. Mitt. Geol.-Paläont. Inst. Univ. Hamburg, 61: 249-279.
- WEITSCHAT W. and BANDEL K. 1991. Organic components in phragmocones of Boreal Triassic ammonoids: implications for ammonoid biology. Palaont. Z., 65: 269-303.
- WEITSCHAT W. and DAGYS A. S. 1989. Triassic biostratigraphy of Svalbard and a comparison with NE-Siberia. Mitt. Geol.-Paläont. Inst. Univ. Hamburg, 68: 179-213.

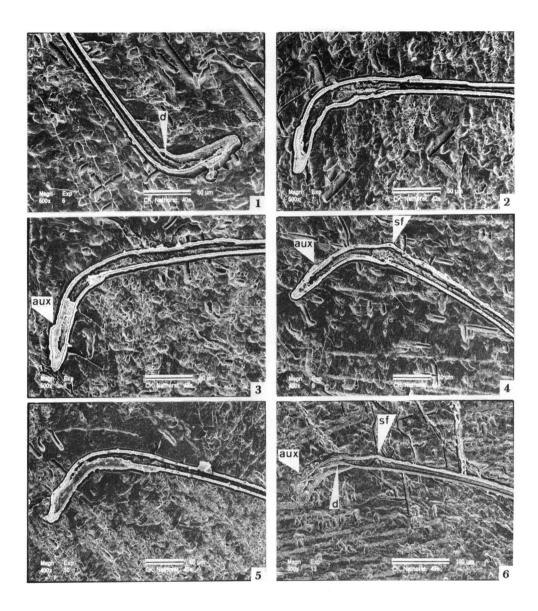
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Streszczenie

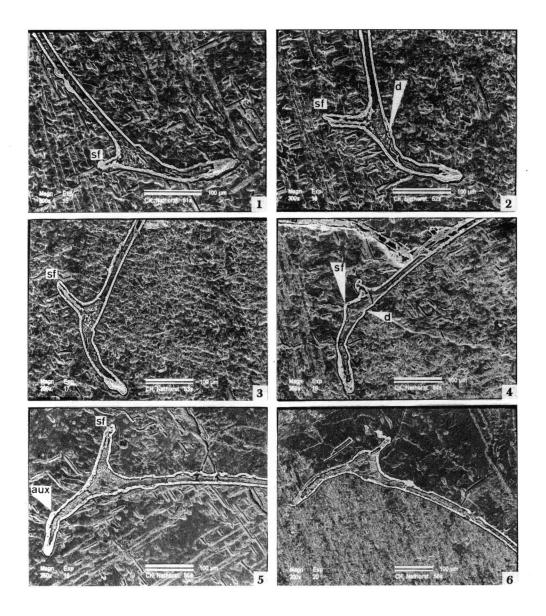
Dokonano redeskrypcji kompleksu syfonalnego oraz rozwoju lejków syfonalnych u triasowego (karnijskiego) ceratyta Stolleyites tenuis (Stolley), z Wyspy Edgeōya, Wschodni Svalbard. Wyróżniono wśród amonitów u których następuje zmiana orientacji od lejków syfonalnych retrochoanitowych poprzez stadia pośrednie do prochoanitowych dwie kategorie form: dorsoprogresywne i wentroprogresywne. W pierwszej kategorii strona na której dochodzi do powstania inicjalnych zmian w kierunku zmiany orientacji lejków syfonalnych, jest strona grzbietowa, gdy w drugiej kategorii strona brzuszna. Szereg rozwojowy lejków syfonalnych jest przedstawiony na ilustracjach (pl. 1, fig. 1–6; pl. 2, fig. 1–6; pl. 3, fig. 2–3), natomiast stosunki kątowe pomiędzy septami na figurze (1). Stwierdzono, że u form z kompleksem syfonalnym silnie przylegającym do ścianki wentralnej jest brak odcinka septum łączącego w planie medialnym lejek i ściankę wentralną oraz że zmiany w kierunku lejków prochoanitowych mogą wystąpić po raz pierwszy w części brzuszno-bocznej. U form takich okołosyfonalna inwaginacja nie obejmowała strony brzusznej fig. (3), a właściwa interpretacja takich form nie może być ograniczona do medialnego planu (fig. 2).

Ścianka rurki syfonalnej w badanym okazie jest wtórnie sfosfatyzowana, lecz po nadtrawieniu w HCl wykazuje pewne cechy budowy pierwotnej to jest wyrażną wielowarstwową budowę, oraz włóknisty charakter poszczególnych warstw. Ułożenie włókien w warstwach jest prostopadłe do osi rurki syfonalnej (pl. 3, fig. 1, pl. 4, figs 1-4).

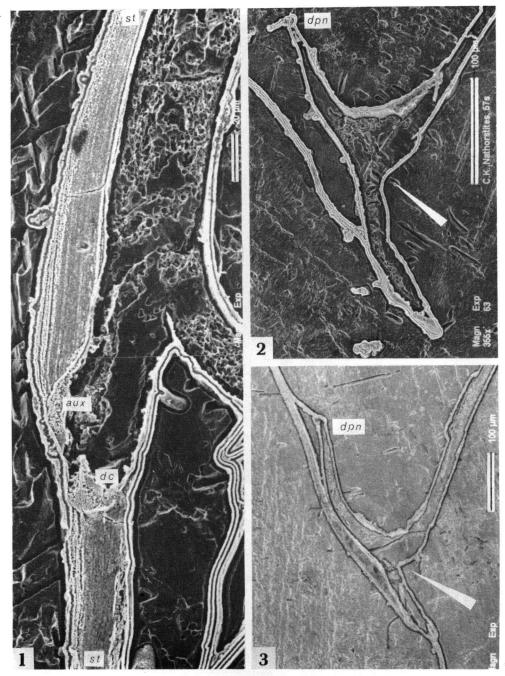
Pomimo, że tkanki mineralne badanego okazu w większej części uległy rekrystalizacji, to na serii kilkunastu septów stwierdzono zachowane pierwotne mikrostruktury utworów auxilarnych przednich i tylnych nie różniące się od pozostałych ammonoidów jurajskich i kredowych, jak również utworów auksilarnych współczesnego Nautilus (pl. 5-6).



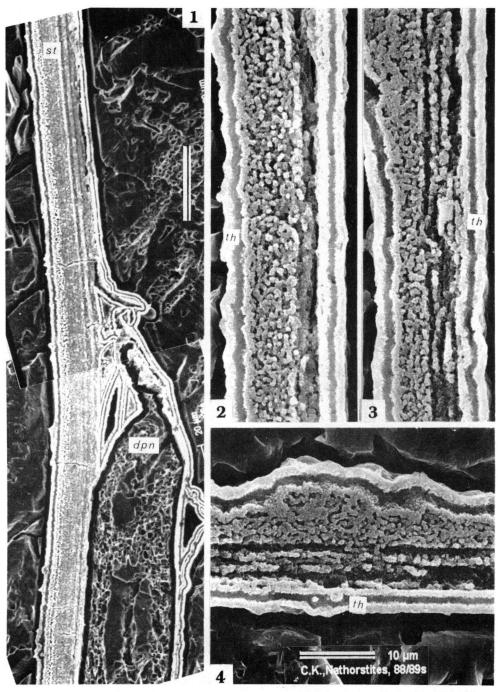
Median sections through dorsal part of septal necks in Stolleyites tenuis (Stolley). 1—40th septum (3.46 whorl). Scale bar = $50 \mu m$, 2—42nd septum (3.62 whorl). Scale bar = $50 \mu m$. 3—43rd septum (3.72 whorl). Scale bar = $50 \mu m$. 4—44th septum (3.83 whorl). Scale bar = $50 \mu m$. 5—45 th septum (3.93 whorl). Scale bar = $50 \mu m$. 6—49th septum (4.31 whorl). Scale bar = $100 \mu m$. 1—3, 5—represent typical retrochoanitic condition. 4, 6—represent intermediate condition, aux—auxiliary ridge, d—discontinuity, separating distal part of retrochoanitic neck from rest of neck and septum, sf—septal rim



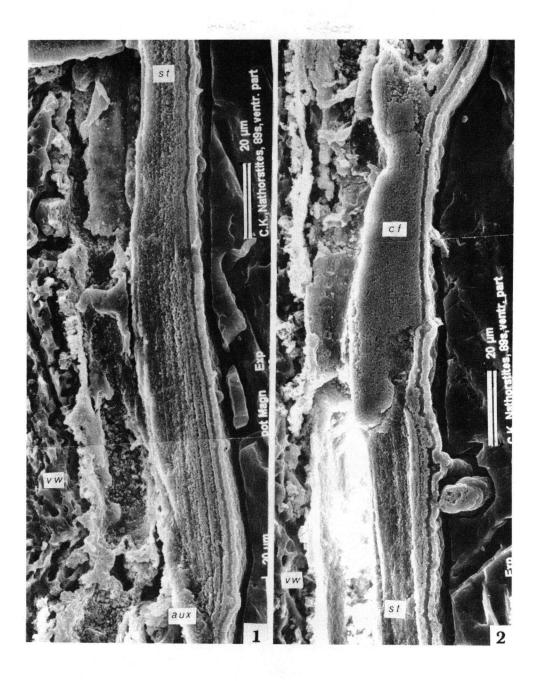
Median sections through dorsal part of septal necks in *Stolleyites tenuis* (Stolley). 1 — 51st septum (4.49 whorl). 2 — 52 nd septum (4.58 whorl). 3 — 53rd septum (4.66 whorl). 4 — 54th septum (4.74 whorl). 5— 55th septum (4.83 whorl). 6 — 56th septum (4.91 whorl). Abbreviations the same as in Pl. 1. Scale bar = $100 \ \mu m$



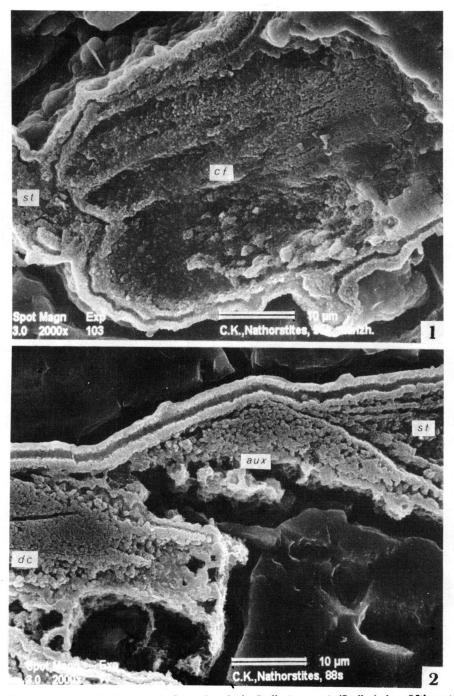
Median sections through dorsal part of septal necks in Stolleyites tenuis (Stolley). 1 — 89th septum (6.94 whorl), proximal part of prochoanitic septal neck. Scale bar = $20 \, \mu \text{m}$. 2 — 57th septum (4.98 whorl). Scale bar = $100 \, \mu \text{m}$. 3 — 71st septum (5.99 whorl). Scale bar = $100 \, \mu \text{m}$, cf — cuff, dc — distal part of cuff, dpn — distal tip of prochoanitic septal neck, st — siphuncular tube, arrows point to the adapertural folding of the adapical surface of the neck and cuff. Other abbreviations are the same as in Pl. 1



Median sections through dorsal part of septal neck and siphuncular tube in Stolleyites tenuis (Stolley). 1 — distal tip of prochoanitic septal neck and its relationship to the siphuncular tube. 89th septum (6.94 whorl), continuation of figure from Pl. 3, Fig. 1. Scale bar = $20 \mu m$. 2—4 — siphuncular tube between septa 88th and 89th. Scale bar = $10 \mu m$, th — secondary phosphatic thickening. Other abbreviations are the same as in Pl. 3



Median section through ventral part of siphuncular tube, cuff and auxiliary deposit in *Stolleyites tenuis* (Stolley), 89th septum (6.94 whorl). 1 — posterior portion of 89-90 section of siphuncular tube and auxiliary deposit. Scale bar = $20 \mu m$. 2 — adaptical continuation of fig (1), vw — ventral wall. Other abbreviations are the same as in Pl. 3



Median section through dorsal part of septal necks in *Stolleyites tenuis* (Stolley). 1 — 95th septum (7.24 whorl), distal part of cuff. Lumen of the siphuncular tube is toward the top. Scale bar = $10 \mu m$. 2 — 88th septum (6.89 whorl), siphuncular tube, auxiliary deposit and distal portion of the cuff.

Orientation and magnification as in Fig. (1) above