

Precursory siphuncular membranes in the body chamber of *Phyllopachyceras* and comparisons with other ammonoids

KAZUSHIGE TANABE, CYPRIAN KULICKI, and NEIL H. LANDMAN



Tanabe, K., Kulicki, C., and Landman, N.H. 2005. Precursory siphuncular membranes in the body chamber of *Phyllopachyceras* and comparisons with other ammonoids. *Acta Palaeontologica Polonica* 50 (1): 9–18.

Organic membranes preserved in the rear part of the body chamber of the Late Cretaceous phylloceratid ammonite *Phyllopachyceras ezoense* were examined with scanning electron microscopy (SEM) on the basis of well-preserved specimens from Hokkaido, Japan. SEM observations revealed that the membranes are continuous with the siphuncular tube wall in the phragmocone and consist of two layers, both of which are made of a dark, primarily conchiolin material; namely, a thinner inner homogeneous layer and a thicker outer layer with gently inclined pillar-like units. Hence, they are interpreted as the precursory siphuncular membranes. The precursory siphuncular membranes are not associated with any other organic components such as the siphuncular sheets reported in some Paleozoic and Mesozoic ammonoids. Unlike the tube-like condition in the phragmocone, the precursory siphuncular membranes in the body chamber of the specimens examined do not form a tube shape; on the ventral side the membranes are truncated and directly contact the outer shell wall. These observations suggest that the inner and outer layers of the precursory siphuncular membranes in the body chamber were respectively formed by the siphuncular epithelium from the inner side and by the invaginated septal epithelium from the outer side. It is also postulated that at the initial stage of septal formation, the rear part of the body moved slowly forward, developing a circumsiphonal invagination of the septal epithelium. Because similar conchiolin membranes are occasionally preserved in the body chambers of other phylloceratids, the above morphogenetic process applies to all members of the Phylloceratina. The tube-shaped structure in the rear part of the body chamber of desmoceratid *Damesites* consists only of nacreous layer. We interpret it as a pathologically overgrown prochoanitic septal neck.

Key words: Ammonoidea, *Phyllopachyceras*, morphogenesis, conchiolin membranes, siphuncle, septal epithelium, chamber formation.

Kazushige Tanabe [tanabe@eps.s.u-tokyo.ac.jp], Department of Earth and Planetary Science, University of Tokyo, Tokyo 113-0033, Japan;

Cyprian Kulicki [kulicki@twarda.pan.pl], Instytut Paleobiologii, Polska Akademia Nauk, ul. Twarda 51/55, PL-00-818 Warszawa, Poland;

Neil H. Landman [landman@amnh.org], Division of Paleontology (Invertebrates), American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192, USA.

Introduction

The chambered shells of extant and extinct cephalopods are distinctly partitioned by septa, and a tube-like organ called the siphuncular tube or the siphonal tube extends from the apex of the shell to the base of the living chamber by passing through each septum around which there is a collar-like projection called the septal neck (Tanabe and Landman 1996). In Recent *Nautilus* and *Spirula*, the siphuncular tube wall is respectively made of a combination of conchiolin and spherulitic prismatic (chalky) layers and of a spherulitic prismatic layer (Denton and Gilpin-Brown 1966; Bandel and Boletzky 1979). The inner space of the tube is occupied by a long and narrow, segmented soft tissue that is connected with the rear part of the main body in the body chamber. This tissue consists mainly of blood vessels, connecting tissue, and a surrounding epithelial layer (siphuncular

epithelium), which serves to transport liquid from chambers to blood vessels by means of osmotic force (Denton and Gilpin-Brown 1973; Greenwald et al. 1980; Tanabe et al. 2000). Tanabe et al. (2000) described similar anatomical features in exceptionally well-preserved siphuncular tissue remains of the Permian prolecanitid ammonoid *Akmilleria* from Nevada, and suggested that the siphuncular epithelium of ammonoids served as the salt-concentrating organ for buoyancy regulation of living animals, as it does in *Nautilus* and *Spirula*.

The siphuncular tube wall of ammonoids is made of multi-layered conchiolin membranes (Erben and Reid 1971; Obata et al. 1980; Westermann 1982; Grégoire 1984), and therefore, it is commonly preserved in fossils in the form of diagenetically replaced phosphates. Together with the septal neck, the siphuncle in ammonoids constitutes the septal neck-siphuncular complex (Tanabe and Landman 1996).

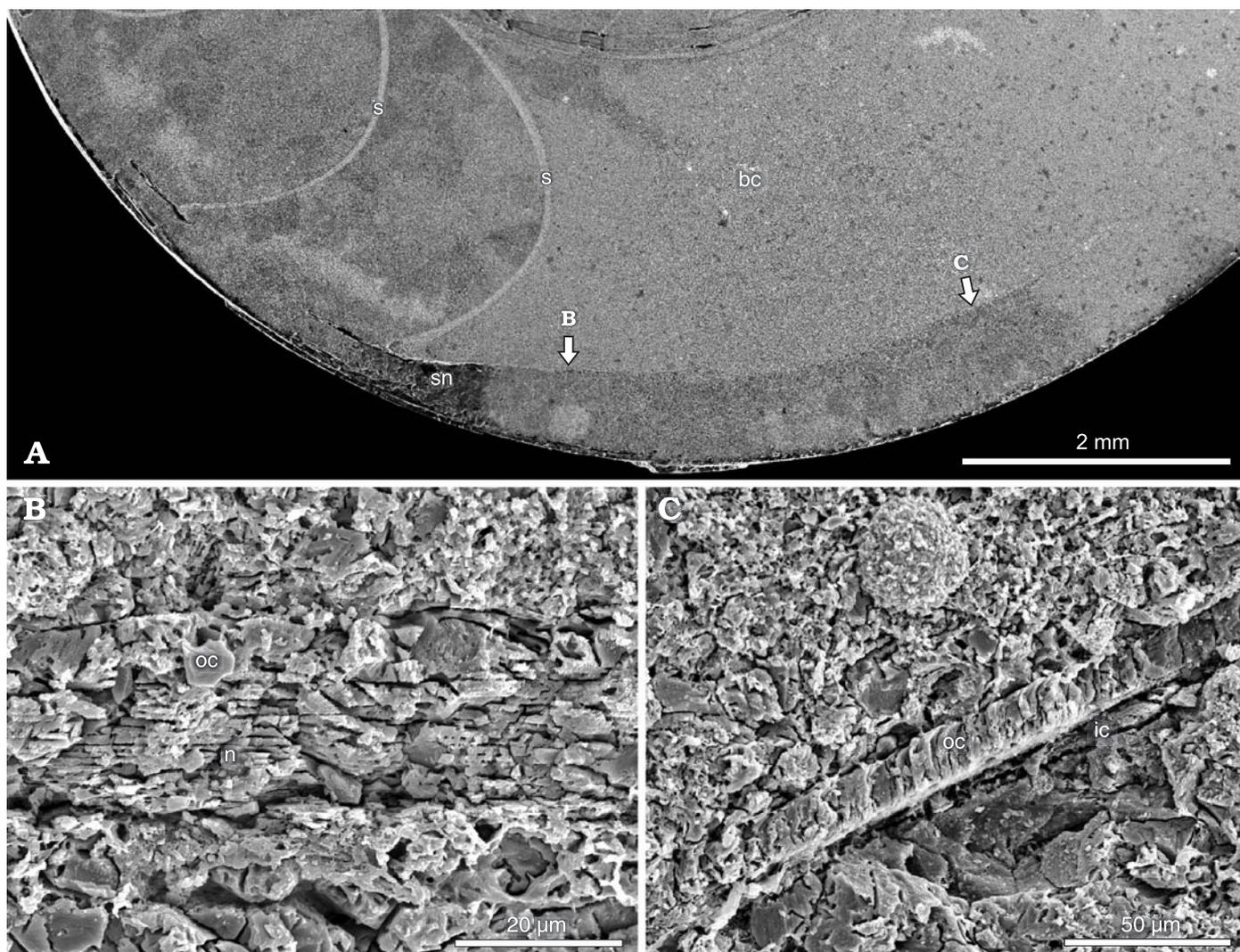


Fig. 1. *Phyllopachyceras ezoense* (Yokoyama, 1890). UMUT MM 28657 from the lower Campanian of the Nakanofutamata-zawa Creek, Haboro area, north-west Hokkaido (median longitudinal section). **A.** Occurrence of precursory siphuncular membranes in the rear part of the body chamber showing locations of photos B and C. **B.** Adoral end of the last septal neck, showing the outer conchiolin layer resting on the nacreous layer of the septal neck. **C.** Adoral portion of the conchiolin membranes in the body chamber, consisting of thinner inner and thicker outer layers. The outer layer consists of adorally tilted pillar-like units. Abbreviations: bc, body chamber; ic, inner conchiolin layer; n, nacreous layer of septal neck; oc, outer conchiolin layer; s, septum; sn, septal neck.

Morphogenetic and evolutionary aspects of the septal neck-siphuncular complex in ammonoids have been discussed by a number of workers (e.g., Branco 1879–1880; Mutvei 1967; Mutvei and Reymont 1973; Kulicki 1979; Bandel 1981; Tanabe et al. 1982; Kulicki and Mutvei 1982; Henderson 1984; Doguzhaeva and Mutvei 1986; Doguzhaeva 1988; Tanabe and Landman 1996). All of these authors assumed that the rear part of the body and the soft tissue of the siphuncle moved forward prior to septum formation. However, the detailed developmental process of the septal neck-siphuncular complex in ammonoids has not yet been clarified to our satisfaction. In this paper, we attempt to consider this process on the basis of SEM observations of well-preserved Late Cretaceous phylloceratid specimens from Hokkaido, northern Japan, by comparison with those in other Ammonoidea.

Institutional abbreviation.—All the specimens described herein are repositied in the University Museum, University of Tokyo, Japan, abbreviated UMUT.

Material and methods

Four juvenile specimens of *Phyllopachyceras ezoense* (Yokoyama, 1890) (Phylloceratina; Phylloceratidae) (UMUT MM 28657, shell diameter (D) = 18.0 mm; UMUT MM 28658, D = 8.2 mm; UMUT MM 28659, D = 18.5 mm; UMUT MM 28660, D = 17.0 mm) were utilized. Three of them came from the lower Campanian of the Haboro area, and one from the middle Campanian of the Nakagawa area, Hokkaido. All specimens were recovered from calcareous nodules and retain

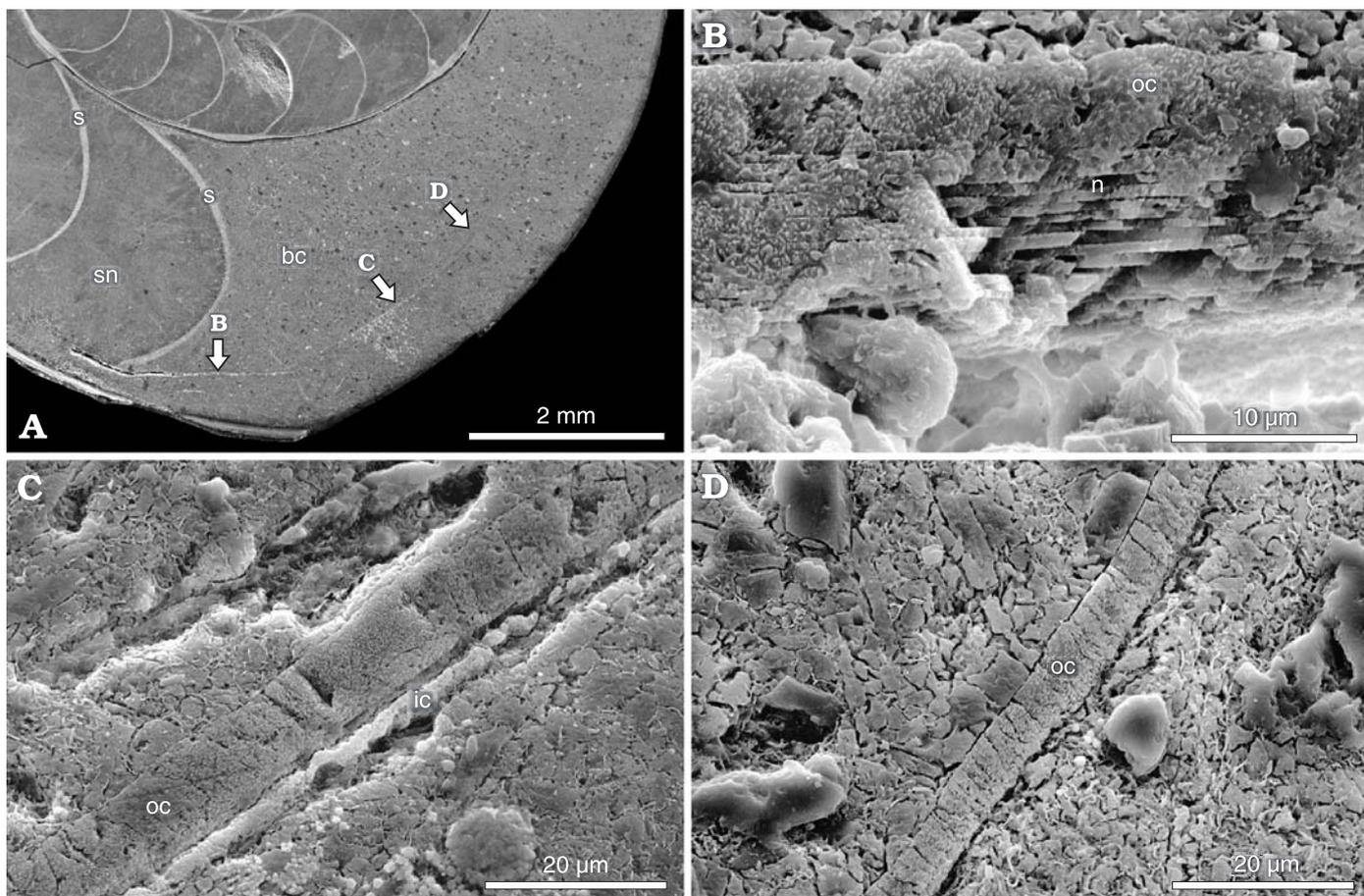


Fig. 2. *Phyllopachyceras ezoense* (Yokoyama, 1890). UMUT MM 28658 from the lower Campanian of the Nakanofutamata-zawa Creek, Haboro area, northwest Hokkaido (median longitudinal section). A. Occurrence of precursory siphuncular membranes in the rear part of the body chamber showing locations of photos B–D. B. Adoral end of the last septal neck, showing the outer conchiolin layer resting on the nacreous layer of the septal neck. C. Conchiolin membranes in the rear part of the body chamber, consisting of thinner inner and thicker outer layers. D. Adoral end of the conchiolin membranes in the body chamber, which consist only of the outer layer. Abbreviations: bc, body chamber; ic, inner conchiolin layer; n, nacreous layer of septal neck; s, septum; sn, septal neck; oc, outer conchiolin layer.

an original aragonitic shell. Every specimen preserves an almost complete body chamber, but is not associated with jaw remains. Furthermore, two juvenile specimens of *Damesites sugata* Forbes, 1846 (Desmoceratidae; Ammonitina) with a tube-shaped structure in their body chambers from the middle Campanian of the Nakagawa area (UMUT MM 28661, 28662) were examined for comparison.

Of the six specimens utilized, three specimens of *Phyllopachyceras ezoense* and two of *Damesites sugata* were cut and polished along the median dorsoventral plane with a graded series of carborundum and diamond pastes. The remaining specimen of *P. ezoense* was cut vertically and its sectioned surface was polished in the same manner to observe the siphuncular tube and dark-colored, organic membranes in the body chamber. The sectioned surface of each specimen was etched with 5% acetic acid for 30–60 seconds, washed with distilled water, dried in air, coated with platinum-palladium using an ion coater, and then observed by scanning electron microscopy (Hitachi S 2400 and Philips XL-20).

Observations

In every specimen of *Phyllopachyceras ezoense* examined, the dark organic membranes in the body chamber are continuous with the siphuncular tube wall in the phragmocone and extend into the rear part of the body chamber to a length equivalent to 2 to 2.5 times that of the last camera (Figs. 1A, 2A, and 3A). In passing adorally from the last septal neck, the membranes are remarkably expanded dorsally and the distance between the membranes and the ventral shell margin is approximately two times wider than the siphuncular tube diameter in the last camera. Unlike the condition in the phragmocone, the organic membranes do not form a complete tube shape; namely, the membranes are truncated on the ventral side and the ventral margin of the membranes directly contacts the outer shell wall (Fig. 4A). In median section, the organic membranes in the body chamber are only visible on the dorsal side (Figs. 1A, 2A, and 3A).

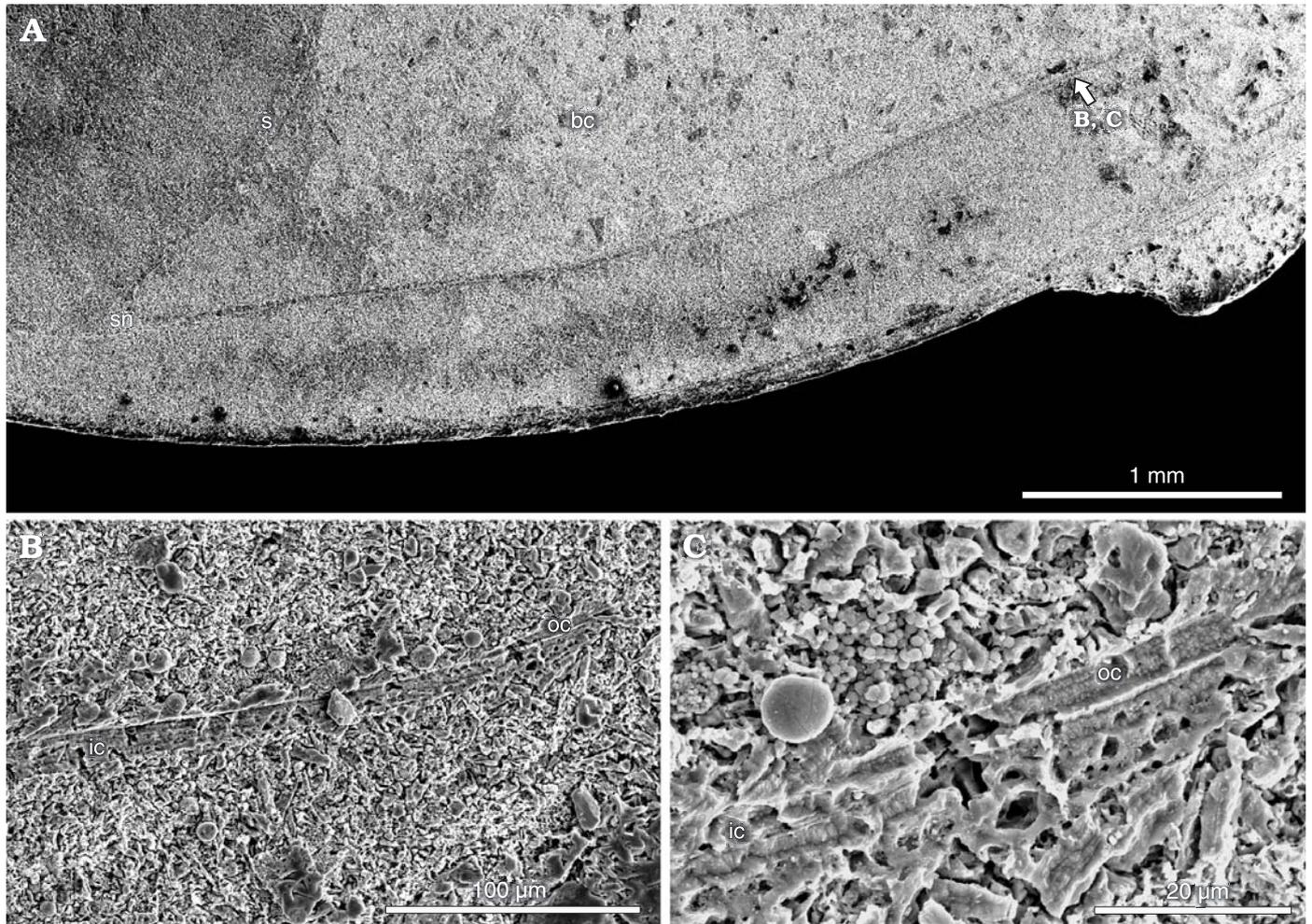


Fig. 3. *Phyllopatryceras ezoense* (Yokoyama, 1890). UMUT MM 28659 from the lower Campanian of the Nakanofutamata-zawa Creek, Haboro area, northwest Hokkaido (median longitudinal section). A. Occurrence of precursory siphuncular membranes in the rear part of the body chamber showing location of photos B, C. The membranes have a length equivalent to that of the two last camerae. B, C. Anterior end and close-up of the conchiolin membranes. The inner layer disappears just before the adoral end, whereas the outer layer still exists. Abbreviations: bc, body chamber; ic, inner conchiolin layer; n, nacreous layer of septal neck; oc, outer conchiolin layer; s, septum; sn, septal neck.

The organic membranes in the body chamber of *P. ezoense* are made of a dark colored, possibly originally conchiolin substance. They are about 10–20 µm thick at shell diameters of 8.2 to 11.0 mm (Figs. 1B, C, 2C, D, 3C, 4B–D) and are distinctly divided into two layers with different microstructures; viz., a thinner inner layer with homogeneous microstructure and a thicker outer layer consisting of pillar-like micro-units, distinctly tilted adorally (Figs. 1C, 2D, 4B–D). In approaching the last septum, the inner layer is replaced by the nacreous-like deposit (auxiliary deposit; Kulicki and Mutvei 1982) that occurs on the adapical side of the septal neck. It becomes thinner adorally and finally disappears just before the anterior end of the outer layer (Fig. 2C, D). The outer layer rests on the anterior extension of the auxiliary deposit (n in Figs. 1B, 2B) and extends to the anterior end of the conchiolin membranes in the body chamber (Fig. 2D).

As in the organic membranes in the body chamber, the siphuncular tube wall of *P. ezoense* consists of two conchio-

lin layers (ic and oc in Fig. 5). The siphuncle in this species initially occupies a subcentral position in the first whorl and then gradually migrates to the ventral position in the second whorl (Tanabe et al. 1979).

Accordingly, after the third whorl the tube wall contacts the outer shell wall on the ventral side, and several thin membranes (= siphuncular sheets of Weitschat and Bandel 1991; see the next chapter for details) branching from the outer layer attach to the ventral shell (Fig. 5B).

Comparison with related structures in other ammonites

Remains of precursory siphuncular membranes have been known in the body chamber of the following Jurassic–Cretaceous Phylloceratina; *Phyllopatryceras* sp. from the Aptian

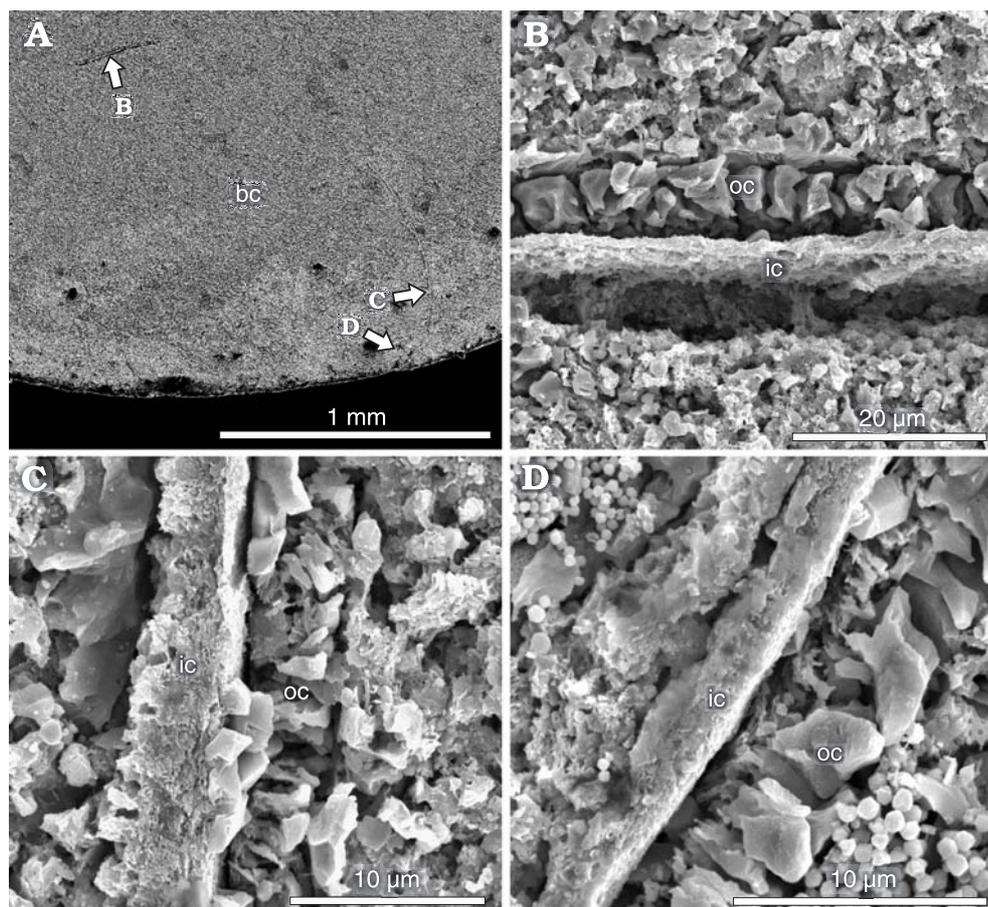


Fig. 4. *Phyllopacchyceras ezoense* (Yokoyama, 1890). UMUT MM 28660 from the middle Campanian of the southern tributary in the Osousyunai Creek, Nakagawa area, northern Hokkaido (dorso-ventral cross section). A. Ventral side of the body chamber, showing the shape of the precursory siphuncular membranes that directly contact the outer shell wall and the locations of photos B–D. B–D. Precursory siphuncular membranes at the dorsal (B), ventrolateral (C) and ventral (D) sides. At every side, the membranes are made up of a thinner homogeneous inner layer and a thicker outer layer with pillar-like units. Abbreviations: bc, body chamber; ic, inner conchiolin layer; oc, outer conchiolin layer.

of Caucasus (Druschits and Doguzhaeva 1974), *Holcophylloceras zignodianum* from the Callovian of Georgia (Kulicki 1979: pl. 40: 1), *Euphylloceras velleidae* from the Aptian of Caucasus (Doguzhaeva and Mikhailova 1982: fig. 1c; Doguzhaeva 1988: text-figs. 2, 3A), and *Ptychophylloceras cf. galoi* (detailed age and locality undescribed; Westermann 1982: fig. 3). In these phylloceratids, the preserved membranes have a length equivalent to that of the last 1.5 to 2 camerae. They are much thinner than the siphuncular wall in the last camera (ca. 30% in *Ptychophylloceras*; Westermann 1982: 376) and occasionally inflated adorally. Although previous authors did not describe the three-dimensional architecture nor the microstructure of the precursory siphuncular membranes in the body chamber, the illustrated pictures and diagrams seem to indicate that in median section, they occur only on the dorsal side (e.g., Westermann 1982: fig. 3; Doguzhaeva 1988: text-figs. 2B, 3A). These features are similar to our observations on *Phyllopacchyceras ezoense*, suggesting a wide distribution of the precursory siphuncular membranes in the Phylloceratina.

Other than the Phylloceratina, Doguzhaeva (1988: text-fig. 1) figured a tube-shaped structure in the rear part of the body chamber of a specimen of the Aptian desmoceratid *Melchiorites* sp. and interpreted it as the fragment of the siphuncular tube. However, further microstructural investigation of the specimen is needed to confirm her interpretation. We have

also found a similar structure in the body chamber of two specimens of the Late Cretaceous desmoceratid *Damesites sugata*. SEM observations of the two specimens reveal that the tube-shaped structure, whose length is equivalent to that of 1.5 to 2 camerae, is continuous with the last septal neck and is made of a nacreous layer only (Fig. 6). We have confirmed that the length of prochoanitic septal necks in the two specimens of *D. sugata* is as less than 1/3 of that of camerae in the phragmocone. We, therefore, believe that the structure represents a pathologically overgrown prochoanitic septal neck and is not homologous with the conchiolin membranes observed in the body chambers of phylloceratids. As far as we know, the precursory siphuncular membranes in the body chamber that are continuous with the siphuncular tube wall have not been described in ammonoids other than phylloceratids.

Other organic structures related to the siphuncular tube wall in ammonoids are intracameral organic membranes. Remains of the intracameral membranes are known to occur in various Paleozoic and Mesozoic ammonoids (Grandjean 1910; Schoulga-Nesterenko 1926; Hölder 1952, 1954; Erben and Reid 1971; Westermann 1971; Bayer 1975; Kulicki 1979; Weitschat 1986; Weitschat and Bandel 1991; Tanabe and Landman 1996; Mapes et al. 2002). In previously described ammonoids, detailed features of intracameral membranes are best preserved in phosphatized specimens of some Triassic ceratites from Spitzbergen and Siberia (Weitschat

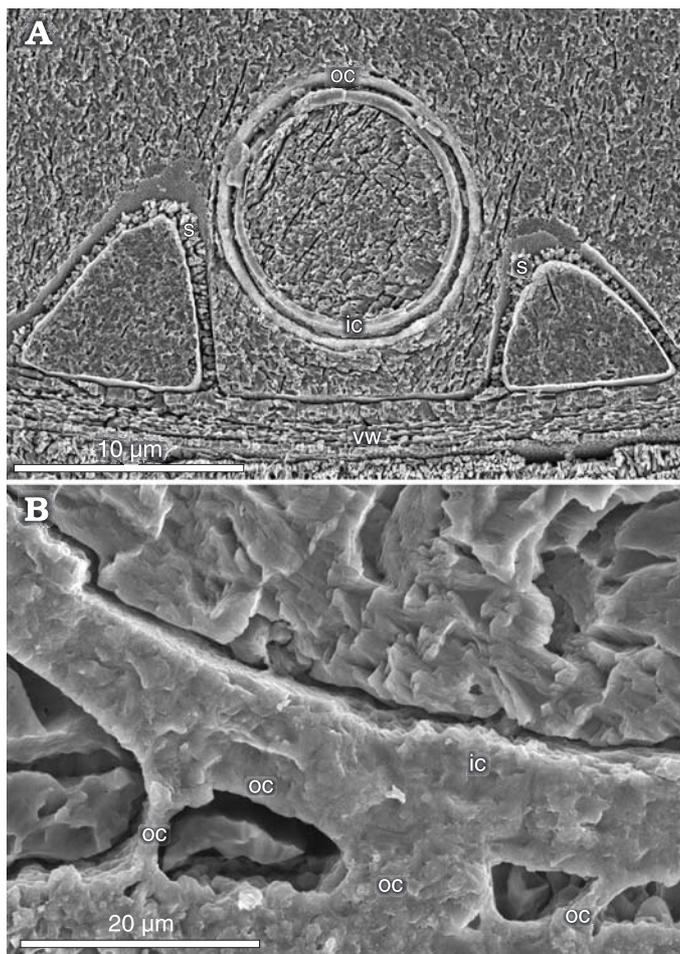


Fig. 5. *Phyllopachyceras ezoense* (Yokoyama, 1890). UMUT MM 28660. Same specimen as that in Fig. 4. **A.** Siphuncular tube at the beginning of the second whorl, consisting of inner and outer conchiolin layers. The ventral side is distinctly detached from the ventral shell wall at this stage. **B.** Close-up of the ventral side of the siphuncular tube in the third whorl, showing that the membranes branching from the outer layer are attached to the ventral shell wall. Abbreviations: ic, inner conchiolin layer; oc, outer conchiolin layer; s, septum; vw, ventral shell wall.

and Bandel 1991; Checa 1996) and Permian prolecanitids from Buck Mountain, Nevada (Tanabe and Landman 1996, fig. 5A; Mapes et al. 2002). According to Weitschat and Bandel (1991), intracameral membranes in the Triassic ceratites form a complex network of sheets and can be classified into three types, based on their distribution and overall shape: (1) siphuncular sheets, (2) transverse sheets, and (3) horizontal (longitudinal) sheets. Of these three types, the siphuncular sheets appear to have originated from the outer organic layer of the siphuncular tube. They are detached from the lateral portion of the siphuncular tube wall at given intervals and are attached ventrally to the inner surface of the outer shell wall and dorsally to horizontal sheets. In median dorsoventral section, the siphuncular sheets are arranged parallel or subparallel to one another and are directed adorally, opposite the adapical direction of septal necks (retrochoanitic necks) (see Weitschat and Bandel 1991: figs. 6–11).

Transverse sheets extend from the inner surface of the dorsal wall in a direction subparallel to the septal surface. Permian prolecanitids from Nevada also retain siphuncular sheets around the siphuncular tube whose overall shape and distribution in each camera are quite similar to those in Triassic ceratites described by Weitschat and Bandel (1991). However, neither transverse sheets nor horizontal sheets are preserved in these prolecanitids (Landman, unpublished data). Remains of siphuncular sheets are widely distributed in Mesozoic ammonoids belonging to the Phylloceratina, Lytoceratina and Ammonitina (Grandjean 1910; Hölder 1952, 1954; Erben and Reid 1971; Westermann 1971; Bayer 1975; Tanabe, unpublished data). In the case of the *Phyllopachyceras* specimens examined, remains of siphuncular sheets appear around the siphuncular tube (see Fig. 5B) in each camera. Yet, organic components other than the conchiolin membranes described herein have not yet been found in the body chamber of ammonoids.

Morphogenetic implications

Because the siphuncle is an element of the chambered cephalopod shell, its morphogenesis should be considered in the context of chamber formation. One of the major evolutionary features in ammonoid chamber structure is the change in the architecture of septal necks (see Tanabe et al. 1993; Tanabe and Landman 1996, for recent reviews). In Paleozoic ammonoids excluding the Goniatitina, the septal necks are directed adapically (retrochoanitic) throughout ontogeny. In the Goniatitina and Ceratitina, retrochoanitic septal necks either persist throughout ontogeny or develop into modified retrochoanitic necks, whose dorsal side is projected adapically, while the ventral side is directed adorally. In the Mesozoic Ammonitida, the septal necks change within the first whorl from retrochoanitic to either amphichoanitic (directed both adorally and adapically) (Phylloceratina) or prochoanitic (totally directed adorally) (Lytoceratina, Ammonitina, and Ancyloceratina). For diagrammatic architectures and median cross-sections of these four septal neck types see Tanabe et al. (1993: figs. 4.1, 4.2) and Tanabe and Landman (1996: fig. 2).

Most previous authors assumed that the rear mantle and siphuncle moved forward prior to septal formation (Branco 1879–80; Mutvei 1967; Mutvei and Reymont 1973; Kulicki, 1979, 1994; Bandel 1981; Kulicki and Mutvei 1982; Doguzhaeva and Mutvei 1986; Doguzhaeva 1988; Tanabe and Landman 1996). These authors also suggested that in ammonoids with retrochoanitic septal necks, the rear part of the mantle and the siphuncle moved forward without changing their shape during chamber formation. This interpretation is supported by the presence of anatomical features without epithelial invagination at the connecting portion of the siphuncle and the rear part of the mantle in Recent *Nautilus* and *Spirula*, both with retrochoanitic septal necks (Fukuda et al. 1981; Tanabe unpublished data). The authors listed above have fur-

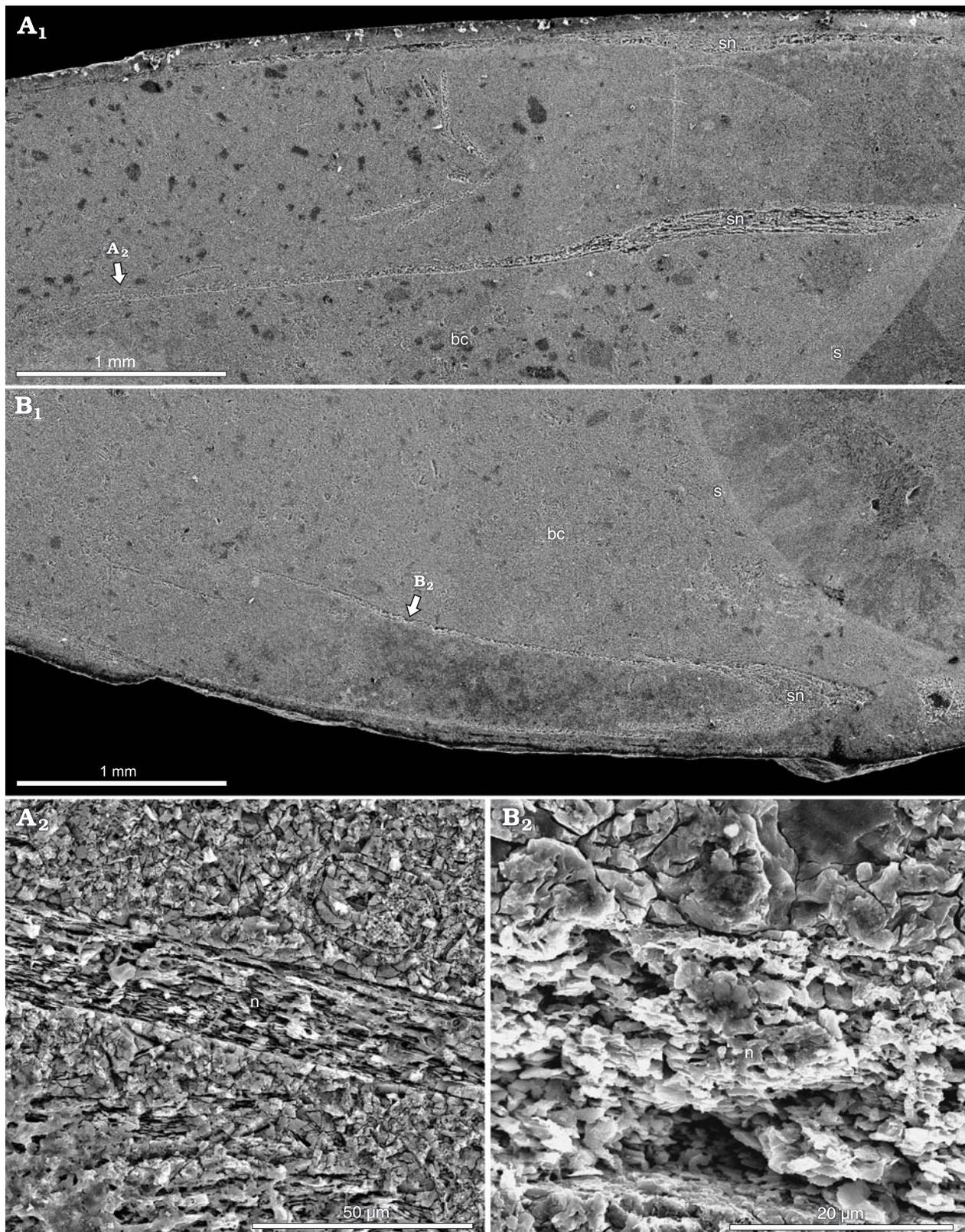


Fig. 6. *Damesites sugata* Forbes, 1846. **A.** UMUT MM 28661 from the middle Campanian in the Nio River, Nakagawa area, north Hokkaido. **B.** UMUT MM 28662 from the middle Campanian in the Nio River, Nakagawa area, north Hokkaido (all in median longitudinal section). **A₁**. Unusually long septal neck, extending into the body chamber, showing locations of photo **A₂**; its length is equivalent to the last cameral distance. **A₂**. Anterior margin of the long septal neck, consisting of a nacreous layer. **B₁**. Unusually long septal neck, extending into the body chamber, showing locations of photo **B₂**; its length is equivalent to the last cameral distance. **B₂**. Anterior margin of the long septal neck, consisting of a nacreous layer. Abbreviations: bc, body chamber; n, nacreous layer of septal neck; s, septum; sn, septal neck.

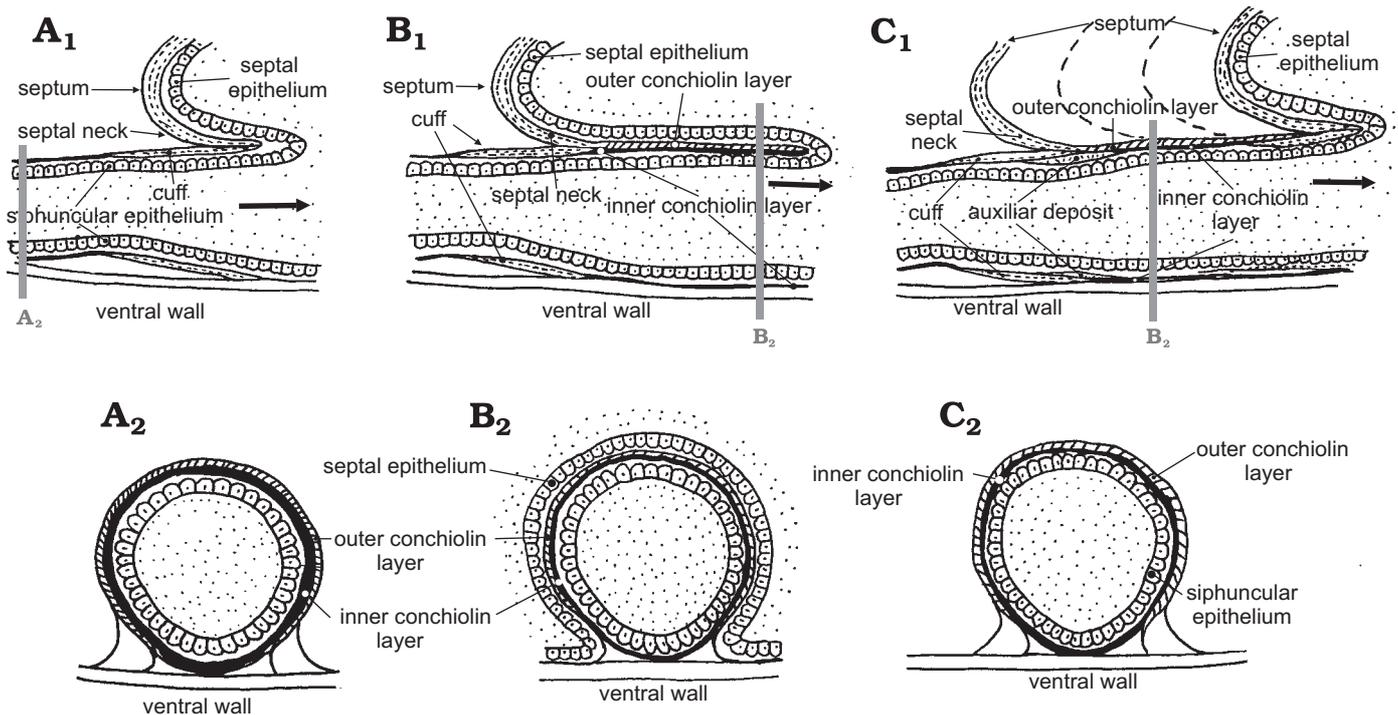


Fig. 7. Successive stages of formation of the septal neck-siphuncular complex in *Phyllopatryceras ezoense*. **A.** Stage before anterior migration of the body and development of invagination of the septal epithelium in median dorsoventral (A_1) and transverse (A_2) sections. **B.** Development of the invagination of the septal epithelium followed by the gradual migration of the circumsiphuncular portion of the body in median dorsoventral (B_1) and transverse (B_2) sections. Inner and outer layers of the primary conchiolin membranes are secreted by the siphuncular and septal epithelia, respectively. **C.** Gradual migration of the body and subsequent secretion of the nacreous septum by the septal epithelium. The inner layer of the siphuncular wall is thickened by additional conchiolin membranes secreted by the siphuncular epithelium, and the siphuncular wall at the preceding septal neck region is partly calcified (auxiliary deposit); median dorsoventral (C_1) and transverse (C_2) sections. Arrows point to the adoral direction.

ther suggested that during the development of modified retro-, amphi-, and prochoanitic septal necks, the anterior portion of the siphuncular epithelium invaginated adapically and changed into the septal epithelium. In other words, invagination of the siphuncular epithelium first occurred only on the dorsal side in the middle to late stages of the Goniatitina and Ceratitina. In Jurassic and Cretaceous ammonoids, the epithelial invagination appeared on both dorsal and ventral sides soon after hatching, coincident with the change from retrochoanitic septal necks to amphichoanitic septal necks in the Phylloceratina or to prochoanitic septal necks in the Lytoceratina, Ammonitina and Ancyloceratina, and the depth of this invagination presumably increased during ontogeny (Tanabe and Landman 1996: fig. 11).

There are currently two views as to the developmental sequence of this invagination during septal formation. The first view, proposed by Kulicki (1979: fig. 3), Tanabe et al. (1982: text-fig. 1), Lominadzé et al. (1993), and Tanabe and Landman (1996, figure 11), is that the invagination of the septal epithelium was initially absent and developed only in the course of septal secretion. Meanwhile, such authors as Mutvei (1967: text-fig. 4), Mutvei and Reymont (1973: text-fig. 6), Henderson (1984: text-fig. 10), Doguzhaeva and Mutvei (1986: text-fig. 8), and Doguzhaeva (1988: text-fig. 5B, C)

have proposed another view that the invagination of the septal epithelium already occurred in the initial stage of chamber formation. According to the second view, the following two major steps are postulated for the formation of the siphuncle and septum; (1) the adorally migrating siphuncular epithelium and the invaginated septal epithelium secrete a thin primary conchiolin membrane prior to new septum formation, and (2) the calcified septum and septal neck are secreted by the invaginated septal epithelium, and simultaneously, the concentric conchiolin membranes of the siphuncular wall and the calcified modification at the septal neck region (cuff, auxiliary deposit) are secreted by the siphuncular epithelium. As already emphasized by Doguzhaeva (1988), a relatively long and thin organic structure observed in the body chamber of several Jurassic and Cretaceous phylloceratids undoubtedly corresponds to the primary conchiolin membrane hypothesized by Mutvei (1967) and Mutvei and Reymont (1973).

Our SEM observations confirm that in *Phyllopatryceras ezoense*, the primary conchiolin membrane in the body chamber at shell diameters larger than 8 mm does not form a tubular shape, since it is in direct contact with the outer shell wall on the ventral side, and that it is not a single membrane but is made up of two layers with different microstructure.

These facts lead to the new model of formation of conchiolin membranes in the body chamber (Fig. 7).

After the formation of a mineralized septum (Fig. 7A₁, A₂), the circumsiphonal portion of the body gradually migrated adorally developing a deep invagination of the septal epithelium prior to septal formation (Fig. 7B₁). In this stage, inner and outer sublayers of the primary conchiolin membrane were respectively formed by the siphuncular epithelium from the inner side and by the invaginated septal epithelium from the outer side (Fig. 7B₂). In the final stage, the invaginated septal epithelium secreted a new nacreous septum, and simultaneously, the siphuncular epithelium secreted a calcified deposit (auxiliary deposit) around the inner surface of the preceding septal neck region (Fig. 7C₁, C₂). As already described, in *P. ezoense*, the siphuncular tube gradually shifts its position from the subcentral to the ventral side in the second whorl. With this change, invagination of the septal epithelium which initially occurred on the dorsal and ventral sides, became restricted to the dorsal side after the third whorl. In summary, available data for the distribution and microstructure of the conchiolin membranes in the body chamber strongly support the deep septal epithelial invagination model by Mutvei (1967) and others for the siphuncle-septum formation in the Phylloceratina.

In our specimens of *P. ezoense*, the conchiolin membranes in the body chamber are expanded relative to the diameter of the siphuncle in the preceding chambers. This is true of some of the phylloceratids previously studied (e.g., *Phyllopachyceras* sp.; Doguzhaeva 1988: text-fig. 3A). We suspect that this expansion is post-mortem and produced by diagenetic deformation of the membranes. In contrast, the extreme length of the membrane in the body chamber relative to the height of the preceding chamber is probably a real phenomenon and reflects the length of the circumsiphonal invagination during life.

Doguzhaeva (1988: text-fig. 5C) postulated that in ammonoids with prochoanitic septal necks, a deeply invaginated septal epithelium was always present before and after septum formation because the primary organic membrane occasionally extends two camera lengths in front of the last formed septum. However, a primary conchiolin membrane has only been confirmed in the Phylloceratina, and therefore, her model cannot be supported by fossil evidence for the other ammonoid suborders. We suggest that a deep invagination of the septal epithelium might also be present in some Cretaceous Lytoceratina (e.g., *Gaudryceras* and *Tetragonites*) that have long prochanitic septal necks. Further research on the conchiolin membranes in the body chamber is needed in these ammonoids to confirm the above hypothesis.

For the morphogenesis of intracamerai membranes associated with the siphuncular tube, there are currently two different opinions. Weitschat and Bandel (1991) interpreted that all of the intracamerai membranes observed in some Triassic ceratites were secreted by the mantle epithelium. Subsequently, on the basis of reexamination of the same material described by Weitschat and Bandel (1991) and experiments

with liquids rich in organic molecules, Checa (1996) proposed another view, that the transverse and siphuncular sheets were the products of desiccation of decoupled hydrogelled cameral liquid and that the horizontal sheets and chamber linings were presumably secreted (not replicated) sequentially and/or stretched across the chamber by the rear mantle. Indeed, in the cuttlefish *Sepia*, a horizontal organic sheet-membrane within the cuttlebone similar in overall features to the ammonoid intracamerai membranes or sheets is formed by organic-rich extrapallial fluid during the early stage of new chamber formation (Bandel and Boletzky 1979; Tanabe et al. 1985). Checa (1996) also suggested that only pseudosepta and septal linings were direct replications of the rear mantle epithelium.

According to Checa's (1996) dehydration model, intracamerai sheets would have formed after new chamber formation, since they were the remnant of organic substances in cameral liquid that was mostly pumped out from the chamber.

Indeed, the conchiolin membranes in the body chamber of phylloceratids do not have any organic sheet around them, being consistent with Checa's (1996) model. A question, however, still remains why the overall features of the siphuncular sheets hitherto described are so uniform and similar among different taxa. Such complicated siphuncular sheets were actually not reproduced by Checa's (1996: fig. 4) experiments using liquids rich in organic molecules. In our interpretation, the outer layer of the ventrally truncated organic membranes observed in the body chamber of *Phyllopachyceras* was secreted by the invaginated septal epithelium from the outside and possibly became part of the future siphuncular sheets during new chamber formation. If the siphuncular sheets were formed by the invaginated septal epithelium from the outside, they should not occur in ammonoids with retrochanitic septal necks. Unexpectedly, they are preserved in the Permian prolecanitid *Akmilleria*, with retrochoanitic septal necks (Tanabe and Landman 1996; Mapes et al. 2002). To sum up the above discussion, a reasonable explanation is not available at this time for the origin of the intracamerai siphuncular sheets of ammonoids. Future comparative anatomical and theoretical morphologic analysis based on well-preserved fossil material will help resolve this problem.

Acknowledgments

We thank Dr. Takashi Okamoto (Ehime University) who provided excellent ammonoid specimens from Hokkaido for this study, and Dr. Yoshio Fukuda (Chiba Prefectural Institute of Public Health, Japan) and two referees, Prof. Royal H. Mapes (Ohio University) and Dr. Harry Mutvei (Swedish Museum of Natural History) for helpful comments to improve this manuscript. Cypryan Kulicki was financially supported by the Polish Academy of Science and the Japan Society for Promotion of Science (JSPS) for his research in Japan in 2003. This work was supported by the Grant-in-Aid of JSPS (no. 1540175) and the scientific research fund of the 21st Century Center of Excellence (COE) Program to the University of Tokyo (G3, Leader, T. Yamagata).

References

- Bandel, K. 1981. The structure and formation of the siphuncular tube of *Quenstedtoceras* compared with that of *Nautilus* (Cephalopoda). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 161: 153–171.
- Bandel, K. and Boletzky, S.v. 1979. A comparative study of the structure, development and morphological relationships of chambered cephalopod shells. *The Veliger* 21: 313–354.
- Bayer, U. 1975. Organische Tapeten im Ammoniten-Phragmokon und ihr Einfluss auf die Fossilization. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1975 (1): 12–25.
- Branco, W. 1879–1880. Beiträge zur Entwicklungsgeschichte der fossilen Cephalopoden. *Palaeontographica* 26 (1879): 15–50; 27 (1880): 17–81.
- Checa, A. 1996. Origin of intracamerals sheets in ammonoids. *Lethaia* 29: 61–75.
- Denton, E.J. and Gilpin-Brown, J.B. 1966. On the buoyancy of the pearly *Nautilus*. *Journal of Marine Biological Association of the United Kingdom* 46: 723–759.
- Denton, E.J. and Gilpin-Brown, J.B. 1973. Floatation mechanisms in modern and fossil cephalopods. In: F.S. Russel and M. Young (eds.) *Advances in Marine Biology, Volume 11*, 197–268. Academic Press, London.
- Doguzhaeva, L. 1988. Siphuncular tube and septal necks in ammonoid evolution. In: J. Wiedmann and J. Kulmann (eds.), *Cephalopods Present and Past*, 291–301. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- Doguzhaeva, L.A. and Mikhailova, I.A. 1982. Siphuncular tube of Cretaceous heteromorphs [in Russian]. *Doklady Akademii Nauk SSSR* 264: 965–968.
- Doguzhaeva, L.A. and Mutvei, H. 1986. Retro- and prochoanitic septal necks in ammonoids, and transition between them. *Palaeontographica, Abteilung A* 195: 1–18.
- Druschits, V.V. and Doguzhaeva, L.A. 1974. Some morphogenetic characteristics of phylloceratids and lycoceratids (Ammonoidea) [in Russian]. *Paleontologičeskij žurnal* 1974 (1): 42–53.
- Erben, H.K. and Reid, R.E.H. 1971. Ultrastructure of shell, origin of conellae and siphuncular membranes in an ammonite. *Biominalisation* 3: 22–31.
- Forbes, E. 1846. Report on the fossil Invertebrata from southern India, collected by Mr. Kaye and Mr. Cunliffe. *Transactions of the Geological Society of London ser. 2*, 7: 97–174.
- Fukuda, Y., Tanabe, K. and Obata, I. 1981. Histology of the siphuncular epithelium in *Nautilus pompilius* (Cephalopoda) and its functional implications [in Japanese with English abstract]. *Kaseki-Kenyūkai shi (Fossil Research Bulletin)* 14: 29–40.
- Grandjean, F. 1910. Le siphon des ammonites et des belemnites. *Bulletin de la Société Géologique de France* 10: 496–519.
- Greenwald, L., Ward, P.D., and Greenwald, O.E. 1980. Cameral liquid transport and buoyancy control in chambered nautilus (*Nautilus macromphalus*). *Nature* 286: 55–56.
- Grégoire, C. 1984. Remains of organic components in the siphonal tube and in the brown membrane of ammonoids and fossil nautiloids. Hydrothermal simulation of their diagenetic alterations. *Akademie der Wissenschaft und Literatur, Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse Jahrgang* 1984 (5): 1–56.
- Henderson, R.A. 1984. A muscle attachment proposal for septal function in Mesozoic ammonites. *Palaeontology* 27: 461–486.
- Hölder, H. 1952. Über Gehäusebau, insbesondere Hohlkiel jurassischer Ammoniten. *Palaeontographica, Abteilung A* 102: 18–48.
- Hölder, H. 1954. Über die Siphonheftung bei Ammoniten. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 1954 (8): 372–379.
- Kulicki, C. 1979. The ammonite shell: Its structure, development and biological significance. *Acta Palaeontologica Polonica* 39: 97–142.
- Kulicki, C. 1994. Septal neck-siphuncular complex in *Stolleyites* (Ammonoidea), Triassic, Svalbard. *Polish Polar Research* 15: 37–49.
- Kulicki, C. and Mutvei, H. 1982. Ultrastructure of the siphonal tube in *Quenstedtoceras* (Ammonitina). *Stockholm Contributions in Geology* 37: 129–138.
- Lominadzé, T.A., Sharikadzé, M.Z., and Kvantaliani, I.V. 1993. On mechanism of soft body movement within body chamber in ammonites. *Geobios Mémoire Spécial* 15: 267–273.
- Mapes, R.H., Landman, N.H., Tanabe, K. and Maeda, H. 2002. Intracamerals membranes in Permian ammonoids from the Buck Mountain, Nevada Lagerstätte. *Geological Society of America, Abstracts with Programs* 34 (6): 354.
- Mutvei, H. 1967. On the microscopic shell structure in some Jurassic ammonoids. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 129: 157–166.
- Mutvei, H. and Reymont, R.A. 1973. Buoyancy control and siphuncle function in ammonoids. *Palaeontology* 16: 623–636.
- Obata, I., Tanabe, K., and Fukuda, Y. 1980. The ammonite siphuncular wall: Its microstructure and functional significance. *Bulletin of the National Science Museum (Tokyo), Series C (Geology and Paleontology)* 6: 59–72.
- Schoulgá-Nesterenko, M. 1926. Nouvelles données sur l'organisation intérieure des conques des ammonites de l'étage d'Artinsk. *Bulletin de la Société des Naturalistes de Moscou, Section Géologique* 2 (34): 81–99.
- Tanabe, K. and Landman, N.H. 1996. Septal neck-siphuncular complex. In: N.H. Landman, K. Tanabe, and R.A. Davis (eds.), *Ammonoid Paleobiology, Volume 13 of Topics in Geobiology*, 129–165. Plenum Press, New York.
- Tanabe, K., Landman, N.H., and Weitschat, W. 1993. Septal necks in Mesozoic Ammonoidea: structure, ontogenetic development and evolution. In: M.R. House (ed.), *The Ammonoidea: Environment, Ecology, and Evolutionary Change*. Systematics Association Special Volume 47, 57–84. Clarendon Press, Oxford.
- Tanabe, K., Obata, I., Fukuda, Y., and Futakami, M. 1979. Early shell growth in some Upper Cretaceous ammonites and its implications to major taxonomy. *Bulletin of the National Science Museum (Tokyo), Series C (Geology and Paleontology)* 5: 153–176.
- Tanabe, K., Fukuda, Y., and Obata, I. 1982. Formation and function of the siphuncle-septal neck structures in two Mesozoic ammonites. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series* 128: 433–443.
- Tanabe, K., Fukuda, Y., and Obata, I. 1985. New chamber formation in the cuttlefish *Sepia esculenta* Hoyle. *Venus* 44: 55–67.
- Tanabe, K., Mapes, R.H., Sasaki, T., and Landman, N.H. 2000. Soft-part anatomy of the siphuncle in Permian prolecanitid ammonoids. *Lethaia* 33: 83–91.
- Weitschat, W. 1986. Phosphatisierte Ammonoideen aus der Mittleren Trias von Central-Spitzbergen. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 61: 249–279.
- Weitschat, W. and Bandel, K. 1991. Organic components in phragmocones of Boreal Triassic ammonoids: implications for ammonoid biology. *Paläontologische Zeitschrift* 65: 269–303.
- Westermann, G.E.G. 1971. Form, structure and function of shell and siphuncle in coiled Mesozoic ammonites. *Life Sciences Contributions, Royal Ontario Museum* 78: 1–39.
- Westermann, G.E.G. 1982. The connecting rings of *Nautilus* and Mesozoic ammonoids: implications for ammonoid bathymetry. *Lethaia* 15: 373–384.
- Yokoyama, M. 1890. Versteinerung aus der japanischen Kreide. *Palaeontographica* 36: 159–202.