Siphuncular structure in Ordovician endocerid cephalopods

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Exceptionally well-preserved shells of the endocerids *Dideroceras wahlenbergi* (Foord, 1887), *Anthoceras vaginatum* (Schlotheim, 1820), and *Suecoceras barrandei* (Dewitz, 1880) from phosphatized Early and Middle Ordovician limestones of Northern Estonia were studied by means of SEM. The septal neck in these endocerids is composed of three, structurally different, aragonite layers: outer spherulitic-prismatic, nacreous, and inner prismatic. The connecting ring is a continuation of the spherulitic-prismatic layer of the septal neck. Its inner surface was probably covered by a thin glycoprotein (conchiolin) sheet. Structural differentiations in the spherulitic-prismatic layer of the connecting ring, such as a layering and 'eyelet', reported by previous writers, were not observed. These differentiations probably result from diagenesis. The siphuncular structure in endocerids agrees in detail with that in Recent *Spirula* and *Nautilus*. The conical endosiphuncular deposits (endocones) of endocerids show extensive intraspecific variation. Morphological and structural differences in these deposits should therefore be used with caution in generic and specific diagnoses.

K e y   w o r d s : endocerids, structure, Ordovician, siphuncle, *Nautilus*, *Spirula*.

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Introduction

Endocerids are characterized by (1) a wide, generally marginal, siphuncle, often with long, holochoantic septal necks, and (2) conical endosiphuncular deposits ('endocones') (e.g., Flower 1941, 1947, 1964; Teichert 1964). Endocerid taxonomy is still imperfectly known. The structure of the shell wall and siphuncle is usually obscured by diagenesis. Therefore, details of this structure need to be studied in well-preserved material.

This paper reports the structure of the siphuncle in three endocerid species: *Anthoceras vaginatum* (Schlotheim, 1820), *Dideroceras wahlenbergi* (Foord, 1887), and *Suecoceras barrandei* (Dewitz, 1880). These species are in need of taxonomic revision, which is outside the scope of the present paper. It is possible that these three species represent, in fact, groups of related species.

The material was collected from the Early and Middle Ordovician of Estonia. The shell is partially phosphatized, and exceptionally well preserved, enabling the study of ultrastructural details with a scanning electron microscope.

The siphuncular structure in endocerids is compared with that in actinocerids and in extant *Nautilus* and *Spirula*.

The present paper also includes a summary of data on the morphology of the conical endosiphuncular deposits ('endocones') and its intraspecific variations, previously studied mainly by the present author (Mutvei 1964b) and by Dzik (1984).

Material and methods

Numerous specimens of *Dideroceras wahlenbergi* (Foord, 1887) and *Anthoceras vaginatum* (Schlotheim, 1820) were collected by the present author from the Harku quarry within the town limits of Tallinn, Estonia. These specimens occur in a phosphatized limestone of the Aluoja Substage, of latest Early Ordovician age (Kundan). The Harku quarry has also yielded well-preserved actinocerids (*Ormoceras*), which are described by the present author in a separate paper (Mutvei 1997). In addition, several specimens of *Suecoceras barrandei* (Dewitz, 1880) were collected from the phosphate quarry at Maardu, about 10 km E of Tallinn. The latter specimens come from a bed with white phosphatic (francolitic) ooids at the boundary between the Aseri and Lasnamägi Stages, Middle Ordovician.

Shell structure was studied on polished sections with a scanning electron microscope (SEM), Philips 35, at the Swedish Museum of Natural History, Stockholm. The polished sections were etched with 1% acetic acid for 10–15 min.
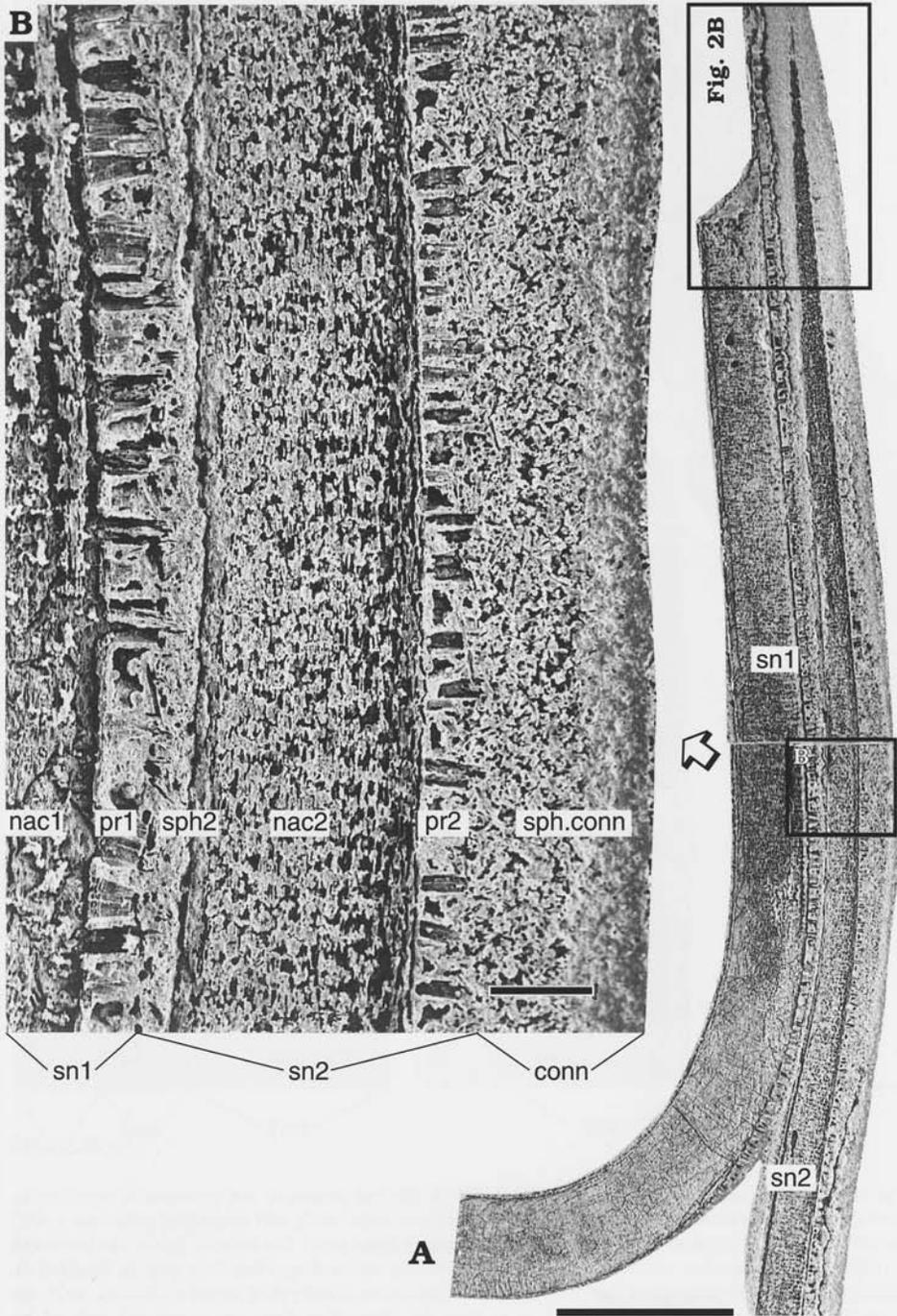
In Figs 1–5, 7–9 the shell aperture is directed downwards.

Observations

Dideroceras wahlenbergi (Foord, 1887)
Figs 1, 2, 3A, B, 4, 6A.
Septal neck. — The septal neck has a length of about one and one quarter of the distance between septa (Fig. 3B). It is composed of three aragonite layers: inner prismatic, nacreous, and outer spherulitic-prismatic. The inner prismatic layer (pr1, pr2 in Figs 1B, 2A) covers the entire inner suface of the neck. Because the adjacent prisms were separated by narrow interspaces, the prismatic layer was originally highly porous. Now, the interspaces are filled by a fine-grained calcium phosphate. During diagenesis,

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Fig. 1. **A**, **B**. *Dideroceras wahlenbergi* (Foord, 1887). **A**. Siphuncular wall in median section, showing two consecutive, overlapping, septal necks (sn1, sn2). **B**. Detail of **A** to show: nacreous (nac1) and prismatic

(pr1) layers of a septal neck (sn1); spherulitic-prismatic (sph2), nacreous (nac2) and prismatic (pr2) layers of the succeeding septal neck (sn2); and spherulitic-prismatic layer (sph.conn) of the succeeding connecting ring (conn). Scale bars: **A** – 1mm, **B** – 0.1 mm.

Fig. 2. **A**, **B**. *Dideroceras wahlenbergi* (Foord, 1887). **A**. Median section of two consecutive septal necks, showing nacreous (nac1) and prismatic (pr1) layers of one septal neck, and spherulitic-prismatic (sph2), nacreous (nac2) and prismatic (pr2) layers of the succeeding septal neck. The inner surface of the latter neck is coated by the spherulitic-prismatic layer (sph.conn3) of the succeeding connecting ring. **B**. Detail of the upper part of Fig. 1A (rectangled there) to show two consecutive, overlapping, septal necks (sn1, sn2), and connecting rings (sph.conn2, sph.conn3). Note that the connecting rings are composed only of the spherulitic-prismatic layer. Scale bar: 0.1 mm.

the prisms have mostly been dissolved, but their shapes are shown as impressions in the phosphatic infilling of the interspaces (pr1, pr2 in Fig. 1B; pr in Fig. 6A). The
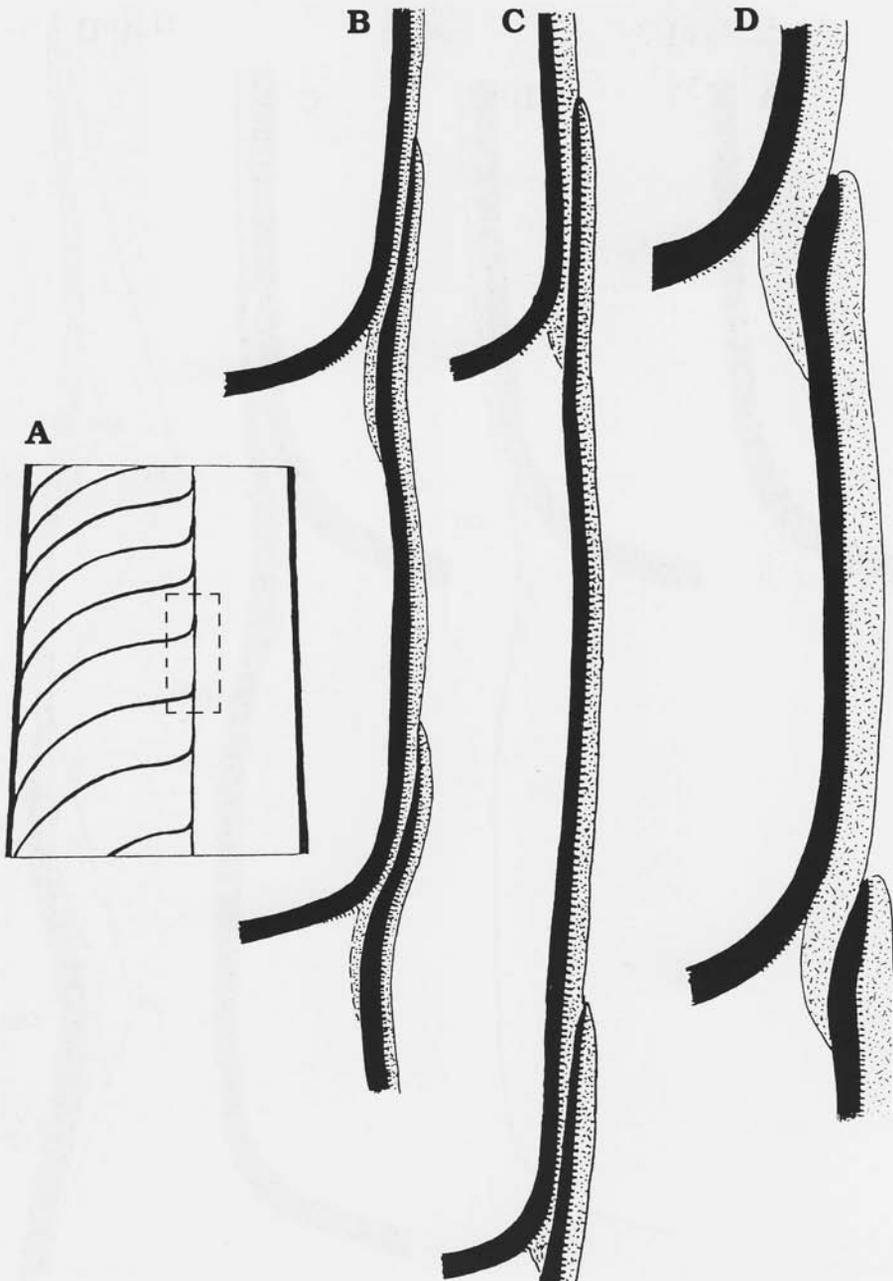
Fig. 3. Diagrammatic median sections of septal necks and connecting rings. **A, B**. *Dideroceras wahlenbergi* (Foord, 1887). **C**. *Suecoceras barrandei* (Dewitz, 1880). **D**. *Anthoceras vaginatum* (Schlotheim, 1820).

prisms are composed of needle-shaped crystallites, oriented at about right angles to the inner surface of the neck. The prismatic layer continues to the adapical surface of the septum, adjacent to the siphuncle (pr1 in Fig. 2A).
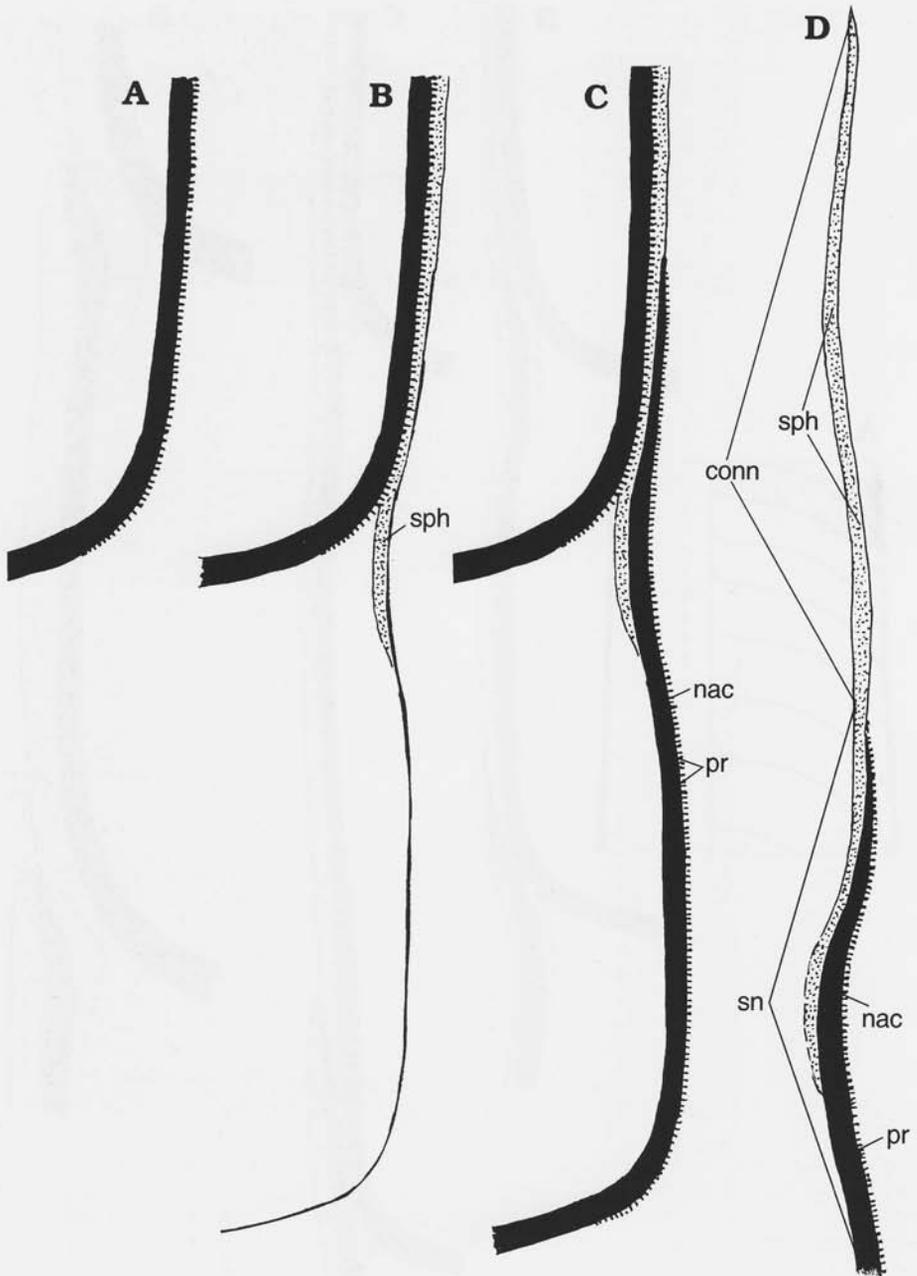
Fig. 4. **A–D**. *Dideroceras wahlenbergi* (Foord, 1887). **A**. Septal neck. **B**. Formation of the spherulitic-prismatic layer (sph) of the succeeding septal neck and connecting ring. **C**. Formation of the nacreous (nac) and prismatic (pr) layers of the septal neck. **D**. Complete septal neck (sn) and connecting ring (conn).

The nacreous layer is thick and constitutes the main portion of the septal neck (nac1, nac2 in Figs 1B, 2A). In the adapical direction it decreases gradually in
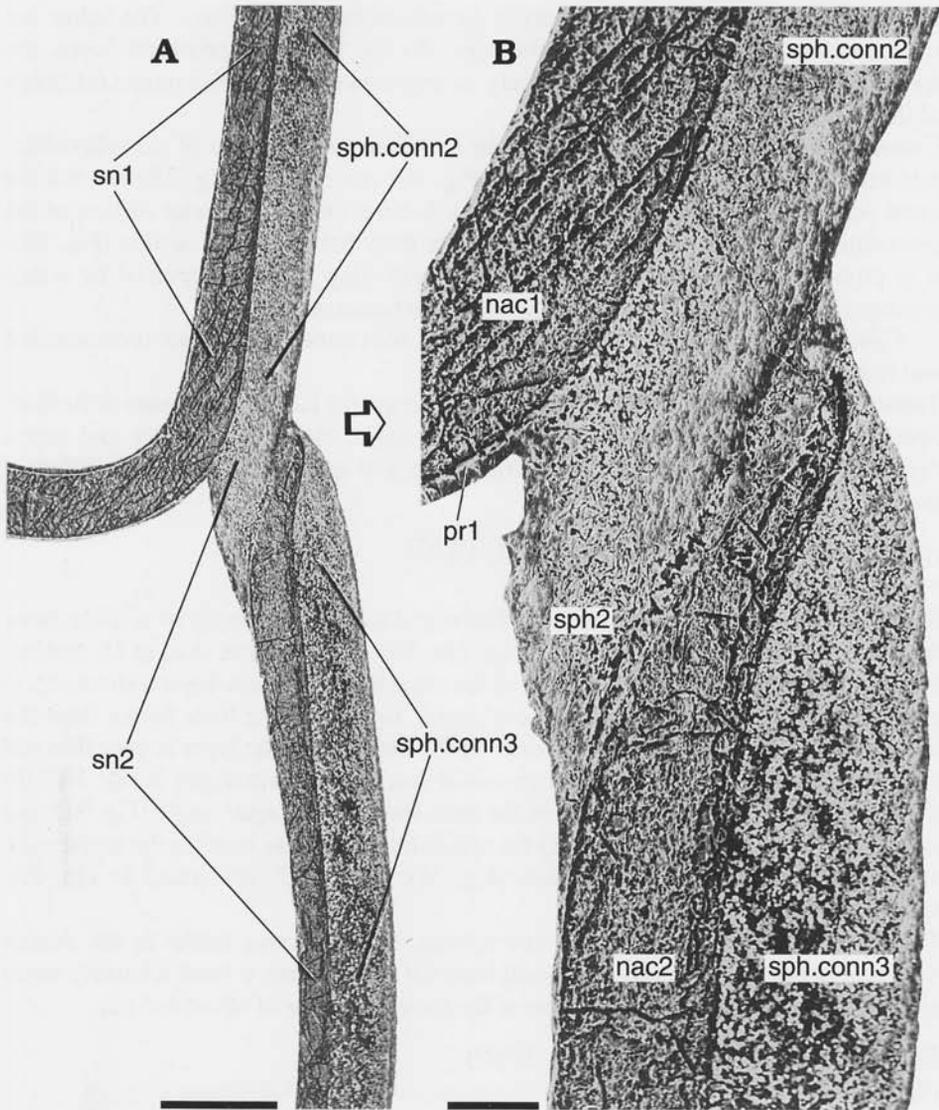
Fig. 5. **A**, **B**. *Anthoceras vaginatum* (Schlotheim, 1820). **A**. Median section of the siphuncle to show comparatively short septal necks (sn1, sn2), and thick spherulitic-prismatic layer of the neck and connecting ring (sph.conn2, sph.conn3). **B**. Detail of A. Note the thin prismatic layer (pr1) of the septal neck, thick spherulitic-prismatic layer of the septal neck (sph2), and connecting ring (sph.conn2, sph.conn3). Scale bars: **A** – 0.5 mm, **B** – 0.1 mm.

thickness, forming an acute angle at the distal end of the neck (nac2 in Fig. 2B). In vertical section the nacreous tablets are arranged in columns, typical of columnar nacre (nac2 in Fig. 2A).

The outer spherulitic-prismatic layer covers the outer surface of the neck, being in contact with the nacreous layer of the neck (sph2 in Figs 1B, 2A). It is composed

of needle-shaped crystallites, arranged in spherulites and prisms. The latter are separated by smaller or larger interspaces. As for the inner prismatic layer, the spherulites and prisms are shown mainly as impressions in the phosphatic infillings of the interspaces.

Connecting ring. — The connecting ring is a direct continuation of the spherulitic-prismatic layer of the septal neck (sph in Fig. 4D; sph.conn2 in Fig. 2B) and has the same porous structure (sph.conn in Fig. 6A). It covers the entire inner surface of the preceding septal neck, being somewhat thinner than that in median section (Fig. 3B). It is probable that the inner surface of the connecting ring was covered by a thin glycoprotein (conchiolin) sheet that has not been preserved.

Consecutive growth stages of the septal neck and connecting ring are reconstructed and illustrated in Fig. 4A–C.

Taxonomic remarks. — *Dideroceras wahlenbergi* still lacks an adequate definition. Specimens which show similarities in apical angle, siphonal diameter and septal distances occur in the latest Early Ordovician and earliest Middle Ordovician of Baltoscandia.

Anthoceras vaginatum (Schlotheim, 1820)
Figs 3D; 5A, B.

Septal neck and connecting ring. — The septal neck has a length of slightly more than the distance between two septa (Figs 3D, 5A), being shorter than in *D. wahlenbergi* and *S. barrandei*. It is composed of the same three aragonite layers. However, in comparison with those in *D. wahlenbergi* and *S. barrandei*, the three layers show the following differences in their thickness: (a) the inner prismatic layer is very thin and can be recognized clearly only at the proximal portion of the neck (pr1 in Fig. 5B); (b) the nacreous layer in the distal end of the neck forms a less acute angle (Fig. 3D; sn2 in Fig. 5A; nac2 in Fig. 5B); and (c) the spherulitic-prismatic layer in the septal neck and connecting ring is much thicker (Fig. 3D; sph.conn2, sph.conn3 in Fig. 5A; sph.conn2, sph.conn3 in Fig. 5B).

Taxonomic remarks. — At least two species of *Anthoceras* occur in the Aluoja Substage of the Harku quarry. The shell material studied here is from relatively small specimens, with diameters at the base of the living chamber of about 4–5 cm.
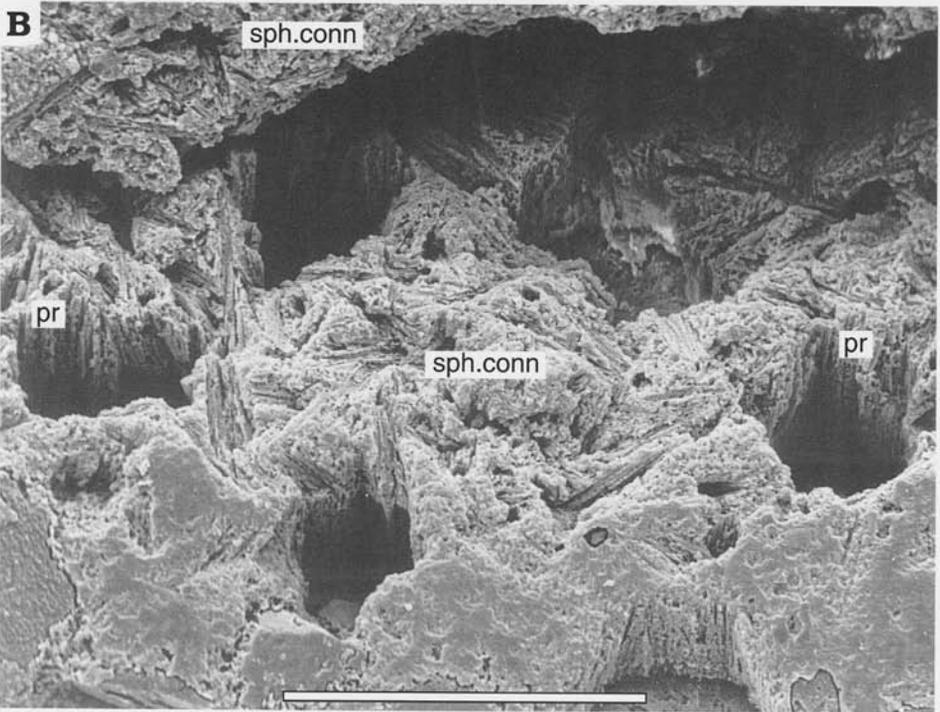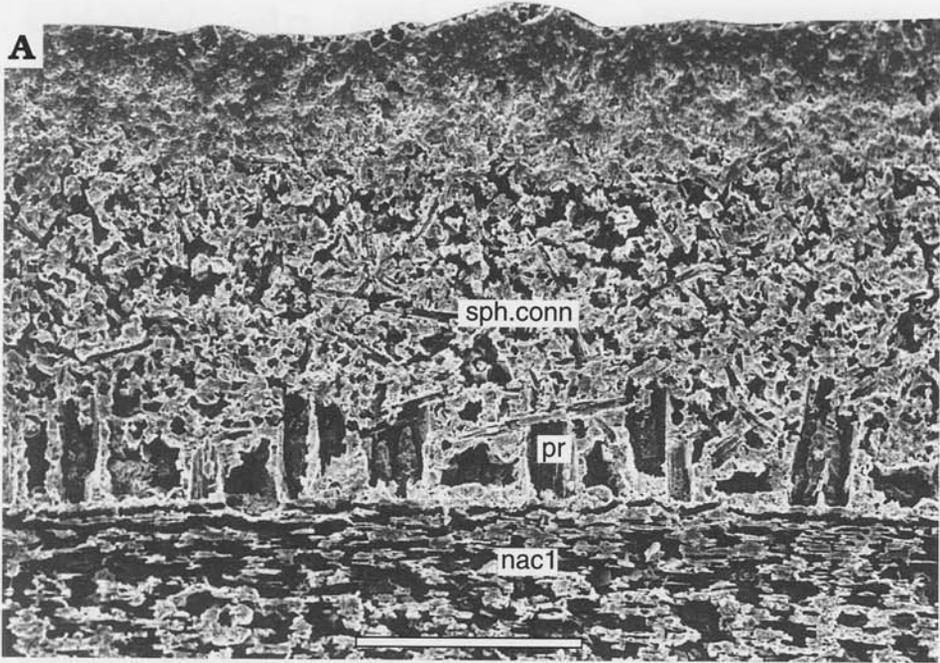
Suecoceras barrandei (Dewitz, 1880)
Figs 3C, 6B.

Septal neck and connecting ring. — The septal neck has similar length and structure as that in *D. wahlenbergi* (compare Fig. 3B and 3C). The structure and thickness of the connecting ring also agrees with that in *D. wahlenbergi*. The porous structure of the prismatic layer of the septal neck and the spherulitic-prismatic layer of the connecting ring is illustrated in Fig. 6B (pr, sph.conn). The impressions of prisms and spherulites, seen in the phosphatic infillings of the interspaces, clearly show the size and orientation of the crystallites.

Fig. 6. **A**. *Dideroceras wahlenbergi* (Foord, 1887), detail of the siphuncular wall, showing the nacreous (nac) and prismatic (pr) layers of a septal neck, in contact with a thick spherulitic-prismatic layer (sph.conn) of the succeeding connecting ring. **B**. *Suecoceras barrandei* (Dewitz, 1880), detail of the inner prismatic layer (pr) of a neck, and spherulitic-prismatic layer of the succeeding connecting ring (sph.conn). Note that

the acicular crystallites in prisms and spherulites are mostly dissolved and visible as imprints on the phosphatic infillings of the interspaces between them. Scale bar: 0.1 mm.
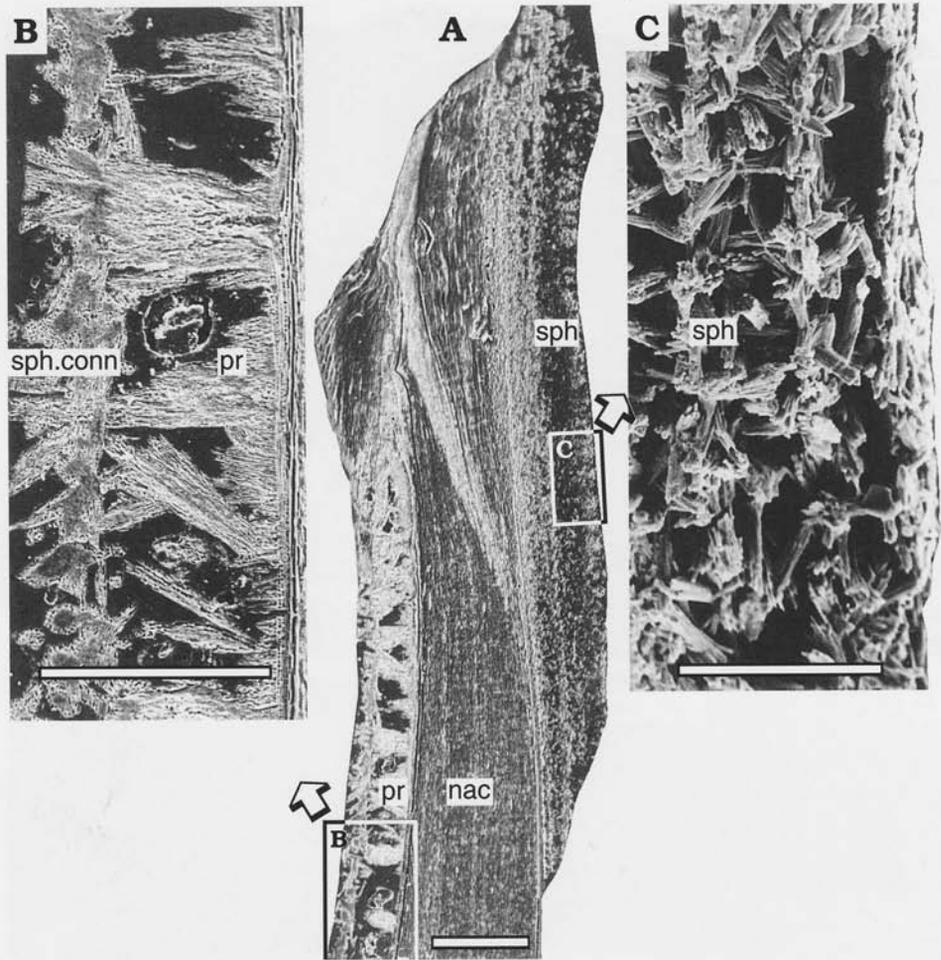
Fig. 7. A–C. *Nautilus pompilius* (Linné, 1758). **A**. Distal portion of the septal neck, showing three aragonite layers: outer spherulitic-prismatic (sph), nacreous (nac), and inner prismatic (pr). **B**. Detail of **A** to show the inner prismatic layer (pr), coated on its inner surface by the spherulitic-prismatic layer (sph.conn) of the succeeding connecting ring. **C**. Detail of **A** to show the outer spherulitic-prismatic layer (sph.conn) of the septal neck. Scale bars: **A** – 0.2 mm; **B**, **C** – 0.1 mm.

Taxonomic remarks. — This species is characterized by its small apical angle, long septal distances, and pitted surface of the wrinkle layer of the shell wall.

Comparison with Recent *Nautilus* and *Spirula*

The septal neck in *Nautilus* is composed of the same three aragonite layers as that in endocerids: outer spherulitic-prismatic, nacreous, and inner prismatic (sph, nac, pr in Figs 7A, 9A). The three layers occur also in the septal neck of *Spirula*, but the inner prismatic and outer spherulitic-prismatic layers there have a somewhat shorter exten-
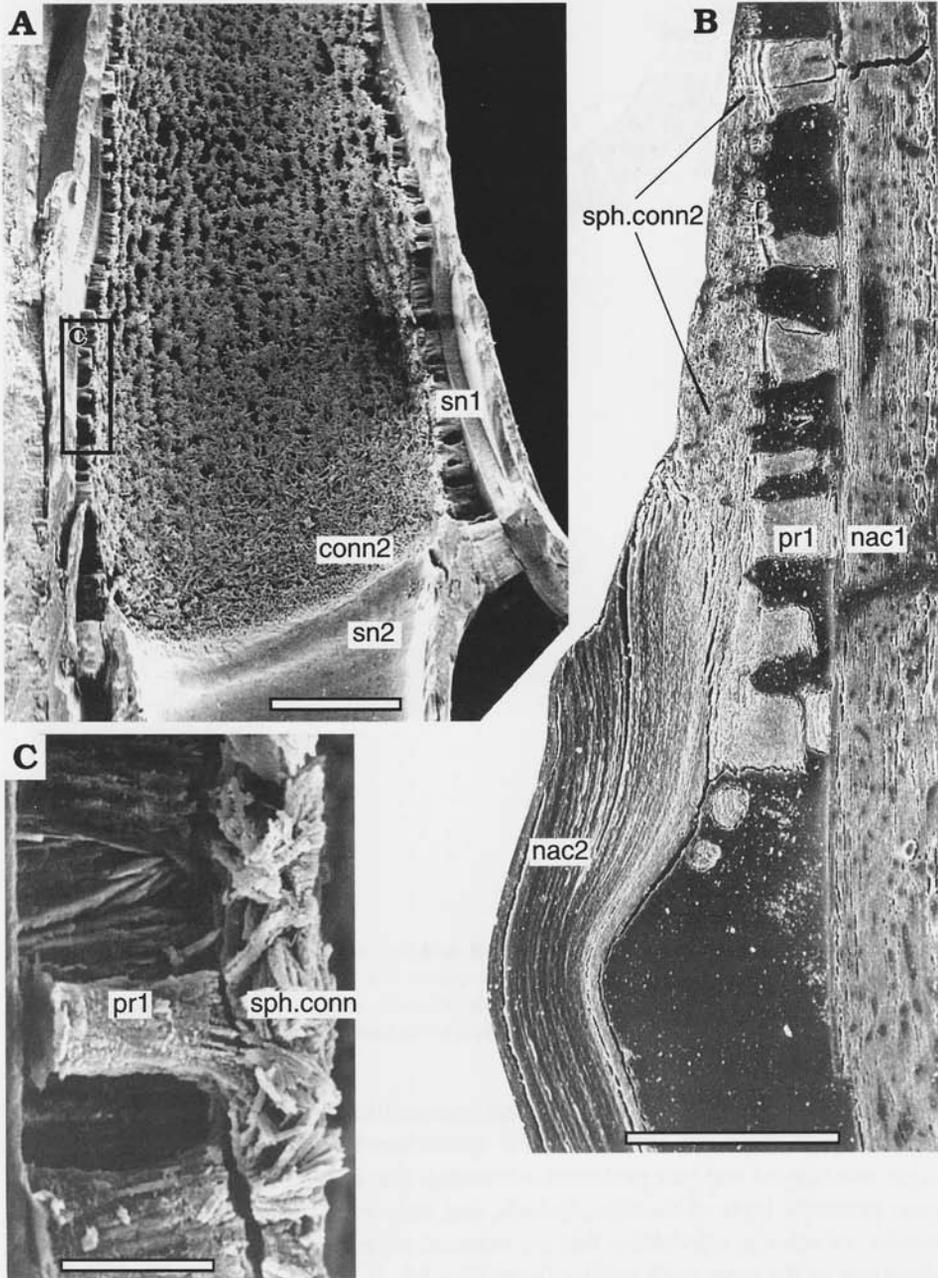
Fig. 8. **A–C**. *Spirula spirula* (Linné, 1758). **A**. General view on the siphuncle, cut medially to show two consecutive septal necks (sn1, sn2) and a connecting ring (conn2). **B**. Apical end of a septal neck, composed mainly of the nacreous layer (nac2); the inner prismatic layer is not developed at the distal end of the neck, but can be seen on the inner surface of the succeeding neck (pr1); the spherulitic-prismatic layer (sph.conn2) forms the connecting ring. **C**. Detail of **A** to show the inner prismatic layer (pr1) of a septal neck and the spherulitic-prismatic layer (sph.conn) of the succeeding connecting ring. Scale bars: **A** – 0.2 mm, **B** – 0.02 mm, **C** – 0.1 mm.
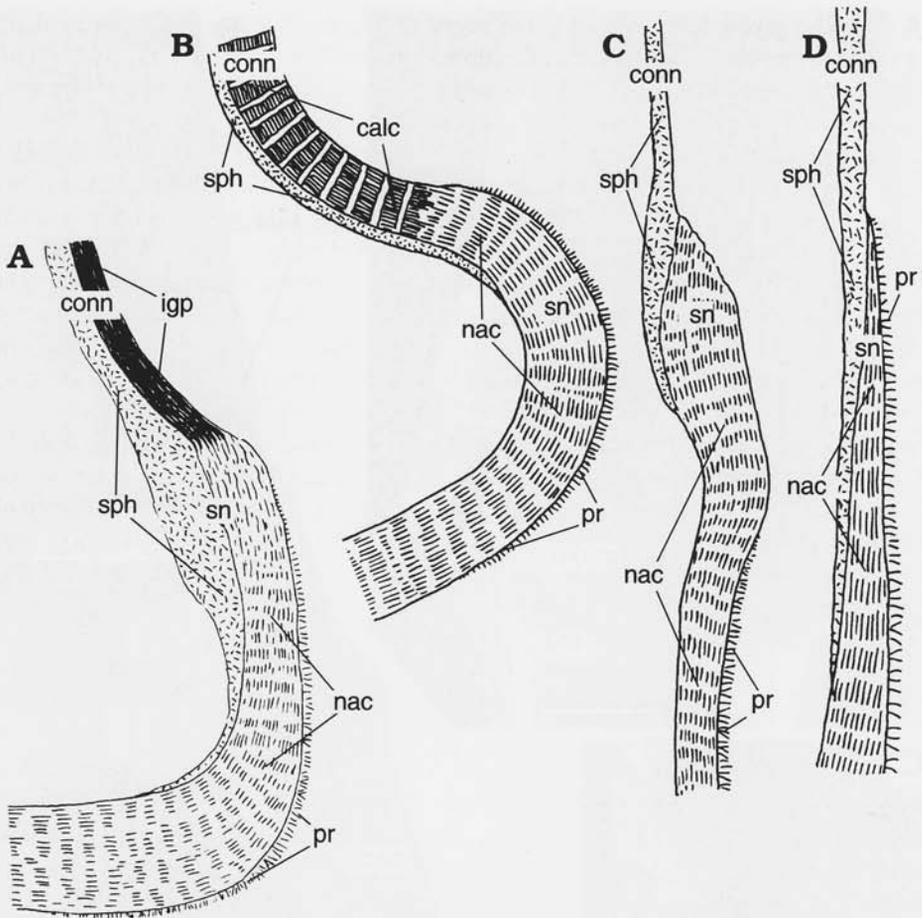
Fig. 9. Comparision between the structure of septal neck (sn) and connecting ring (conn) in: *Nautilus pompilius* (**A**), actinocerid *Ormoceras* (**B**), *Spirula spirula* (**C**), and endocerid *Dideroceras* (**D**); nac – nacreous layer, pr – prismatic layer, sph – spherulitic-prismatic layer, calc – calcified inner glycoprotein layer of connecting ring, igp – uncalcified, inner glycoprotein layer of connecting ring.

sion (Fig. 9C). In *Nautilus*, *Spirula*, and endocerids, the outer spherulitic-prismatic layer consists of prisms and incomplete spherulites that are separated by smaller or larger interspaces and lack preferred orientation (see also Mutvei 1964a, 1972). In the inner prismatic layer of *Nautilus*, *Spirula*, and endocerids, the prisms are composed of bundles of acicular crystallites that are oriented either at right angles, or more or less obliquely, to the inner neck surface (pr in Figs 6A, B, 7A, B; pr, pr1 in Fig. 8B, C).

Thus, by the Early Ordovician, the structure of the endocerid septal neck had already become practically identical to that in Recent *Nautilus* and *Spirula* (sn in Fig. 9A, C, D).

The connecting ring of *Nautilus* consists of an outer spherulitic-prismatic layer (sph.conn in Fig. 7B) and an inner, uncalcified, comparatively thick, glycoprotein (conchiolin) layer (igp in Fig. 9A). The inner layer is a direct continuation of the

interlamellar glycoprotein sheets in the nacreous layer of the neck (nac), with alone provided the mechanical strength of the siphuncle needed to withstand the hydrostatic pressure corresponding to depths of 600–700 m. In endocerids the inner glycoprotein layer was probably thin and therefore not preserved.

The connecting ring in *Spirula* shows the closest similarity to that in endocerids. Its main component is the porous spherulitic-prismatic layer in both taxa (sph.conn in Figs 6A, B, 9C, D; sph.conn2 in Fig. 8B; sph.conn in Fig. 8C). However, this layer is much thicker in endocerids than in *Spirula*. (compare sph.conn in Figs 6A, 8C). What the functional significance was of this thickening is still unknown. One may speculate that the thick porous layer was needed as an enlarged reservoir for cameral liquid, probably because the osmotic pumping ability of the siphuncular epithelium was less efficient than that in *Nautilus* and *Spirula*. A similarly thick spherulitic-prismatic layer also occurs in tarphycerids and ellesmerocerids.

The inner-surface of the spherulitic-prismatic layer of the connecting ring in *Spirula* is covered by a thin glycoprotein sheet which is difficult to distinguish in dry shells. A similar glycoprotein sheet probably occurred also in endocerids. The long septal necks in *Spirula* provide sufficient mechanical strength against hydrostatic pressure. This was also the case in endocerids. The thick glycoprotein inner layer of the connecting ring, as occurring in *Nautilus*, is therefore not needed.

Comparison with actinocerids

The structure of the siphonal tube in some Ordovician and Silurian actinocerids has been recently dealt with by the present author (Mutvei 1997). As in *Nautilus*, *Spirula*, and in endocerids, the septal neck (sn) is composed of the outer spherulitic-prismatic layer, the nacreous layer, and the inner prismatic layer (sph, nac, pr in Fig. 9B). In the connecting ring (conn), the outer spherulitic-prismatic layer is thin (sph). The main portion of the connecting ring is composed of a layer of calcified lamellae (calc). The latter layer is a direct continuation from the nacreous layer of the septal neck (nac), and corresponds with the inner glycoprotein layer of *Nautilus* (compare Fig. 9A, B). In order to make the calcified connecting ring of actinocerids permeable for cameral liquid, the lamellar layer is perforated by numerous pores (calc in Fig. 9B; Mutvei 1997: figs 1A, 2B, C, 7D). The cavities of these pores were probably traversed by glycoprotein sheets.

The inflated connecting rings in actinocerids have a great surface area which increases the number of pores across it, probably increasing the emptying rates and permeability of the cameral liquid. In addition, the calcified ring increased the mechanical strength against hydrostatic pressure (Mutvei 1997). It is probable that actinocerids had a more advanced system for chamber emptying than endocerids.

Conical endosiphonal deposits

The conical endosiphuncular deposits ('endocones') are characteristic of endocerids. The present author (Mutvei 1964b) showed that these deposits were secreted by the
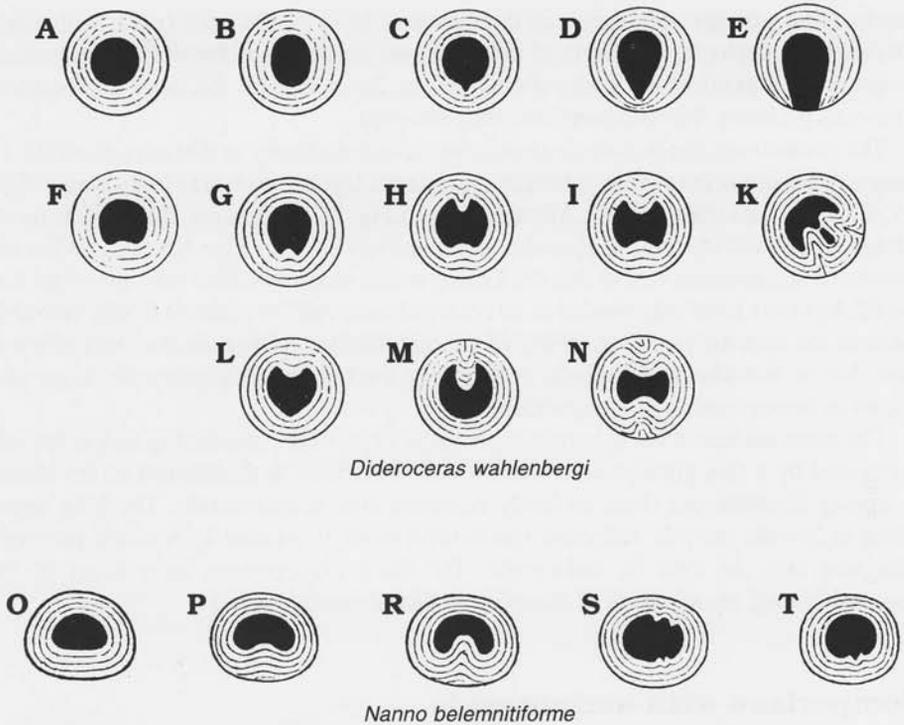
Dideroceras wahlenbergi

Nanno belemnitiforme

Fig. 10. Diagrammatic representation of cross-sections of conical endosiphuncular deposits to show intraspecific variations. **A–N.** *Dideroceras wahlenbergi* (Foord, 1887). **O–T.** *Nanno belemnitiforme* (Holm, 1885).

siphuncular epithelium, and that they have a prismatic structure, with more or less distinct growth lamellae ('endocones').

Intraspecific variations of the shape of these deposits have been studied by the present author in two species: *Dideroceras wahlenbergi* and *Nanno belemnitiforme* (Mutvei 1964b). The material of the former species comprises more than one hundred isolated siphuncles, found on a bedding plane of the Valastean Substage of Kunda Stage, Early Ordovician, northern part of the Island of Öland (Hälludden), Sweden (Jaanusson & Mutvei 1982). In the majority of specimens belonging to the two species, the endosiphuncular deposit has a practically uniform thickness on all sides (Figs 10A, B, O). Less frequently, the deposit is considerably thickened in either its ventral or dorsal portion, or both. As a consequence, the inner surface of the deposit forms one or two crests (Fig. 10F–N, P–T). The formation of these crests is often initiated by a secretion of a thin and high, glycoprotein crest on the inner surface of the ectosiphuncle, termed the initial conchiolin crest (Mutvei 1964b: con.cr in text-figs 5–7, pls 4, 5: 3). In a few cases, finally, the deposit is thinner dorsally than on the other sides. The inner surface of the deposit here forms a more or less conspicuous groove (Fig. 10C–E).

Dzik (1984) confirmed these observations, and illustrated considerable intraspecific variations in the endosiphuncular deposit of *Dideroceras glauconiticum* (Dzik 1984: pp. 24–30, fig. 3). On the other hand, Flower (e.g., 1964, 1968) neglected such

variations and used minor structural and morphological differences in the endosiphuncular deposits as major diagnostic features.

Taxonomic importance has also been ascribed to the radially oriented endosiphoblades within the endosiphuncular deposits. As pointed out by Mutvei (1964b: p. 385), certain 'endosiphoblades' seem to represent post-mortem fractures (e.g., 'blattartige Gebilde', Holm 1885: pl. 3: 1g–i; Balashov 1968: pls 19, 27; Flower 1964: fig. 16), whereas other appear to correspond to the initial conchiolin crests (e.g., 'vertical blades', Flower 1968: pl. 17).

Discussion

Already 450–500 my ago, in the Early Ordovician, the siphuncle of several nautiloid taxa, including endocerids, attained a structure which has remained virtually unchanged to the present day.

Flower (1941, 1964) and Teichert & Glenister (1954) described, in several endocerid taxa, structurally different layers within the spherulitic-prismatic layer of the connecting ring. In addition, Flower (1941: p. 157) described in some other taxa 'a pattern in which dense and apparently amorphous material termed the eyelet, tended to concentrate in the tip of the ring'.

In the three endoceroid species here studied the spherulitic-prismatic layer of the connecting ring does not show any structural differentiations into layers or dense portions ('eyelets'), contrary to what has been previously reported (Flower 1941). Nor do such structural differentiations occur in Recent *Nautilus* and *Spirula*. It is therefore probable that the structural differentations may be the result of diagenesis.

The conical endosiphuncular deposits in endocerids show considerable intraspecific variation. These variations have been previously studied in *Dideroceras wahlenbergi* and *Nanno belemnitiforme* (Mutvei 1964b), and confirmed by Dzik (1984) in *Anthoceras vaginatum* and *Dideroceras glauconiticum*. Correspondingly large intraspecific variation occurs also in the actinocerid annular endosiphuncular deposits (Mutvei 1964b, 1997). Consequently, the morphology of the endosiphuncular deposits should be used with caution as a diagnostic (specific or generic) character.

Acknowledgements

References

Balashov, Z.G. 1968. Endoceratoidei Ordovika SSSR [in Russian]. 278 pp. Leningrad University Publication, Leningrad.

Dzik, J. 1984. Phylogeny of Nautiloidea. — *Palaeontologia Polonica* **45**, 3–203.

Flower, R.H. 1941. Notes on structure and phylogeny of eurysiphonate cephalopods. — *Palaeontographica Americana* **3**, 1–56.

Flower, R.H. 1947. Holochoanites are endoceroids. — *Ohio Journal of Sciences* **47**, 155–172.

Flower, R.H. 1964. Nautiloid shell morphology. — *New Mexico Bureau of Mines, Memoir* **13**, 1–78.

Flower, R.H. 1968. Some additional Whiterock cephalopods. — *New Mexico Bureau of Mines, Memoir* **19**, 19–55.

Holm, G. 1885. Die innere Organisation einiger silurischer Cephalopoden. — *Palaeontologische Abhandlungen* **3**, 1–27.

Jaanusson, V. & Mutvei, H. 1982. Ordovician of Öland. *Guide to Excursion 3, IV International Symposium on the Ordovician System, Oslo*, 1–23.

Mutvei, H. 1964a. On the shells of *Nautilus* and *Spirula* with notes on the shell secretion in non-cephalopod molluscs. — *Arkiv för Zoologi. Serie 2*, **16**, 221–278.

Mutvei, H. 1964b. On the secondary internal calcareous lining of the wall of the siphonal tube in certain fossil 'nautiloid' cephalopods. — *Arkiv för Zoologi. Serie 2*, **16**, 375–424.

Mutvei, H. 1972. Ultrastructural studies of cephalopod shells. Part I. The septa and siphonal tube in *Nautilus*. — *Bulletin of the geological Institutions of the University of Uppsala. New Series* **3**, 263–272.

Mutvei, H. 1997. Characterization of actinoceratoids (Mollusca: Cephalopoda) by their siphuncular structure. — *Lethaia* **29**, 339–348.

Teichert, C. 1964. Endoceratoidea. *In:* R.C. Moore (ed.), *Treatise on Invertebrate Paleontology*, Part K, 160–189. Geological Society of America Boulder and University of Kansas Press, Lawrence.

Teichert C. & Glenister, B.F. 1954. Early Ordovician cephalopod fauna from northwestern Australia. — *Bulletins of American Paleontology*, **35**, 7–112.

Budowa syfona ordowickich endoceratydów

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Streszczenie

Fosfatyzacja jest wyjątkowo korzystnym stanem zachowania w przypadku aragonitowo-organicznych muszli mięczaków, umożliwiającym zachowanie wielu pierwotnych elementów. Ordowickie endoceratydy *Dideroceras wahlenbergi* (Foord, 1887), *Anthoceras vaginatum* (Schlotheim, 1820) i *Suecoceras barrandei* (Dewitz, 1880) ze sfosfatyzowanych wapieni północnej Estonii posłużyły do szczegółowych badań w SEM struktur syfonalnych i porównania ich ze współczesnymi głowonogami z rodzajów *Nautilus* i *Spirula*. Lejek syfonalny u tych endoceratydów jest zbudowany z trzech różnych warstw aragonitowych: zewnętrznej warstwy sferolityczno-pryzmatycznej, środkowej perłowej i wewnętrznej pryzmatycznej. Rurka syfonalna łącząca poszczególne lejki jest przedłużeniem sferolityczno-pryzmatycznej warstwy lejka. Jej wewnętrzna powierzchnia była prawdopodobnie pokryta cienką, glikoproteinową (konchiolinową) wyściółką. Nie zaobserwowano cech, opisywanych wcześniej: warstwowania ani zgęstnień („eyelets") w obrębie sferolityczno-pryzmatycznej warstwy rurki syfonalnej. Struktury te należy prawdopodobnie uznać za artefakty powstałe w wyniku diagenezy. Ogólny plan budowy syfona endoceratydów jest podobny do planu budowy spiruli i łodzika. Stożkowate złogi endosyfonalne (endokony) wykazują u endoceratydów znaczne wewnątrzgatunkowe zróżnicowanie, dlatego też ich wartość diagnostyczna na poziomie rodzajowym i gatunkowym jest ograniczona.