

Connecting ring structure and its significance for classification of the orthoceratid cephalopods

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The connecting ring in orthoceratids is composed of two calcified layers: an outer spherulitic-prismatic and an inner calcified-perforate. The spherulitic-prismatic layer is a direct continuation of that layer in the septal neck, whereas the calcified-perforate layer is a structurally modified continuation of the nacreous layer of the septal neck. The latter layer is traversed by numerous pores which are oriented either transversally to the siphuncular surface, or have a somewhat irregularly anastomosing course. The connecting ring structure is positively correlated to the dorsal position of the scars of the cephalic retractor muscles. A similar type of connecting ring and a dorsal position of retractor muscle scars also occur in lituitids, previously assigned to tarphyceratids, and in baltoceratids, previously assigned to ellesmeroceratids. These two taxa are therefore included in the suborder Orthoceratina, which, together with the suborder Actinoceratina, are assigned to the order Orthoceratida Kuhn, 1940.

Key words: Orthoceratina, Actinoceratina, siphuncular structure, connecting ring.

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Introduction

Shell structure in most Paleozoic nautiloids is imperfectly preserved owing to diagenetic transformation of shell aragonite into calcite. This has made it difficult to use microstructural features for taxonomy.

Mutvei (1972, 1997a, 1998) has shown that the connecting ring in Recent *Nautilus* is a structurally modified continuation of the septal neck. This is also the situation in fossil nautiloids. Details of the connecting ring structure have previously been described by the present writer in three actinoceratid families (Mutvei 1997a), one orthoceratid family (Mutvei 1997b) and one endoceratid family (Mutvei 1998). A short review on the connecting ring structure in tarphyceratids, orthoceratids and actinoceratids has been given in a fourth paper (Mutvei in press). In the present paper the connecting ring structure is described in nine orthoceratid families, including ten taxa. Furthermore, the position of the scars of the cephalic retractor muscles in orthoceratids is reviewed and used, together with connecting ring structure, for characterisation of higher systematic groups.

Material and methods

The following orthoceratids were studied: Ordovician: *Orthoceras regulare* Schlotheim, 1820, *O. scabridum* Angelin, 1880

(Orthoceratidae); “*Michelinoceras*” sp. (Michelinoceratidae); *Geisonoceras kinnekullense* (Foord, 1887) (Geisonoceratidae); *Polygrammoceras oelandicum* Troedsson, 1932 (Troedssonellidae); *Lituites* sp., *Rhynchoceras* sp. (Lituitidae); *Cochlioceras* spp. (Baltoceratidae). Silurian: *Dawsonoceras* sp. (Dawsonoceratidae); *Lycoceras* spp. (Paraphragmitidae); *Danacoceras gotlandense* Mutvei, 1998 (Nartheoceratidae).

The shells were cut medially, tangentially and transversely. Section surfaces were ground with carborundum, polished with aluminum oxide, and studied in incident light using a Wild M400 photomicroscope. The preservation did not allow studies with the scanning electron microscope, except in one shell of *Orthoceras regulare* and one shell of “*Michelinoceras*” sp.

Shell preservation

Shells of Recent *Nautilus* and *Spirula*, as well as those of fossil nautiloids and ammonoids, are composed of aragonite. In Ordovician and Silurian nautiloids, the shell aragonite is usually diagenetically replaced by calcite and the shell glycoprotein matrix is completely destroyed. Even in favourable cases only traces of the original shell structure are preserved after this replacement. However, if phosphate was available in the depositional environment, aragonite can be transformed into calcium phosphate in early diagenesis owing to

topotactic reaction of aragonite to hydroxyapatite and similarity of their crystal structures (Eysel and Roy 1975). Therefore, to carry out structural studies of fossils with originally aragonitic skeletons, it is essential to find sedimentary environments where this process has taken place.

Phosphatization occurred more easily in porous structures, such as connecting rings, than in solid septal necks, shell wall and septa. In porous structures small amounts of phosphate seem to have been sufficient to allow replacement of the original aragonite.

Highly phosphatized limestones occur in the Lower Ordovician of the island of Öland, Sweden and the Middle Ordovician of northern Estonia. On Öland not only are nautiloid shells well preserved but also receptaculitid skeletons (Nitecki et al. 1999) and other fossils with aragonitic skeletons. The structural preservation is less favourable in Silurian nautiloids from the island of Gotland even though their shells are externally well preserved.

General characteristics of siphuncular structure

Mutvei (1957, 1964, 1972, 1997a, b, 1998) has described the septal neck in *Nautilus* as consisting of three calcareous layers: a thin inner prismatic layer, a thick nacreous layer, and a thin outer spherulitic-prismatic layer. The prismatic and spherulitic-prismatic layers are both highly porous. Towards the distal end of the septal neck the organic matter in the nacreous layer gradually increases and the layer loses its typical nacreous structure, becoming semi-prismatic. The connecting ring is a direct, structurally modified continuation of the septal neck. It consists of two layers: an outer spherulitic-prismatic layer that is a continuation of that layer from the septal neck, and an inner, fibrous, glycoprotein (conchiolin) layer that is an uncalcified continuation of the nacreous layer of the septal neck.

The septal neck in orthoceratids and actinoceratids consists of the same three layers as that in *Nautilus*: an inner prismatic, a nacreous, and an outer spherulitic-prismatic (Mutvei 1997a, b, and in press). In some specimens the prismatic and spherulitic-prismatic layers are thin and therefore not clearly discernible. As in *Nautilus*, the spherulitic-prismatic layer of the neck continues into the wall of the connecting ring and forms its outer layer. The inner layer of the connecting ring is a continuation of the nacreous layer of the neck but, unlike the corresponding layer in *Nautilus*, it is not a glycoprotein layer but a structurally modified, calcified layer perforated by pores termed the calcified-perforate layer. The pores show differences in shape, size and distribution in different taxa. During the lifetime, the pores were not open but traversed by a number of thin glycoprotein sheets (indicated in Mutvei 1997a: fig. 1B). The microscopic structure of the calcified-perforate layer is either granular or laminated.

Connecting ring structure and the position of retractor muscle scars

Ordovician orthoceratids

Orthoceras regulare (Schlotheim, 1820) (Orthoceratidae)

Figs. 1, 7A.

The material of this species comes from the Middle Ordovician Uhaku Stage, Kandle, northern Estonia. It comprises ten specimens collected by Gerhard Holm in the nineteenth century and previously studied by Troedsson (1931).

The wall of the connecting ring is about as thick as the septum and septal neck, and fully calcified (conn, sn in Fig. 1A, Fig. 7A). The outer spherulitic-prismatic layer is somewhat thinner than the inner calcified-perforate layer. A few long acicular crystallites from this layer project at various angles into the shell chamber (sph in Fig. 1B, D, Fig. 7A). The inner calcified-perforate layer is composed of phosphatic granules of various sizes and shapes (Figs. 1B, C, 7A). In paramedian section, the pores in this layer show a varying diameter and shape, the majority being more or less elongated in apical-oral direction (Figs. 1C, 7A). In cross-section, most pores penetrate the layer at right angles to the siphuncular surface, but some have an oblique course and some are branching (Figs. 1D, 7A). At the boundary to the spherulitic-prismatic layer the calcified-perforate layer has a more compact structure with smaller pores than in the main portion of the layer (Figs. 1D, 7A).

This species has paired dorsal retractor muscle scar (Dewitz 1879; Schröder 1881; Mutvei 1957).

Orthoceras scabridum (Angelin, 1880) (Orthoceratidae)

Figs. 2A–C, 7A.

The material comprises five shells from the Middle Ordovician Folkeslunda Limestone, Södra Bäck, island of Öland.

The outer spherulitic-prismatic layer and the inner calcified-perforate layer of the connecting ring have a similar structure to those in *O. regulare* (sph in Fig. 2B, Fig. 7A). The inner calcified-perforate layer is granular (cp in Fig. 2B, Fig. 7A). In median section, the pores have an irregular course and vary in diameter, in places branching into two (Figs. 2A, B, 7A). In paramedian section, the pore openings towards the siphuncular cavity vary in shape but are mostly elongated in apical-oral direction (Figs. 2C, 7A). As in *O. regulare* and other orthoceratids dealt with here, the structure of the outermost portion of the calcified-perforate layer is more compact than the main portion, due to smaller pores (Figs. 2A, B, 7A).

The retractor muscle scars are similar to those in *O. regulare* in being paired and situated dorsally (Rüdiger 1889; Mutvei 1957; Dzik 1984).

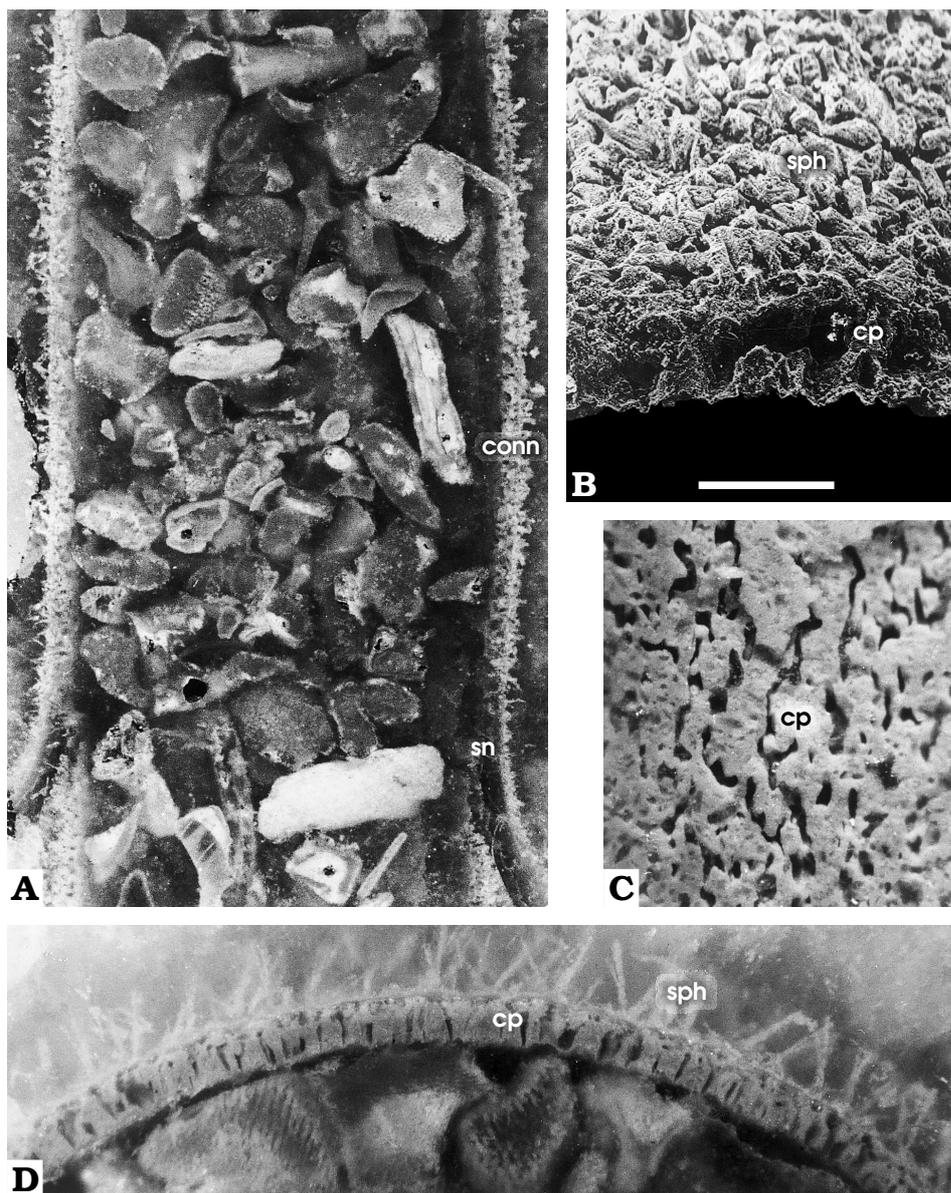


Fig. 1. A–D. *Orthoceras regulare* Schlotheim, 1820. A. Median section of a septal neck (sn) and connecting ring (conn), $\times 25$. B. SEM photograph of the surface and transverse section of a connecting ring to show a thin outer spherulitic-prismatic layer (sph) and a thick calcified-perforate layer (cp) with pores; scale bar 0.1 mm. C. Tangential section through the calcified-perforate layer (cp) of the connecting ring to show the number, size and outlines of the pores, $\times 50$. D. Transverse section of the connecting ring; note the pores in the calcified-perforate layer (cp) and the acicular crystallites in the spherulitic-prismatic layer, $\times 50$.

“*Michelinoceras*” sp. (Michelinoceratidae)

Fig. 3A–C.

The material comprises one fragmentary specimen, collected from the Middle Ordovician Lasnamägian Stage, Palmse, Estonia. The specimen has a 11 cm long proximal portion of its living chamber preserved. The shell diameter at the base of the living chamber is 3 cm. The cross section is circular and the apical angle is small. The siphuncle is central and its diameter is one-eighth of the shell diameter. Shell ornamentation is not preserved.

The wall of the connecting ring is somewhat thinner than the septal neck, and only the calcified-perforate layer can be recognized (cp in Fig. 3A–C). If the outer spherulitic-prismatic layer was originally present it must have been thin. On an oblique fracture plane through the siphuncle, the pores in the

calcified-perforate layer are narrow and elongated in an apical-oral direction (cp in Fig. 3A). As in *O. regulare* and *O. scabridum*, the outermost portion of the calcified-perforate layer seems to be more solid (cp in Fig. 3B, C) and to have smaller pores than the rest of the layer. This is often the only portion preserved. In contrast to other orthoceratids studied here, the calcified-perforate layer is not granular, but shows a lamellar structure in median section (cp in Fig. 3B, C). A similar lamellar structure was found in the calcified-perforate layer in three families of actinoceratids (Mutvei 1998: figs. 1, 5C, 6D, E).

In addition to the Palmse specimen, less well-preserved lamellar structure in the calcified-perforate layer of the connecting ring was observed in another, fragmentary, Estonian specimen from Moholm, Aserian Stage, Middle Ordovician.

Retractor muscle scars are unknown.

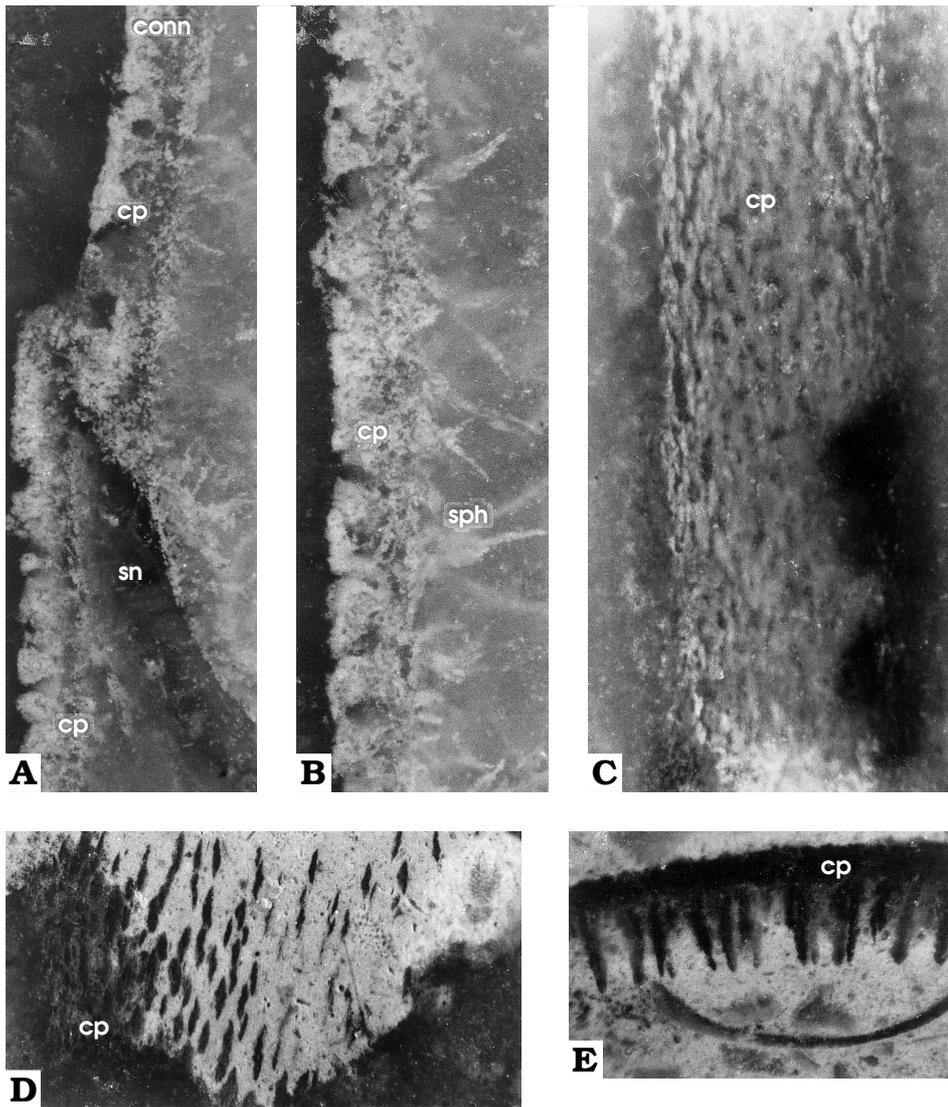


Fig. 2. A–C. *Orthoceras scabridum* Angelin, 1880. A. Median section of a septal neck (sn) and connecting ring (conn); note that the calcified-perforate layer (cp) of the connecting ring is a direct continuation of the nacreous layer of the septal neck, $\times 50$. B. Median section of a connecting ring to show the calcified-perforate layer (cp) with pores and the spherulitic-prismatic layer (sph), $\times 50$. C. Tangential section of a connecting ring to show numerous, elongated pores in the calcified-perforate layer (cp), $\times 50$. D, E. *Rynchorthisceras* sp. D. Tangential section of the calcified-perforate layer (cp) of the connecting ring to show numerous elongated pores, $\times 40$. E. Transverse section of the calcified-perforate layer (cp) with numerous pores, $\times 40$.

Polygrammoceras oelandicum Troedsson, 1932 (Troedssonellidae)

Fig. 4A, B.

The material comprises one shell of *P. oelandicum*, determined by Troedsson. It was collected from the Middle Ordovician Folkeslunda Limestone, Folkeslunda, island of Öland.

The wall of the connecting ring has about the same thickness as the septum and septal neck. The outer spherulitic-prismatic layer is thicker than that layer in *O. regulare* and *O. scabridum*, attaining about half of the thickness of the inner calcified-perforate layer (sph, cp in Fig. 4A). The inner calcified-perforate layer has a granular structure. In tangential section, the pores are numerous and elongated in the apical-oral direction (cp in Fig. 4B). Thus, the morphology of the pores is similar to that in other orthoceratids dealt with here. At the boundary to the outer spherulitic-prismatic layer, the calcified-perforate layer forms a brown lamella in which the pores decrease much in diameter (cp in Fig. 4A). In several places only this lamella of the connecting ring is preserved.

Retractor muscle scars are unknown.

The connecting ring structure in *Geisonoceras kinnekullense* (Foord 1887) (Geisonoceratidae) from the Lower Ordovician Kunda stage, Hälludden, island of Öland, is similar to that in *P. oelandicum*.

Lituities sp. (Lituitidae)

Figs. 4C, D, 7B.

The material of this species comprises four shells from the Middle Ordovician Kundan Stage, Kandle, Estonia.

The wall of the connecting ring is slightly thicker than the adjacent septum and septal neck. The spherulitic-prismatic layer has a typical porous structure and attains about half of the thickness of the calcareous-perforate layer (Fig. 7B). As seen in a tangential section, the pores in the latter layer are numerous, elongated in the apical-oral direction, and have a comparatively large diameter (cp in Fig. 4C, Fig. 7B). Also in transverse section, the pores in the calcified-perforate layer are large (cp in Fig. 4D, Fig. 7B). As in other orthoceratids described here, the

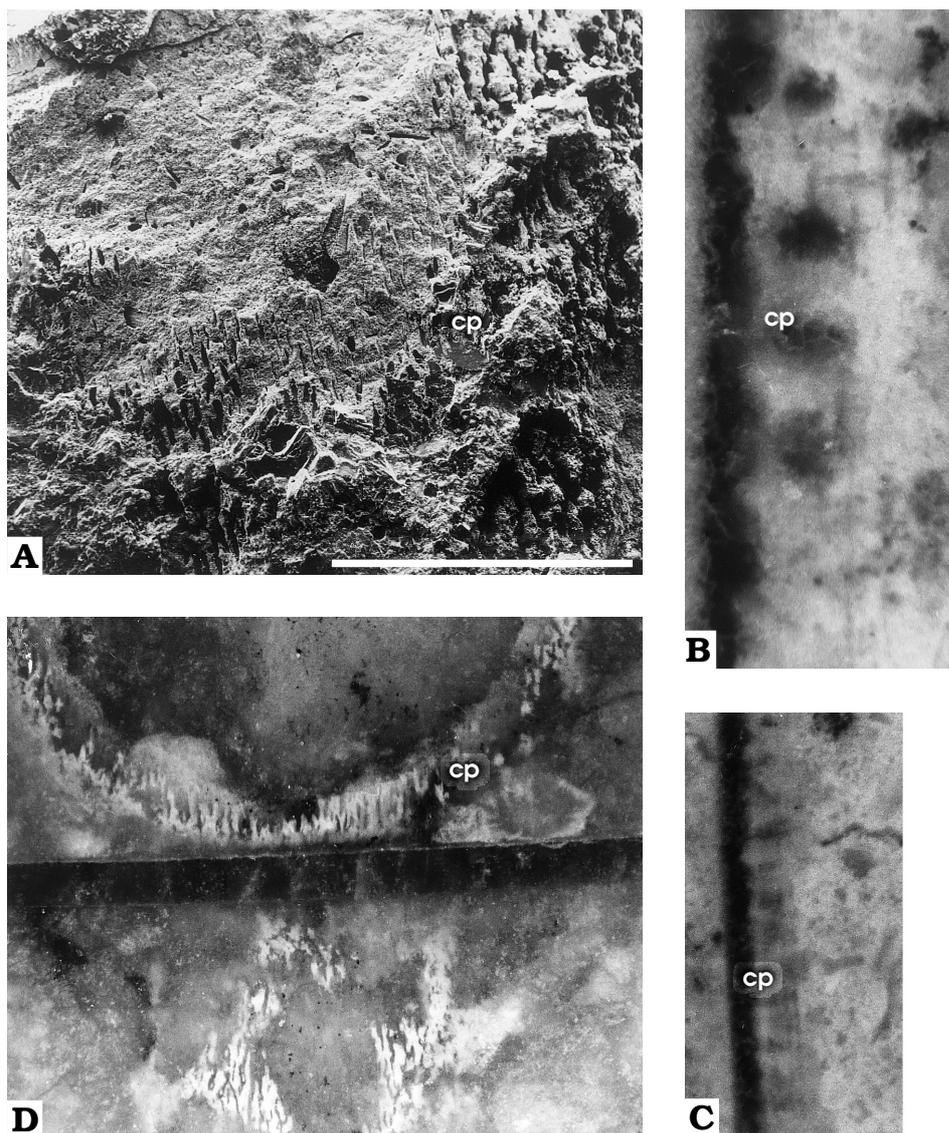


Fig. 3. A–C. “*Michelinoceras*” sp. A. SEM photograph of an oblique fracture plane of a connecting ring to show numerous elongated pores in the calcified-perforate layer (cp); scale bar 1 mm. B, C. Median sections of a connecting ring to show the lamellar structure of the calcified-perforate layer (cp), $\times 120$ and $\times 40$, respectively. D. *Dawsonoceras* sp. Paramedian section of a connecting ring to show numerous pores in the calcified-perforate layer (cp) of the connecting ring, $\times 50$.

outermost portion of the calcified-perforate layer has smaller pores and therefore a denser structure (Figs. 4D, 7B).

According to Schröder (1881) and Noetling (1882) the genus *Lituites* has a dorsal scar of the retractor muscle, similar to that in orthoceratids.

The family Lituitidae has previously been assigned to tarphyceratids (Flower and Kummel 1950; Furnish and Glenister 1964). Because this family has thin connecting rings, Dzik (1984) and King (1993) removed it from the tarphyceratids to the orthoceratids. The connecting ring structure, here described for the first time, and the dorsal position of retractor muscle scars, clearly confirm that Lituitidae has to be classified with orthoceratids.

Rhynchorthoceras sp. (Lituitidae)

Fig. 2D, E.

The material of this species is a single shell, collected from the Middle Ordovician Kundan Stage, Kandle, Estonia.

The connecting ring structure is similar to that in *Lituites* sp. In both tangential and transverse sections, the pores in the calcified-perforate layer (cp) are seen to be large and numerous (Fig. 2D, E).

This genus has similar paired dorsal scars of retractor muscles as *Lituites* (Sweet 1958).

Both *Lituites* and *Rhynchorthoceras* differ from other orthoceratids in having large pores in the calcified-perforate layer of the connecting ring.

Cochlioceras sp. (Baltoceratidae)

Figs. 5, 7C.

The material of this species comprises one well-preserved shell from Sjöstorp, island of Öland, Middle Ordovician Folkeslunda Limestone.

The outer spherulitic-prismatic layer of the connecting ring is thin at the distal end of the septal neck (sn, sph in Fig. 5A). Passing into the connecting ring, it increases rapidly in thick-

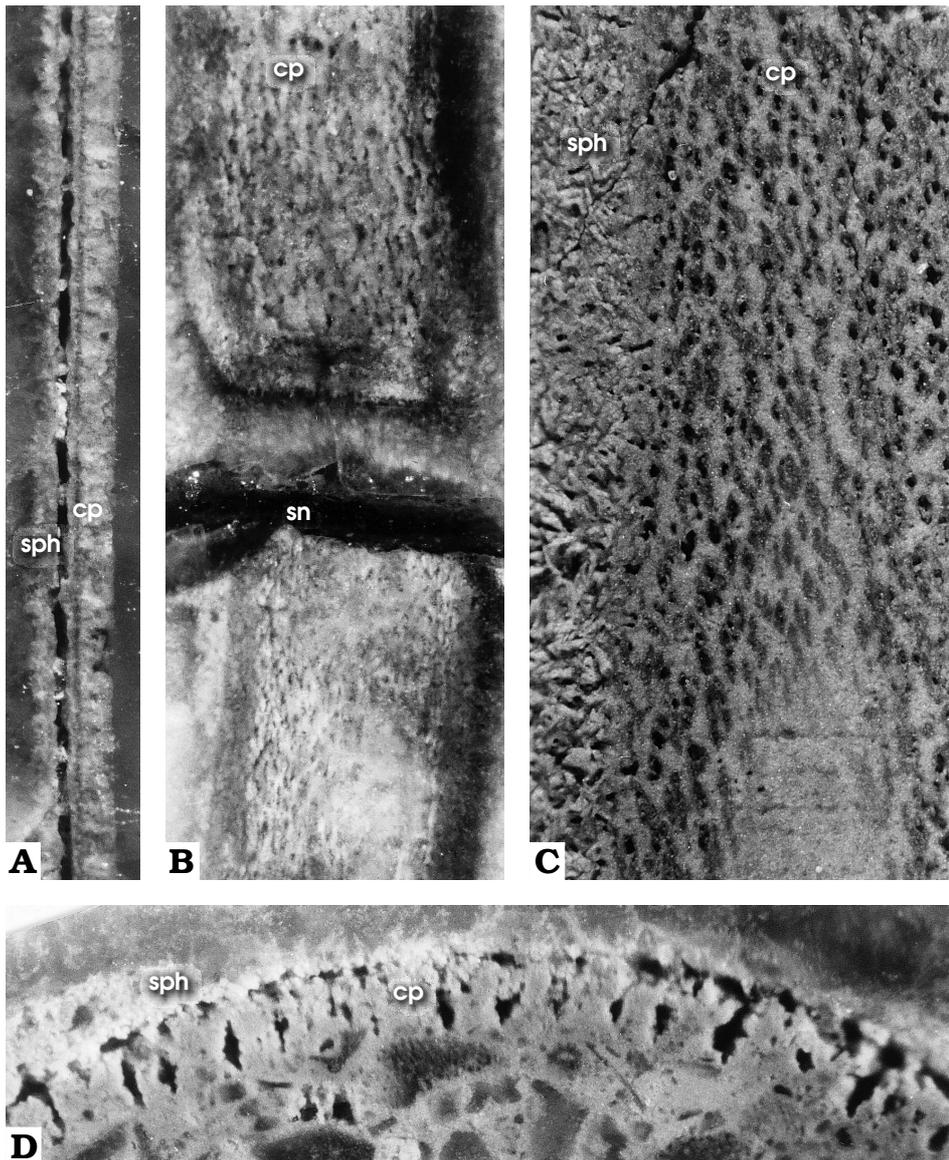


Fig. 4. **A, B.** *Polygrammoceras oelandicum* Troedsson, 1932. **A.** Median section of a connecting ring to show the calcified-perforate layer (cp) with a thin outermost lamellae of a dense structure, and the spherulitic-prismatic layer (sph), $\times 40$. **B.** Tangential section through a septal neck (sn) and the calcified-perforate layer (cp) of two successive connecting rings to show numerous elongated pores, $\times 30$. **C–D.** *Lituites* sp. **C.** Tangential section of a connecting ring to show the spherulitic-prismatic layer (sph), and the calcified-perforate layer (cp) with large pores, $\times 40$. **E.** Transverse section of a connecting ring to show the spherulitic-prismatic layer (sph), and the calcified-perforate layer (cp) with pores; note that the pores decrease in size in the outermost portion of the latter layer, $\times 50$.

ness, attaining two-thirds of the total thickness of the connecting ring wall (sph in Fig. 5A, Fig. 7C). It is porous and composed of acicular crystallites. As seen in median sections, and particularly in cross-sections, the calcified-perforate layer is traversed by numerous pores (cp in Fig. 5A, C, Fig. 7C). In tangential section, the shape of the pores is similar to the other orthoceratids dealt with here, being narrow and elongated in the apical-oral direction (cp in Fig. 5B, Fig. 7C).

The genus *Cochlioceras* has an unpaired, broad, dorsal scar of retractor muscle (Dewitz 1879; Schröder 1881; Mutvei 1957).

Cochlioceras is a member of the family Baltoceratidae that has been previously classified with ellesmeroceratids (Flower 1964; Furnish and Glenister 1964; King 1999). However, the connecting ring structure in this genus is identical to that in orthoceratids except that the outer spherulitic-prismatic layer is thicker. Also the dorsal position of the retractor muscle scar

agrees with that in orthoceratids. Thus, the family Baltoceratidae is a typical member of the orthoceratids and not of the ellesmeroceratids. The latter taxon still lacks a satisfactory definition (see also Mutvei in press).

Silurian orthoceratids

Danacoceras gotlandense Mutvei, 1998 (Narthecoceratidae)

The material of this species comprises ten isolated, large siphuncles, collected from the Llandoveryan Lower Visby Bed, island of Gotland, Sweden.

As previously described (Mutvei 1998), the calcified-perforate layer of the connecting ring is thick and traversed by large pores, arranged in longitudinal rows, about 0.5 mm apart. The pores seem to be elongated in the apical-oral direc-

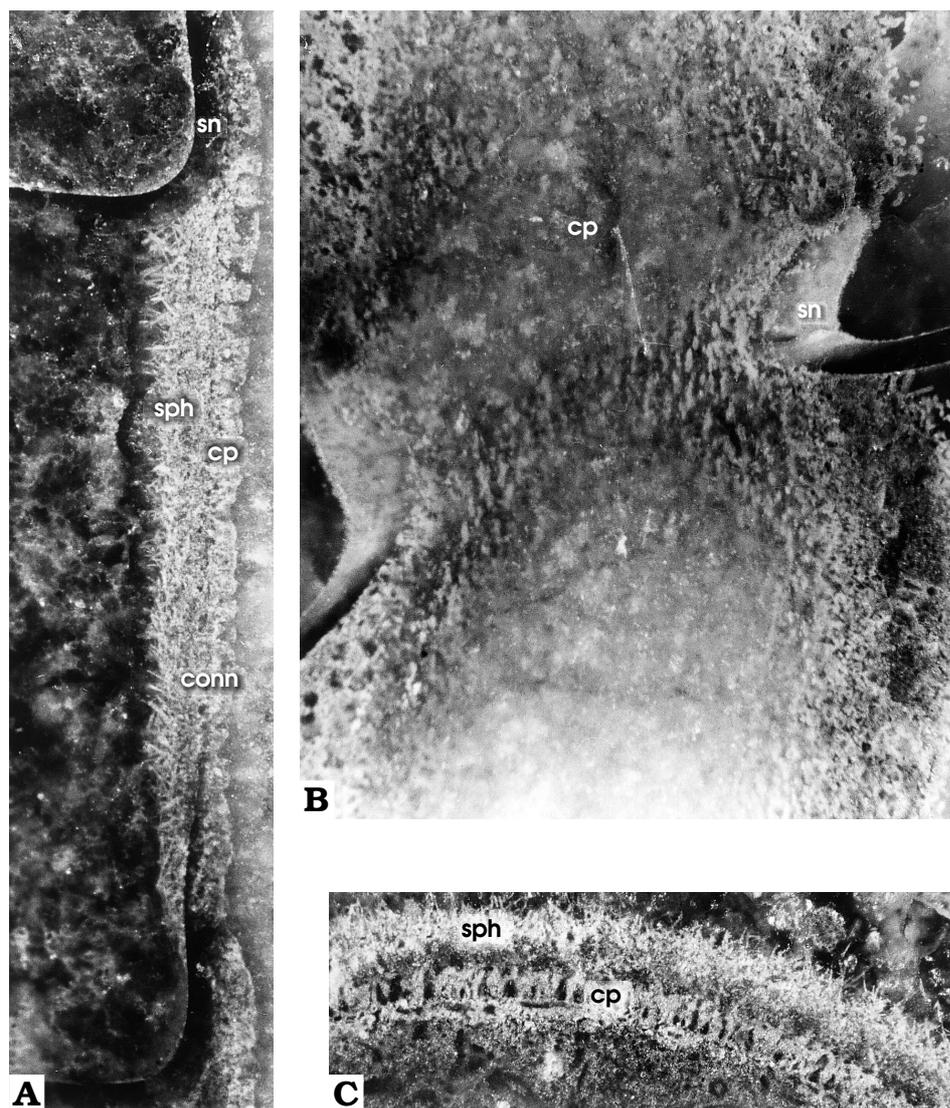


Fig. 5. A–C. *Cochlioceras* sp. **A.** Median section of two septal necks (sn) and a connecting ring (conn); note that the outer spherulitic-prismatic layer (sph) of the connecting ring is much thicker than the inner calcified-perforate layer (cp), and that the calcified-perforate layer is a direct continuation of the nacreous layer of the septal neck, $\times 40$. **B.** Tangential section of the calcified-perforate layer (cp) of the connecting ring to show numerous elongated pores, $\times 40$. **C.** Transverse section of the connecting ring to show numerous pores in the calcified-perforate layer (cp) and a thick spherulitic-prismatic layer (sph), $\times 40$.

tion. Their outer diameter is about 0.1 mm at a siphuncular diameter of 15 mm (Mutvei 1998: figs. 1C–E, 3B). Because of the imperfect preservation, it could not be ascertained if the outer spherulitic-prismatic layer was present in the connecting ring.

Retractor muscle scars.—Unknown.

Remarks.—The pores in the calcified-perforate layer of the connecting ring differ from those in other orthoceratids in their arrangement in longitudinal rows. Also other members of the family Narthecoceratidae seem to have similar pores, best illustrated by Flower (1968: pl. 16: 4, 5) in *Narthecoceras sinclairi*.

Lyecoceras spp. (Paraphragmitidae)

Fig. 6D.

Material of these species comprises numerous shells from the Silurian Hemse-Group, Lower Ludlow, Lye, island of Gotland.

Only one specimen shows the structure of the connecting ring in a transverse section. The pores in the calcified-perforate layer seem to be narrower and more numerous than in other orthoceratids (cp in Fig. 6D). The outer spherulitic-prismatic layer is not preserved.

The retractor muscle scars in this genus are paired and situated dorsally (Mutvei 1957).

Dawsonoceras sp. (Dawsonoceratidae)

Fig. 3D.

The material of this species comprises several specimens from the Middle Silurian Mulde Marl, Eksta, Djupvik, island of Gotland, but only one specimen has the connecting ring structure sufficiently well preserved for a detailed study.

In median section only the calcareous-perforate layer of the connecting ring is preserved. This layer is comparatively thin, about half of the thickness of the septum. The outer spherulitic-prismatic layer of the connecting ring is either ab-

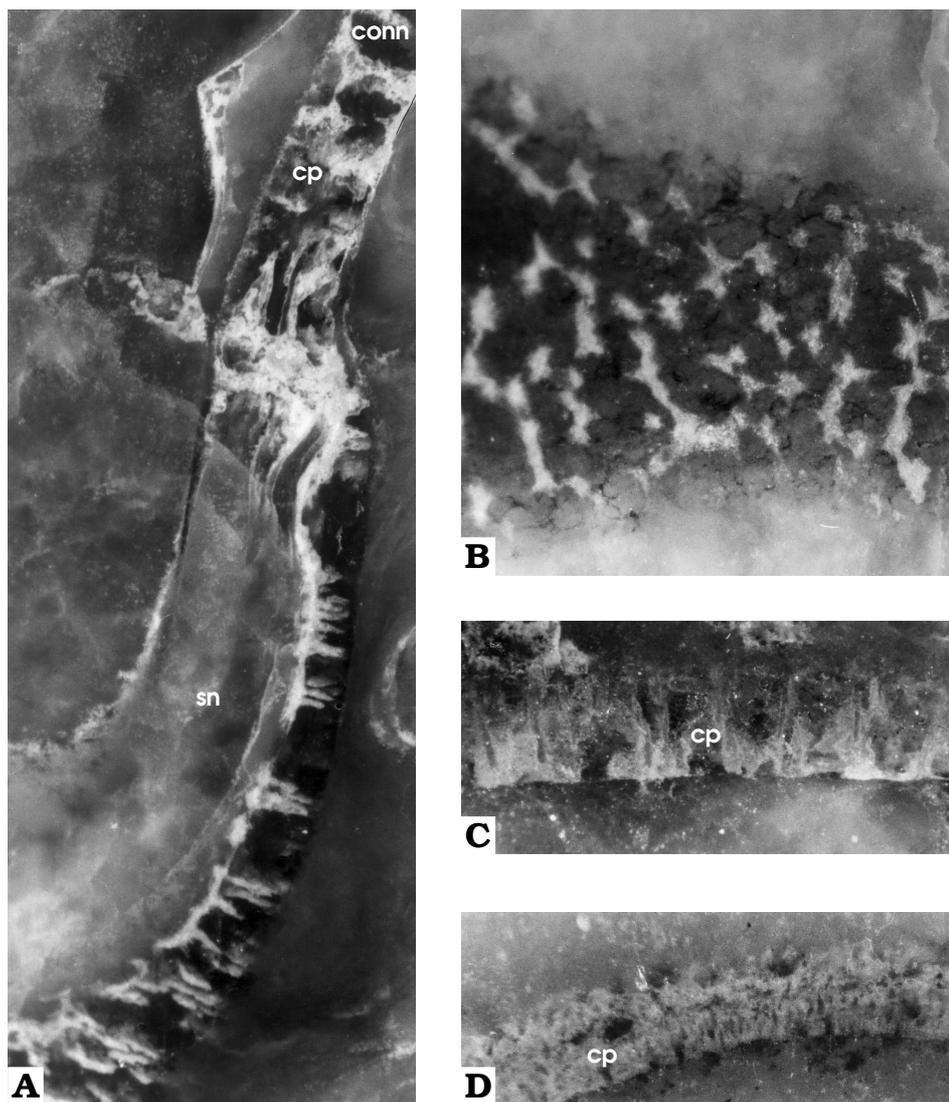


Fig. 6. A–C. *Adamsoceras holmi* (Troedsson, 1926). A. Median section of a sepal neck (sn) and a connecting ring (conn) with pores; note that the calcified-perforate layer (cp) of the connecting ring is a continuation of the nacreous layer of the sepal neck (sn), $\times 50$. B. Tangential section of the calcified-perforate layer (cp) of the connecting ring to show that pores have angular outlines, $\times 50$. C. Transverse section of the connecting ring to show pores in the calcified-perforate layer (cp), $\times 50$. D. *Lycoceras* sp. Transverse section of the connecting ring to show that pores in the calcified-perforate layer (cp) are numerous and very narrow, $\times 80$.

sent or too thin to be recognized. The pores in the calcified-perforate layer are numerous. In tangential section their shape is narrow and much elongated in the apical-oral direction (cp in Fig. 3D).

Retractor muscle scars are unknown.

The connecting ring structure is so far one of the best preserved among Silurian nautiloids, probably because the shells were embedded in marly sediment.

Summary of connecting ring structure in orthoceratids and actinoceratids

The outer spherulitic-prismatic layer in orthoceratids and actinoceratids has a different thickness in different taxa: it is

much thinner than the calcified-perforate layer in the actinoceratid *Adamsoceras holmi* (Ormoceratidae) and in the orthoceratids *Orthoceras regulare* and *O. scabridum* (Orthoceratidae); it is half as thick as the calcified-perforate layer in the orthoceratids *Polygrammoceras oelandicum* (Troedssonellidae), *Geisonoeras kinnekullense* (Geisonoceratidae), and *Lituites* sp. (Lituitidae); it is twice as thick as the calcified-perforate layer in *Cochlioceras* sp. (Baltoceratidae).

Morphology of pores in the calcified-perforate layer also shows certain differences in different taxa. The pores are numerous and narrow, and elongated in the apical-oral direction in all orthoceratids dealt with here. However, the diameter of the pores seems to be larger in the representatives of the family Lituitidae than in other families. *Donacoceras gotlandense* (Narthecoceratidae) differs from other orthoceratids in having pores arranged in longitudinal rows (Mutvei 1998: fig. 1H). In the actinoceratid *Adamsoceras holmi* (Ormoceratidae) the pores (Fig. 6A, C) have angular outlines in cross section (Figs. 6B, 7D).

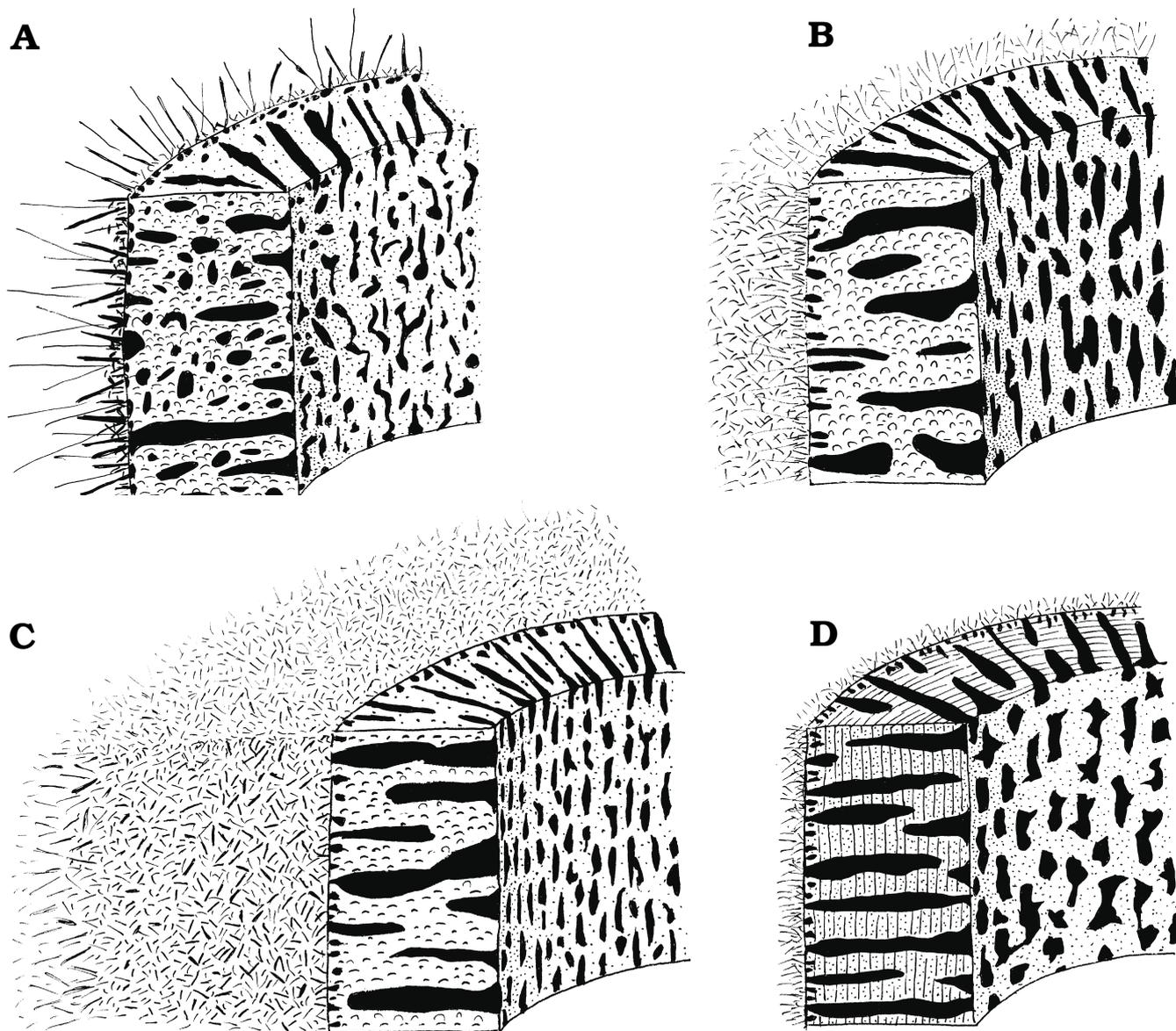


Fig. 7. Diagrammatic representation of connecting ring structure. A. *Orthoceras regulare* and *O. scabridum* (Orthoceratidae). B. *Lituites* sp. (Lituitidae). C. *Cochlioceras* sp. (Baltoceratidae). D. *Adamsoceras holmi* (Actinoceratida: Ormoceratidae).

As observed in the actinoceratid *Adamsoceras holmi* (Mutvei 1997a: figs. 1A, 2A) and in most orthoceratids, the pores usually decrease in diameter towards the outermost portion of the calcified-perforate layer, at the border to the outer spherulitic-prismatic layer. The outermost portion of this layer therefore acquires a more dense structure, and is often the only portion of the connecting ring that is preserved.

In most orthoceratids here dealt with the calcified-perforate layer is composed of small granules of irregular size and shape (cp in Figs. 1B, 2B). Only in "*Michelinoceras*" sp. (cp in Fig. 3B, C) does this layer show a lamellar structure similar to that in the actinoceratids *Adamsoceras holmi*, *Eushantungoceras pseudoimbricatum*, and *Huroniella* sp. (Mutvei 1997a: fig. 1B, C; ll in figs. 3C, D; 7D, E).

Cameral deposits

As shown herein, a common feature of orthoceratids and actinoceratids is a calcified connecting ring, perforated by numerous and comparatively large pores. This feature is positively correlated with the occurrence of cameral deposits, described by several writers in orthoceratids and actinoceratids, and interpreted as having been secreted in the shell chambers during the lifetime of the animal. On the other hand, in nautiloid taxa where the connecting ring has a different structure, the cameral deposits are lacking or have a doubtful occurrence.

As pointed out (Mutvei in press), the cameral deposits are still poorly studied and their origin imperfectly understood.

These deposits may have had a post-mortem origin. After the death of the animal the glycoprotein sheets in the pores were rapidly destroyed leaving the pores open. In those shells that were post-mortally deposited on the surface of a calcareous bottom sediment, the water, supersaturated by calcium carbonate, rapidly penetrated through the pores into the shell chambers and gave rise to the calcareous cameral deposits. Taxa with more extensive cameral deposits, such as *Lituites* and *Rhynchorthoceras*, seem to have had larger pores than other taxa (Figs. 2D, E, 4C, D). In contrast, orthoceratid shells preserved in shales are usually completely flattened owing to compaction of the sediment, which indicates that their chambers did not contain cameral deposits but were empty.

Position of retractor muscle scars in orthoceratids-actinoceratids in comparison with *Nautilus*

***Nautilus*.**—The retractor muscle scars are paired and situated on the lateral sides of the shell wall in front of the last septum (Mutvei 1957, 1964; Mutvei et al. 1993; Mutvei and Doguzhaeva 1997). These muscles extend from their origin on the shell wall to the cephalic cartilage on which they are rigidly inserted. They are powerful and form the roof of the entire ventral and lateral portions of the mantle cavity. Rapid swimming is produced by contractions of these muscles, which pull the body into the shell, accompanied by simultaneous contraction of the hyponome. As a result, the water is forcibly expelled from the mantle cavity through the hyponome.

Orthoceratids, actinoceratids, and endoceratids.—In orthoceratids, as defined here, the retractor muscle scars are known in six genera: *Orthoceras*, *Geisonoceras*, *Lycoceras*, *Lituites*, *Rhynchorthoceras*, and *Cochlioceras* (Mutvei 1957, 1964; Sweet 1959; the present paper). The position of the retractor muscle scars in these genera is dorsal, termed the dorsomyarian type by Sweet (1959). These scars are mostly paired and considerably smaller than the laterally and/or ventrally situated scars in *Nautilus* and fossil tarphyceratids. In their course to the cephalic cartilage, the retractor muscles in orthoceratids did not form a roof above the ventral and lateral portions of the mantle cavity as they do in *Nautilus*. Their function seems to have been to attach the body to the shell and pull the head into the living chamber when threatened. Because of their different position in relation to the ventral and lateral portions of the mantle cavity, their contractions could not be used to expel water from the mantle cavity for swimming by jet propulsion, as in *Nautilus*.

In actinoceratids the retractor muscle scars are usually indistinct. However, Frey (1995) reported that these scars in this taxon also have a dorsal position.

As in actinoceratids, the retractor muscle scars in endoceratids are usually indistinct except in *Anthoceras vaginatum* (Endoceratidae) in which their dorsal position is distinctly indicated (Schröder 1881: pl. 2: 5A; Mutvei in press).

Mode of life

Most authors believe that fossil nautiloids with orthoconic shells were capable of jet-powered swimming. For this the long axis of the shell and body must have been horizontal. According to these authors, horizontal posture in orthoceratids and actinoceratids was achieved with the help of cameral deposits. These deposits filled the early shell chambers and functioned as ballast to increase the weight of posterior portion of the shell.

The view that orthoceratids and actinoceratids were capable of jet-powered swimming is here refuted on the following grounds: 1) Orthoconic shells were often long but very seldom completely straight; without fins for steering the animal would have been unable to keep a straight course or to change its swimming direction. 2) As indicated by the position and size of their attachment scars, the retractor muscles were small and, unlike those in *Nautilus*, did not form a roof above the ventral mantle cavity—their contractions therefore could not expel water from the mantle cavity, which is necessary for jet-powered swimming. 3) Formation of cameral deposits during the lifetime of the animal is still controversial (see above). Instead, the occurrence of a calcified inner layer of the connecting ring with numerous pores strongly suggests that orthoceratids and actinoceratids were capable of comparatively rapid, probably diurnal, changes of volume of cameral liquid. This made it possible to migrate vertically in the water column. Among Recent cephalopods *Spirula* has a similar mode of life.

Classification

Taxonomic features such as shell ornamentation, length and curvature of septal necks, and morphology of endosiphuncular deposits have usually been used for orthoceratid classification. However, these features show a high degree of variability, and taxa based on them cannot be therefore properly defined (Mutvei 1964, 1997a, b, 1998; Ristedt 1968; Dzik 1984).

As pointed out by several writers (e.g., Schindewolf 1933; Ristedt 1968; Engeser 1996; Zakharov 1996), the shape of the initial portion of the shell in orthoceratids is either globular or cup-shaped. However, the structure of the initial shell portion can only be studied in extremely well preserved material. Studies by Blind (1987) on the Pennsylvanian Boggy Formation (Buckhorn Asphalt) orthoceratids reveal that cup-shaped initial shell portion with cicatrix is structurally similar to that

in *Nautilus* (Mutvei and Doguzhaeva 1996). As indicated by studies of Doguzhaeva et al. (1999), the globular initial shell portion, which also occurs in bactritids, ammonoids and belemnites, has a different structure in different taxa. The globular shape itself cannot therefore be used for classification. Besides, in Baltoscandian Ordovician and Silurian orthoceratids, the initial shell portion is rarely preserved, and its morphology and structure cannot therefore be studied.

The present writer emphasized (Mutvei 1964 and in press) that the position of the retractor muscle scars indicates differences in anatomy and mode of life in fossil nautiloids. On the other hand, the position of muscle scars was considered of minor taxonomic and phylogenetic significance by Sweet (1959), because the dorsal position of these scars occurs in ellesmeroceratids (*Cochlioceras*) and tarphyceratids (*Lituites*), as well as in orthoceratids. However, as demonstrated in the present paper (see also Mutvei in press), *Cochlioceras* and *Lituites* have to be classified with orthoceratids because they possess not only dorsal muscle scars but also the orthoceratid type of connecting ring.

Ammonoids belonging to goniatitids, ceratitids, phylloceratids, lytoceratids and ammonitids all seem to have paired dorsal attachment scars (Doguzhaeva and Mutvei 1996). This demonstrates that the position of the retractor muscle scars is characteristic for large taxonomic units, and is not influenced by differences in shell morphology.

On the basis of number and position of the retractor muscle scars, Mutvei (1964) preliminarily classified fossil nautiloids in three major taxa: Orthoceratomorphi, Nautilomorphi and Oncoceratomorphi. Orthoceratomorphi was characterized by dorsal position of the scars.

Recently (Mutvei in press), Orthoceratomorphi were classified as an order (Orthoceratida herein) that includes two suborders: Orthoceratina and Actinoceratina, both characterized by calcified connecting rings perforated by numerous, comparatively large, pores. Retractor muscle scars in orthoceratids are dorsal; in actinoceratids they are either dorsal or difficult to distinguish owing to their small size.

The characteristic pore system in the connecting ring is at the present known in nine families of the suborder Orthoceratina (Orthoceratidae, Michelinoceratidae, Geisonoceratidae, Troedssonellidae, Dawsonoceratidae, Paraphragmitidae, Baltoceratidae, Lituitidae, and Narthecoceratidae) and two families of the suborder Actinoceratina (Ormoceratidae and Huroniidae). In Carbonactinoceratidae (*Rayonnoceras*) and Armenoceratidae (*Eushantungoceras*) the connecting ring is calcified but the pores could not be clearly recognized (Mutvei 1997a).

It should be pointed out that calcified connecting rings with a different pore system may occur in taxa other than orthoceratids and actinoceratids.

Endoceratids have a dorsal position of the retractor muscle scars (Mutvei in press). On the basis of this character, endoceratids are preliminarily included as a separate suborder to the order Orthoceratida. The endoceratid siphuncle has been studied in detail only in the family Endoceratidae

(Mutvei 1998). The connecting ring here consists of a comparatively thick spherulitic-prismatic layer. Because the septal necks are long, the inner calcified layer of the connecting ring is not developed.

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