



Nautiloid Systematics Based on Siphuncular Structure and Position of Muscle Scars

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3 Text-Figures and 3 Plates

Nautiloids
Systematics
Muscle scar
Siphuncle
Connecting ring

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Die Systematik der Nautiloideen auf Basis der Verbindungsringstrukturen und der Ansatznarben des Retraktormuskels

Zusammenfassung

Verbindungsringstrukturen und die Position der Ansatznarben des Retraktormuskels werden zur Unterscheidung und Definition größerer Nautiloideengruppen herangezogen. Bei Orthoceratiden und Actinoceratiden besteht der Verbindungsring aus zwei calcifizierten Lagen: einer äußeren sphärolitisch-prismatischen und einer inneren calcifiziert-perforierten Lage, letztere von zahlreichen Poren durchquert. Zusätzlich besitzen Orthoceratiden und Actinoceratiden dorsale Ansatzstellen des Retraktormuskels. Dorsale Narben sind auch bei Endoceratiden vorhanden, aber im Gegensatz zu Orthoceratiden und Actinoceratiden besteht deren Verbindungsring nur aus einer einzigen sphärolitisch-prismatischen Lage, während die innere, calcifiziert-perforierte Lage durch eine lange Siphonaldüte ersetzt ist. Die Endoceratiden stehen daher den Orthoceratiden und Actinoceratiden näher als den Ellesmeroceratiden.

Der Verbindungsring der Tarphyceratiden besteht aus einer dicken sphärolitisch-prismatischen Lage. Wie bei *Nautilus* war diese Lage innen mit einer Glycoproteinschichte überzogen (Conchiolin), die nicht erhalten ist. Diese letztere Lage entspricht der calcifiziert-perforierten Lage bei Orthoceratiden und Actinoceratiden: beide bilden eine strukturell modifizierte Fortsetzung der Perlmutter-schichte der Siphonaldüte. Die Tarphyceratiden haben ventrale und/oder laterale Ansatznarben des Retraktormuskels, was auf ähnliche innere Organisation des Weichkörpers wie bei *Nautilus* hinweist, unterschiedlich jedoch zu Orthoceratiden, Actinoceratiden und Endoceratiden. Die Familie Lituitidae, früher zu den Tarphyceratiden gestellt, zählt zum Typus mit calcifiziert-perforiertem Verbindungsring, ähnlich dem der Orthoceratiden und Actinoceratiden.

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Die Ellesmoceratiden sind ein sehr heterogenes Taxon. Eine ihrer Familien, die Baltoceratidae, zählt zu den Orthoceratiden, weil sie den calcifiziert-perforierten Typus des Verbindungsringes und dorsale Retraktormuskelnarben besitzt. Drei andere Familien, Bathmoceratidae, Cyrtocerinidae und Cyclostomiceratidae sind anscheinend mit dem Rest der Ellesmoceratidae nicht näher verwandt; die letztgenannte Gruppe ist noch immer undefiniert.

Das Auftreten von Ablagerungen in den Kammern korreliert mit dem calcifiziert-perforierten Typus Verbindungsring. Die Herkunft der Kammerablagerungen wird immer noch unzureichend verstanden.

Auf der Basis dorsaler Retraktormuskelnarben werden Orthoceratide, Actinoceratide und Endoceratide in die Ordnung Orthoceratida KUHN 1940 gestellt. Orthoceratiden, Actinoceratiden werden darüber hinaus durch den Besitz einer inneren calcifiziert-perforierten Lage des Verbindungsringes gekennzeichnet.

Abstract

Connecting ring structure and position of retractor muscle scars are used here to distinguish and define major groups of nautiloids. In orthoceratids and actinoceratids the connecting ring is composed of two calcified layers: an outer spherulitic-prismatic and an inner calcified-perforate, the latter traversed by numerous pores. In addition, orthoceratids and actinoceratids have dorsal retractor muscle scars. Dorsal scars also occur in endoceratids, but unlike orthoceratids and actinoceratids, the connecting ring is here composed of only a spherulitic-prismatic layer, whereas the inner calcified-perforate layer has been replaced by a long septal neck. Endoceratids were therefore closely related to orthoceratids and actinoceratids, rather than to ellesmoceratids.

The tarphyceratid connecting ring is composed of a thick spherulitic-prismatic layer. As in *Nautilus*, this layer was internally coated by a glycoprotein (conchiolin) layer that is not preserved. The latter layer corresponds to the calcified-perforate layer in orthoceratids and actinoceratids: they both form a structurally modified continuation of the nacreous layer of the septal neck. Tarphyceratids have ventral and/or lateral scars of retractor muscles, indicating an organization of soft anatomy similar to that in *Nautilus*, but different from that in orthoceratids, actinoceratids and endoceratids. The family Lituitidae, previously assigned to tarphyceratids, has a calcified-perforate type of connecting ring, similar to that in orthoceratids and actinoceratids.

Ellesmoceratids is a highly heterogeneous taxon. One of its families, Baltoceratidae, belongs to the orthoceratids because it has a calcified-perforate type of connecting ring and dorsal retractor muscle scars. Three other families, Bathmoceratidae, Cyrtocerinidae and Cyclostomiceratidae, seemingly have no close relationship to the rest of the ellesmoceratids; this latter group still lacks a precise definition.

Occurrence of cameral deposits shows a positive correlation with the calcified-perforate type of connecting ring. The origin of these deposits is still poorly understood.

On the basis of the dorsal position of the retractor muscle scars, orthoceratids, actinoceratids and endoceratids are assigned to the order Orthoceratida KUHN 1940. Orthoceratids and actinoceratids are furthermore characterized by possessing an inner calcified-perforate layer of connecting ring.

1. Introduction

Palaeozoic nautiloids had their main evolutionary radiation in the Ordovician and Silurian. Owing to poor preservation, caused by transformation of shell aragonite to calcite during diagenesis, it has been difficult to study structural differences between the numerous new taxa that appeared, and to give a satisfactory definition to these taxa. Only when aragonite has been transformed into calcium phosphate before diagenesis is the structure partially preserved and can then be studied in some detail. Phosphatization and good structural preservation has been found in nautiloid shells from the Lower and Middle Ordovician limestones in Sweden and Estonia. On the other hand, in the rich, externally well preserved, Silurian nautiloid faunas from the Island of Gotland, Sweden, most shells are completely recrystallized into calcite, and have lost their structure. In these nautiloids detailed studies on siphuncular structures are therefore more difficult to carry out than on Ordovician nautiloids.

A short review of siphuncular structures in four taxa of Ordovician and Silurian nautiloids: orthoceratids, actinoceratids, endoceratids and tarphyceratids (MUTVEI, 1997a,b, 1998, and unpublished) is given here. Siphuncular structures show a positive correlation with the position of retractor muscle scars. These two features are used here to define and classify the above mentioned taxa.

2. Material and Methods

The material studied comprises:

- Recent *Nautilus*.
- Orthoceratids

Orthoceras regulare SCHLOTHEIM and *Lituities* sp. from the Middle Ordovician Lasnamägian Stage, Kandle,

Estonia; *Orthoceras scabridum* Angelin from the Middle Ordovician Folkeslunda Limestone, Stenösa kanal, Öland, Sweden; *Cochlioceras* sp. from the Lower Ordovician Kundan Stage, Hälludden, Öland, Sweden.

○ Actinoceratid

Adamsoceras holmi (TROEDSSON) from the Lower Ordovician Kundan Stage (Aluoja Substage), Harku quarry, Tallinn, Estonia.

○ Tarphyceratids

Estonioceras sp. from the Middle Ordovician Lasnamägian Stage, Tallinn Estonia; *Planctoceras falcatus* (SCHLOTHEIM) from the Lower Ordovician Kundan Stage (Aluoja Substage), Harku quarry, Tallinn, Estonia.

The shells were cut medially, paramedially and transversely. The sections were ground with carborundum, polished with aluminium oxide, and studied and photographed in incident light with a Wild M400 photomicroscope.

3. Siphuncular Structures and Retractor Muscle Scars

3.1. *Nautilus*

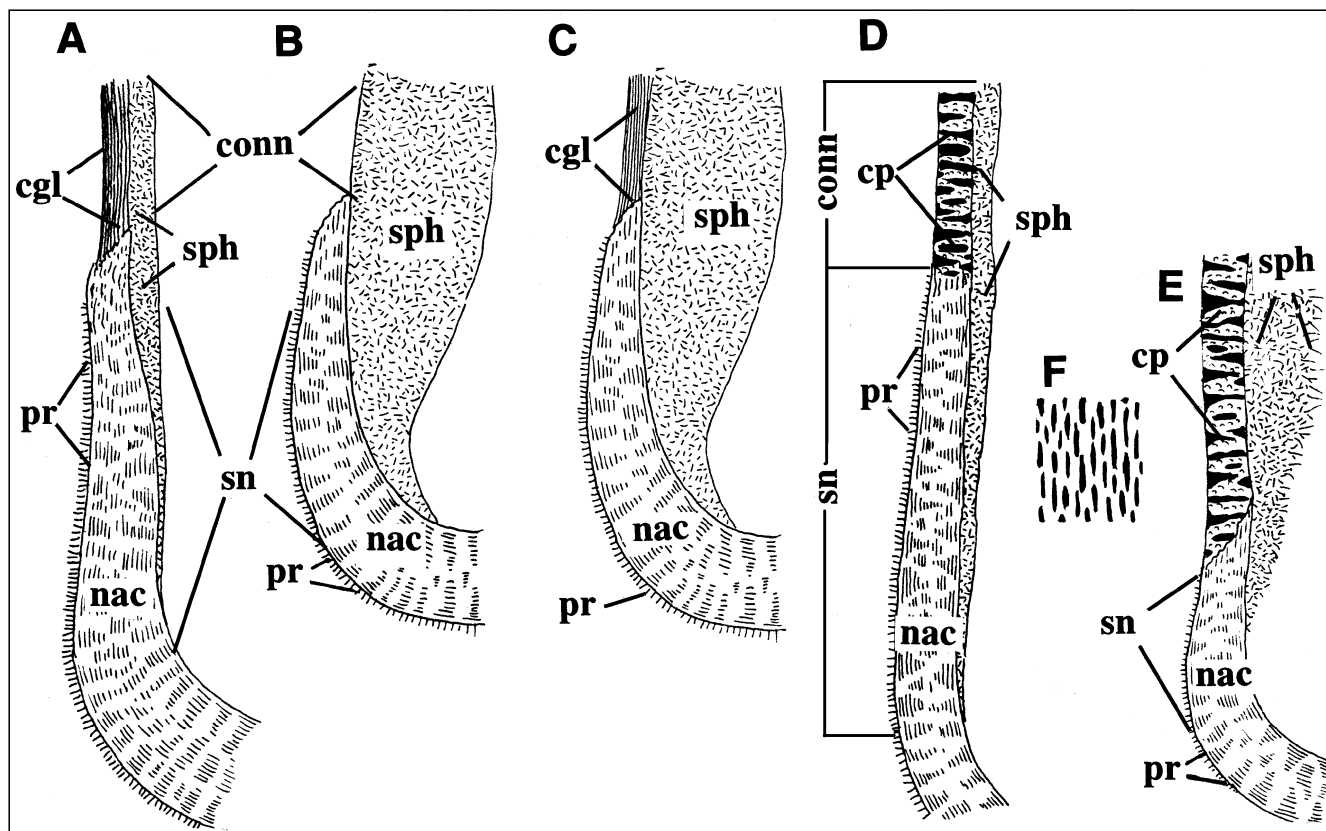
3.1.1. Siphuncle

As emphasized in several papers (MUTVEI, 1964, 1972, 1997a), the siphuncle in *Nautilus* and in fossil nautiloids is formed of tubular prolongations of consecutive septa, each composed of a solid septal neck and a permeable connecting ring.

The septal neck in *Nautilus* (sn, Text-Fig. 1A) is composed of three calcareous layers:

- 1) an outer spherulitic-prismatic (sph)
- 2) a median nacreous (nac)
- 3) an inner prismatic (pr).

The outer spherulitic-prismatic layer is porous and consists of acicular crystallites and incomplete spherulites



Text-Fig. 1.

Median sections of a septal neck and connecting ring in:

- A) *Nautilus*, showing three layers of the septal neck (sn): inner prismatic (pr), nacreous (nac) and outer spherulitic-prismatic (sph), and two layers of the connecting ring (conn): inner glycoprotein (conchiolin) (cgl) and outer spherulitic-prismatic (sph).
- B) Tarphyceratid *Estonioceras* sp. showing similar three layers of the septal neck (sn) as in *Nautilus* (pr, nac, sph); the inner glycoprotein (conchiolin) layer of the connecting ring (conn) has been destroyed by diagenesis.
- C) *Estonioceras* sp., same as in B, except that it shows a reconstruction of the inner glycoprotein (conchiolin) layer (cgl) of the connecting ring.
- D) Orthoceratid *Orthoceras scabridum*: septal neck with the same three layers (pr, nac, sph) as in *Nautilus* and *Estonioceras*; connecting ring with two calcareous layers, a thin, outer, spherulitic-prismatic layer (sph) and a calcified-perforate inner layer (cp).
- E) Orthoceratid *Cochlioceras* sp.: same layers in the septal neck (sn) and connecting ring as in *O. scabridum*, but the spherulitic-prismatic layer (sph) of the ring is much thicker.
- F) Outer surface of the inner calcified-perforate layer in *O. scabridum* to show the density and outlines of the pores.

Note that the calcified-perforate layer of the connecting ring in orthoceratids, and the glycoprotein (conchiolin) layer of the connecting ring in *Nautilus* and tarphyceratids, are both structurally modified continuations of the nacreous layer of the septal neck.

without preferred orientation, separated by smaller or larger interspaces. Also the inner prismatic layer is porous. Here, the acicular crystallites are oriented either at right angles, or more or less obliquely, to the inner neck surface. In the thick nacreous layer the amount of organic matrix increases towards the distal end of the septal neck where its structure becomes semi-prismatic.

The connecting ring (conn, Text-Fig. 1A) consists of two layers:

- 1) an outer spherulitic-prismatic layer (sph), which continues from that layer of the septal neck; and
- 2) an inner, fibrous, glyco-protein (conchiolin) layer (cgl), which is a continuation of the nacreous layer of the septal neck but uncalcified.

The latter layer alone provided the mechanical strength the siphuncle needed to withstand hydrostatic pressure corresponding to depths of 600–700 m.

3.1.2. Retractor Muscle Scars

Cephalic retractor muscles, longitudinal mantle muscles and sub-epithelial muscles of the posterior part of the body all have their origin on the annular elevation of the shell wall in front of the last septum. The cephalic retractor muscles are paired and situated laterally. The position of

their attachment scars on the shell wall is marked by large anterior lobes of the annular elevation (rms, Text-Fig. 2H). These muscles extend to the cephalic cartilage in which they are rigidly inserted (MUTVEI, 1957, 1964).

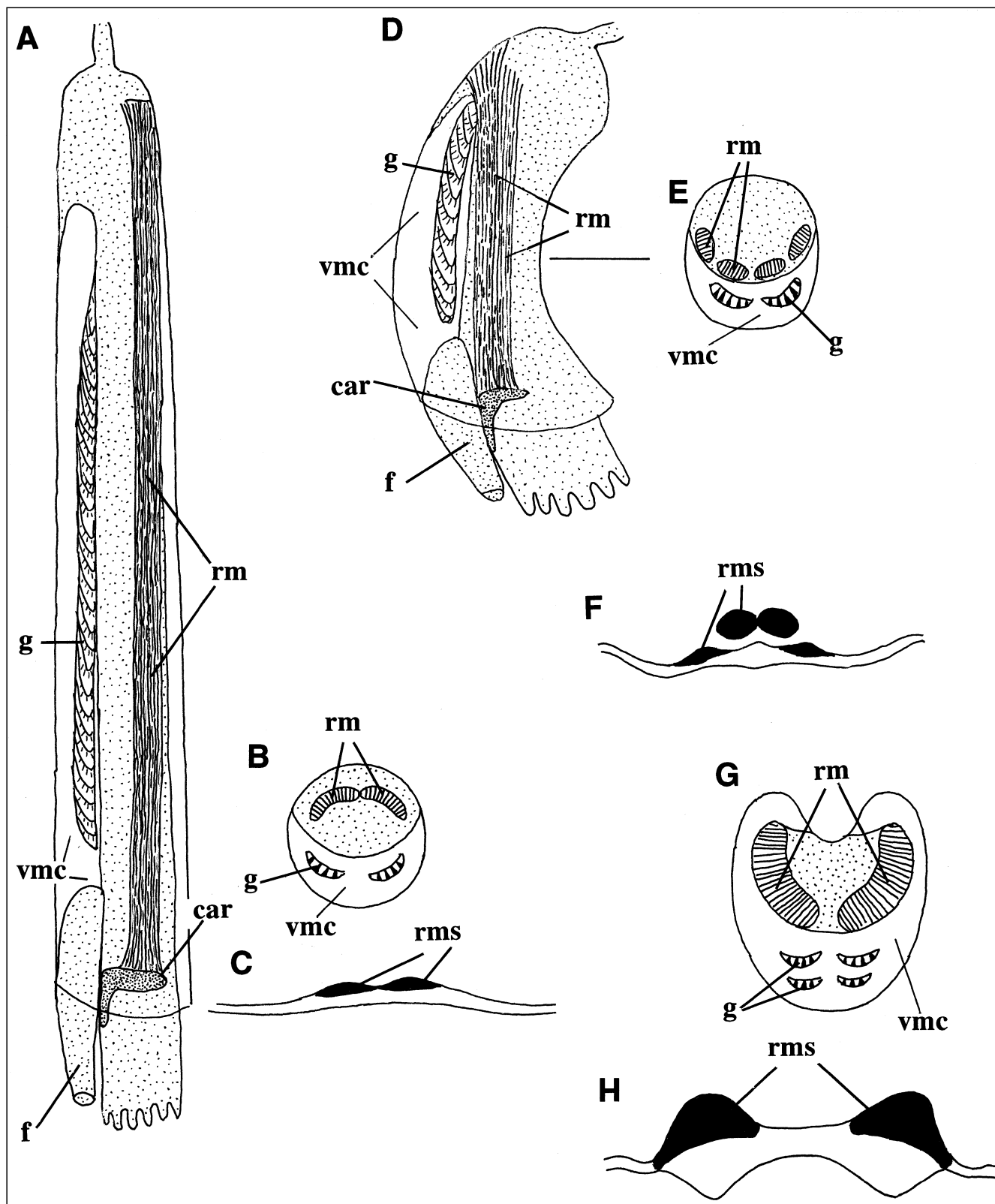
Weakly developed hyponome retractor muscles are situated on the ventral surface of the cephalic retractor muscles (MUTVEI et al., 1993, hr, Fig. 8B). The cephalic retractor muscles (rm, Text-Fig. 2G) are powerful and form a roof of the entire ventral and lateral portions of the mantle cavity (vmc).

Rapid swimming is produced by contractions of these muscles, which pull the body into the shell, accompanied by simultaneous contractions of the hyponome. As a result water is forcibly expelled from the mantle cavity through the hyponome.

The ventilatory flow of the water to the gills is created by contraction of the hyponome wings,

“... aided at times by contraction ... of head retractor muscles ...” (WELLS, 1988, p. 339).

In squids the cephalic and hyponome retractors originate from the dorsal gladius. Unlike in *Nautilus*, swimming by jet propulsion is produced by contractions of the mantle muscles. Mantle contractions are also used for normal ventilation (WELLS, 1988).



Text-Fig. 2.
Orthoceratid.

- A) Schematic median section of the body to show the extension of the retractor muscles (rm) from the dorsal side of the living chamber to the cephalic cartilage (car); note that the muscles have no spatial relationship to the ventral mantle cavity (vmc) with gills (g) and funnel (f).
B) Cross section of the body to show the relationship between the retractor muscles (rm) and ventral mantle cavity (vmc).
C) Annular elevation with retractor muscle scars (rms).

Tarphyceratid.

- D) Median section of the body to show the extension of the retractor muscles (rm) from the ventral and lateral sides of the living chamber

to the cephalic cartilage (car), and their close spatial relationship to the ventral mantle cavity (vmc) with gills (g) and funnel (f).

- E) Cross section of the body to show that the retractor muscles (rm) formed a roof above the ventral mantle cavity (vmc).
F) Annular elevation with retractor muscle scars (rms).

Nautilus.

- G) Cross section of the body to show the position of the retractor muscles (rm) above the ventral mantle cavity (vmc).
H) Annular elevation with retractor muscle scars (rms).

3.2. Tarphyceratids

3.2.1. Siphuncle

Siphuncular structure was studied in *Estonioceras* sp. and *Planctoceras falcatum* (Fam. Estonioceratidae). The septal neck (sn, Text-Fig. 1B, C; Pl. 1, Fig. 2) consists of the same three calcareous layers as that in *Nautilus*: outer spherulitic-prismatic (sph), nacreous (nac), and inner prismatic (pr). However, the outer spherulitic-prismatic layer is thicker than the corresponding layer in *Nautilus* (compare Text-Fig. 1A with 1C). The inner portion of the spherulitic-prismatic layer, in contact with the nacreous layer of the septal neck, seems to have a more solid structure than the rest of the layer (x, Pl. 1, Figs. 2–4). The distal end of the septal neck therefore looks bifurcated in longitudinal sections.

Only the thick, outer, spherulitic-prismatic layer of the septal neck continues into the connecting ring (sph, Text-Fig. 1B; Pl. 1, Figs. 1–4). This layer shows often two or more sublayers of different orientation of acicular crystallites (MUTVEI, unpublished). It is, however, certain that the connecting ring in tarphyceratids was originally composed of the same two layers as those in *Nautilus*: an outer spherulitic-prismatic layer and an inner glycoprotein (conchiolin) layer. The latter layer was a continuation of the nacreous layer of the neck (cgl, Text-Fig. 1C), but uncalcified and therefore destroyed by diagenesis. Thus, the main difference between *Nautilus* and tarphyceratids is that the latter had a much thicker outer spherulitic-prismatic layer, often subdivided into sublayers.

The present author did not have access to well preserved material of barrandeoceratids for studies of siphuncular structure. As reported by MUTVEI (1957), the retractor muscle scars have a ventral position in *Uranoceras* (?), currently classified with barrandeoceratids, and this indicates their close relationship with tarphyceratids.

The family Lituitidae, previously assigned to tarphyceratids (FURNISH & GLENISTER, 1964), resembles orthoceratids in connecting ring structure and the dorsal position of muscle scars (see below).

3.2.2. Retractor Muscle Scars

Retractor muscle scars are known in Estonioceratidae and Trocholitidae (MUTVEI, 1957, 1964; SWEET, 1959). Their position is often marked by a distinct anterior lobe of the annular elevation. On this lobe two pairs of scars can often be distinguished, the largest pair situated on both sides of the median line (rms, Text-Fig. 2F). As in *Nautilus*, the retractor muscles probably extended to the cephalic cartilage (rm, car, Text-Fig. 2D) on which they were rigidly fixed, forming a roof on the ventral portion of the mantle cavity (rm, vmc, Text-Fig. 2E). It is therefore possible that these tarphyceratids which possessed an evolute-involute shell may have been able to swim by jet propulsion, produced by contractions of retractor muscles and muscular hyponome.

3.3. Ellesmeroceratids

The order Ellesmeroceratida was erected by FLOWER (in FLOWER & KUMMEL, 1951). However, as pointed out by FURNISH & GLENISTER (1964), ellesmeroceratids lack an adequate definition because of great morphological variability and poor preservation. The majority of ellesmeroceratids were reported to have thickened connecting rings. However, as emphasized by MUTVEI (1964), the main part of the thick “connecting rings” in the family Bathmooceratidae, assigned to ellesmeroceratids, represents a spe-

cial type of endosiphuncular deposit. This family, and probably also the family Cyrtoceratidae, cannot therefore be included in ellesmeroceratids. The family Baltoceratidae, currently assigned to ellesmeroceratids, has connecting rings of calcified-perforate type (see below) and dorsal scars of retractor muscles (MUTVEI, 1957), both features characteristic of orthoceratids. This family is therefore classified with orthoceratids, and not with ellesmeroceratids. Another family, Cyclostomiceratidae, included by FLOWER (1964) and FURNISH & GLENISTER (1964) in the family Ellesmeroceratidae, has thick connecting rings of tarphyceratid type and ventral retractor muscle scars (MUTVEI & STUMBUR, 1971; KING, 1998, 1999). Because we lack information for the rest of ellesmeroceratids on the position of retractor muscle scars, and their connecting ring structure is imperfectly known, the classification of Cyclostomiceratidae with ellesmeroceratids remains uncertain.

3.4. Actinoceratids and Orthoceratids

3.4.1. Siphuncle

Septal neck in actinoceratids (MUTVEI, 1997a) is composed of the same three calcareous layers as in *Nautilus* and tarphyceratids: an outer spherulitic-prismatic, a nacreous, and an inner prismatic. On the other hand, the connecting ring has a structure different from that in *Nautilus* and tarphyceratids. In *Adamsoceras holmi* (family Ormoceratidae), it is composed of two calcareous layers: a thin, outer spherulitic-prismatic layer, being a continuation of that layer in the neck (MUTVEI, 1997a, sph, Figs. 1A, 3B); and a thick calcified-perforate, inner layer traversed by numerous pores (conn, cp, Pl. 3, Figs. 4, 5). As shown on Plate 3, Fig. 4 the latter layer (cp) is a direct, structurally modified, continuation of the nacreous layer (nac) of the neck. It does not have a nacreous structure, but consists of thin lamellae (MUTVEI, 1997a, Fig. 1B, C). Thus, unlike in *Nautilus* and tarphyceratids, both layers in the connecting ring of actinoceratids are fully calcified, and the regulation of the volume of cameral liquid took place through the porous outer layer and through the pores in the inner layer.

The siphuncular structure in orthoceratids fully agrees with that in actinoceratids. Each septal neck (sn) consists of an outer spherulitic-prismatic layer, a nacreous layer, and an inner prismatic layer (sph, nac, pr, Text-Fig. 1D, E), and each connecting ring (conn) of an outer spherulitic-prismatic layer and an inner calcified-perforate layer (sph, cp, Text-Fig. 1D, E).

In the connecting ring of *Orthoceras regulare* and *Orthoceras scabridum* (family Orthoceratidae) the spherulitic-prismatic layer is usually thinner than the calcified-perforate layer (sph, cp, Text-Fig. 1D; Pl. 2, Figs. 2, 5; Pl. 3, Figs. 2, 3). The pores in the latter layer have a somewhat irregular, anastomosing course in *O. regulare* (cp, Pl. 3, Fig. 3), whereas they are oriented transversally to the siphuncular surface in *O. scabridum* (cp, Pl. 2, Fig. 5).

The family Baltoceratidae has been classified with ellesmeroceratids because the connecting ring is considerably thickened. However, as shown in the baltoceratid genus *Cochlioceras* (Text-Fig. 1E; Pl. 2, Figs. 1, 6) only the outer spherulitic-prismatic layer (sph) is much thicker than that in *O. regulare* and *O. scabridum*, whereas the inner layer is a typical calcareous-perforate layer (cp) with numerous transverse pores. On the basis of connecting ring structure and dorsal position of retractor muscle scars (see below), the family Baltoceratidae is assigned here to orthoceratids and not to ellesmeroceratids.

DZIK (1984) moved the family Lituitidae from tarphyceratids to orthoceratids, and erected for this family a new suborder Lituitina, characterized by shell shape and thin connecting rings. Also KING (1993, 1998) assigned lituitids to orthoceratids. However, the connecting ring structure in this family remained unknown. My studies show that the connecting ring (conn, Pl. 2, Fig. 3) in the lituitid genus *Lituites* has an outer spherulitic-prismatic layer and an inner calcified-perforate layer, the latter traversed by numerous, elongated pores (sph, cp, Pl. 2, Fig. 4). Thus, the connecting ring structure in lituitids fully agrees to that in orthoceratids.

The shape, size and number of pores in the calcified-perforate layer of the connecting ring varies: in *Donacoceras* the pores are large and sparse (MUTVEI, 1998), whereas in most other genera hitherto studied (*Orthoceras*, *Polygrammoceras*, *Cochlioceras*, "*Geisonoceras*", *Lituites*, *Rhynchorthoceras*, *Michlinoceras*) (MUTVEI, here and unpublished) they are small, elongated and abundant (Text-Fig. 1F).

3.4.2. Retractor Muscle Scars

The annular elevation in orthoceratids forms an unpaired or paired, low anterior lobe or lobes on the dorsal side of the living chamber. This lobe or these lobes were the site of retractor muscle scars (rms, Text-Fig. 2C). In relation to the size of the living chamber, the area of the retractor muscle scars is often smaller than that in *Nautilus* and tarphyceratids.

In actinoceratids here examined, the annular elevation is indistinct and forms a narrow band around the living chamber. Therefore, it has not been possible to distinguish the position of the retractor muscle scars. However, FREY (1995) reported the presence of dorsal retractor muscle scars in actinoceratids.

As pointed out by MUTVEI (1957, Text-Fig. 7E; 1964, Figs. 3C, 6A–C), the retractor muscles in orthoceratids (rm, Text-Fig. 2A, B) did not form a roof on the ventral mantle cavity (vmc) as do/did those in *Nautilus* and tarphyceratids. Their contractions could not therefore have been used to expel water from the mantle cavity in order to make jet-powered swimming possible.

3.5. Endoceratids

3.5.1. Siphuncle

As defined in the "Treatise" (TEICHERT, 1964), endoceratids include several taxa in which detailed siphuncular structure is still inadequately known. According to the present writer (MUTVEI, 1997b), the septal neck in *Dideroceras*, *Anthoceras* and *Suecoceras*, all assigned to Endoceratidae, is long, being equal or longer than the distance between septa. It is composed of the same three, structurally different, aragonite layers as in other nautiloids considered above: the outer spherulitic-prismatic, nacreous, and the inner prismatic. In the apical direction the nacreous layer gradually decreases in thickness, forming an acute angle at the distal end of the neck.

The connecting ring in endoceratids is thick, unilayered, and composed of a continuation of the porous spherulitic-prismatic layer of the septal neck. The inner layer of the connecting ring is absent and replaced by the long septal neck.

3.5.2. Retractor Muscle Scars

In three shells of *Anthoceras* cf. *vaginatum*, two collected in Tallinn and one in Kandle, Estonia (Lower Ordovician Kundan Stage and Middle Ordovician Lasnamägi Stage,

respectively), the annular elevation is clearly visible (MUTVEI, unpublished). It is narrow ventrally and laterally but forms an adorally directed, low lobe dorsally, indicating the dorsal position of the scars of the retractor muscles. Thus, the retractor muscle scars in endoceratids had the same size and the same dorsal position as those in orthoceratids. On the basis of siphuncular structure and position of retractor muscle scars it seems justified to classify endoceratids with orthoceratids, and not with ellesmeroceratids, as suggested by DZIK (1984).

4. Cameral Deposits

Cameral deposits have been reported in a great number of orthoconic nautiloids belonging to orthoceratids and actinoceratids. As described above, these nautiloids have the calcified inner layer of the connecting rings traversed by numerous pores. The cameral deposits are rare or absent in other nautiloids which possessed a different type of connecting ring.

According to most authors, the cameral deposits have been secreted during the lifetime of the animal; a minority have advocated a post-mortem origin for these deposits. Chemical analyses show that well preserved aragonitic cameral deposits have twice the Sr content of shell wall and septa (CRICK & OTTENSMA, 1983). The high Sr content in cameral deposits was confirmed by DAUPHIN (1989). The writer also noted that the Sr content in the cameral deposits is closer to that in the adjacent sediment than to that in the shell.

It has been proposed that the cameral deposits in orthoconic shells functioned as ballast to increase the weight of the posterior portion of the shell so that the shell and the hyponome became oriented horizontally. The latter was considered as a requirement for jet-powered swimming. However, actinoceratids and orthoceratids were probably unable to perform jet-powered swimming because:

- 1) The animals had an external, long, slightly exogastrically coiled shell, lacked fins and were therefore unable to steer; and
- 2) the retractor muscles were small, originated dorsally and, consequently, had a different spatial relationship to the ventral mantle cavity than those in *Nautilus*, and they could not effect jet-powered swimming (MUTVEI, 1964).

Satisfactorily to explain the origin of the cameral deposits the following problems still need to be resolved:

- 1) As pointed out by MUTVEI (1956, Pl. I: 1, 2, 4), cameral lamellae in *Lamellorthoceras* often project into the siphuncular cavity. This indicates that at least distal parts of the lamellae had an epitaxial post-mortem growth, and that we have no means of distinguishing which part of the deposit was formed during the lifetime of the animal and which post-mortally.
- 2) In the Mediterranean, and in tropical and sub-tropical seas, precipitation of aragonite and calcite invariably takes place post-mortally in shell cavities (ALEXANDERSSON, 1972, 1974). Much of these precipitates are similar to cameral deposits.
- 3) GRÉGOIRE & TEICHERT (1965) found organic sheets within cameral deposits and considered this as an important proof of the organic origin of these deposits. However, organic sheets have also been reported often to occur in inorganically formed ooids (MITTERER, 1971, 1972a,b).

- 4) In *Nautilus* the siphuncular epithelium first secretes the septal neck and connecting ring. After this secretory phase, the epithelial cells undergo a structural change and begin to pump the cameral liquid out through the connecting ring. Thus, the epithelial cells cannot secrete calcium carbonate and simultaneously pump the liquid from the shell chambers. Precipitation of cameral deposits required that the chambers were completely filled with liquid. This is in conflict with the hydrostatic function of the chambered shell.

4. Discussion and Conclusions

Buoyancy regulation has been considered by several authors as one of the major factor in nautiloid evolution. This regulation was aimed to give the animal maximum stability and the most favourable orientation for swimming. However, as in ammonoids, only a minority of nautiloids seem to have had an anatomical design and shell shape adapted for jet-powered swimming.

In tarphyceratids the retractor muscle scars were often much larger than in orthoceratids-endoceratids, and situated ventrally and/or laterally. These muscles had a similar spatial relationship to the ventral mantle cavity as those in *Nautilus*, forming a roof over this cavity. Consequently, they could have been used for jet-powered swimming by expelling the water from the mantle cavity. However, although fulfilling this requirement, tarphyceratid shells seem to be often poorly streamlined. For example, the genus *Estonioceras* includes species with evolute and gyroconic shells with no sign of selection towards streamlining.

Specializations of connecting ring structures indicate that many nautiloid taxa were capable of vertical migrations by changing the volume of cameral liquid. This function seems to have been a more important factor in nautiloid evolution than a capability for jet-powered swimming. Several types of connecting ring structure emerged in the Ordovician. In the present paper only two types are dealt with: the tarphyceratid type and the calcified-perforate

type (MUTVEI, 1997a, and unpublished). The tarphyceratid type resembles that in *Nautilus* except that the outer spherulitic-prismatic layer was thicker, sometimes much thicker. The inner glycoprotein (conchiolin) layer, present in *Nautilus*, has been diagenetically destroyed in tarphyceratids. How many other taxa share the tarphyceratid type of connecting ring is still unknown. In the calcified-perforate type of connecting ring of orthoceratids and actinoceratids, the inner glycoprotein layer was substituted by a calcified layer perforated with pores, generally very numerous. The latter type of connecting ring seems to occur in all members of the orthoceratids and actinoceratids, and thus represents an important distinctive feature for these taxa.

The present writer (MUTVEI, 1964) emphasized that the position of retractor muscle scars is an important systematic feature, and that different positions of retractor muscle scars indicate anatomical differences in fossil nautiloids. This was opposed by SWEET (1959) who believed that the position of these scars could be easily changed. However, despite different shell shapes most ammonoids have paired dorsal scars indicating a dorsal position of retractor muscle scars (DOGUZHAIEVA & MUTVEI, 1996), probably inherited from orthoceratid ancestors.

On the basis of the number and position of retractor muscle scars, MUTVEI (1964) classified fossil nautiloids in three major taxa: Orthoceratomorphi, Nautilomorphi and Oncoceratomorphi. Orthoceratomorphi were characterized by a dorsal position for retractor muscle scars. This taxonomic category is replaced here by the order Orthoceratida KUHN 1940 that includes orthoceratids, actinoceratids and endoceratids. A common diagnostic feature for orthoceratids and actinoceratids is the occurrence of an inner calcified-perforate layer of the connecting ring, traversed by numerous pores.

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Plate 1

Tarphyceratid *Estonioceras* sp.

Fig. 1: Median section of a connecting ring (conn) and two septal necks (sn); note that the connecting ring (conn) consists only of the spherulitic-prismatic layer (sph), and that the inner surface of the septal neck (sn) and adoral surface of the septum is covered by a prismatic layer (pr).
× 15.

Fig. 2: Higher magnification of a median section to show the prismatic (pr), nacreous (nac) and spherulitic-prismatic (sph) layers of the septal neck (sn), and the spherulitic-prismatic layer (sph) of the connecting ring; note that the inner portion of the spherulitic-prismatic layer of the neck is more dense (x) than the rest of the layer.
× 35.

Tarphyceratid *Planctoceras falcatum*

Figs. 3,4: Median sections of a connecting ring (conn) and septal neck (sn) to show close structural similarity with those in *Estonioceras* sp.
× 35.

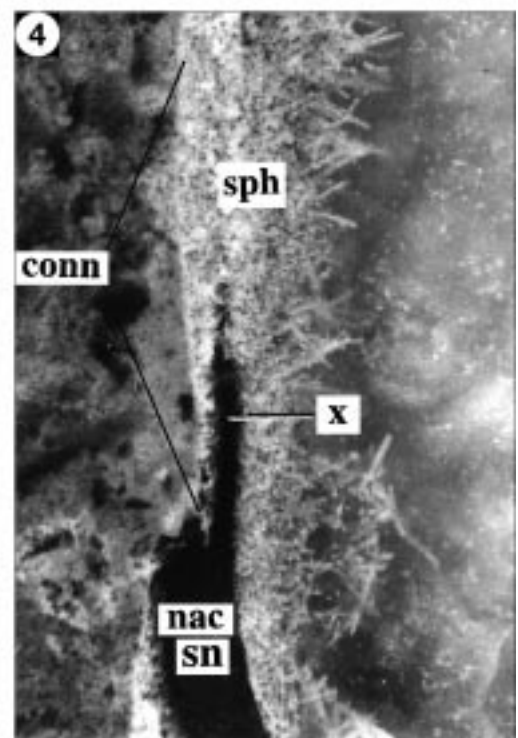
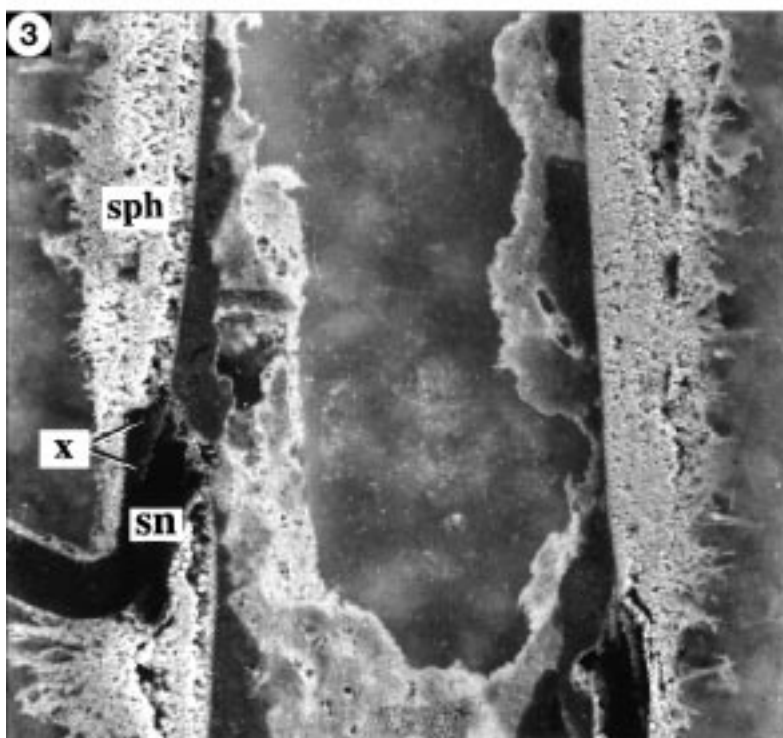
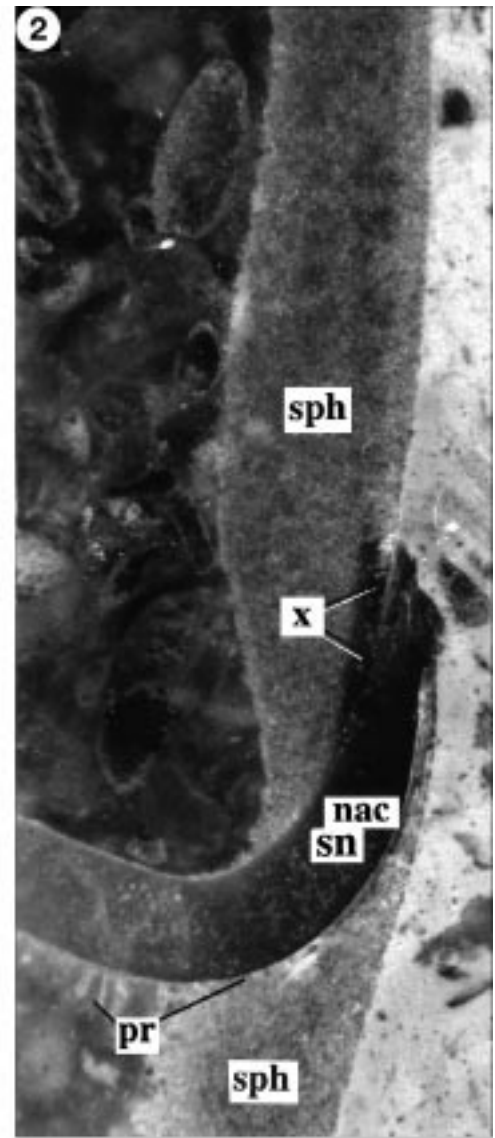
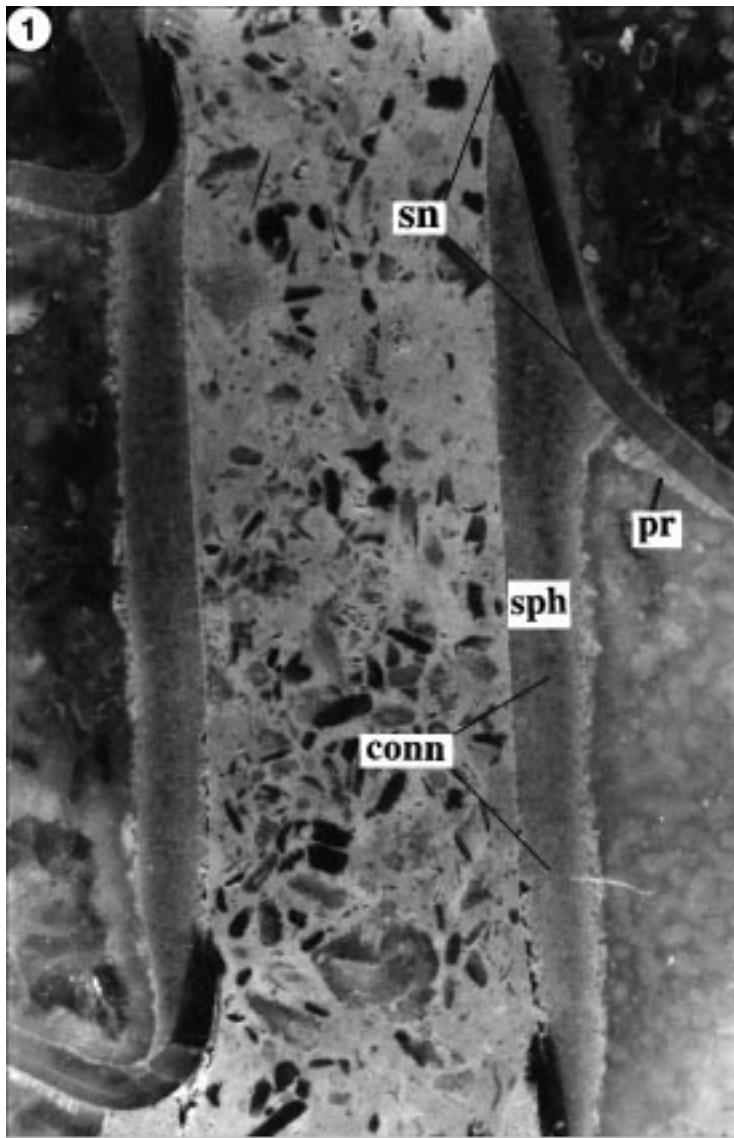


Plate 2

Orthoceratid *Cochlioceras* sp.

Fig. 1: Median section of a connecting ring and a septal neck (sn); the connecting ring consists of a thick outer spherulitic-prismatic layer (sph) and an inner calcified-perforate layer (cp) with pores; note that the calcified-perforate layer (cp) is a direct, structurally modified, continuation of the nacreous layer of the neck (nac).
× 40.

Fig. 6: Cross section of a connecting ring to show the thick spherulitic-prismatic layer (sph) and calcified-perforate layer (cp) with pores.
× 30.

Orthoceratid *Orthoceras scabridum*

Fig. 2: Median section of a connecting ring showing a thin spherulitic-prismatic layer (sph) and a calcified-perforate layer (cp) with pores.
× 50.

Fig. 5: Cross section of a connecting ring with spherulitic-prismatic layer (sph) and calcified-perforate layer (cp) with pores.
× 40.

Orthoceratid *Lituiles* sp.

Fig. 3: Median section of the connecting ring (conn) showing two layers.
× 50.

Fig. 4: Paramedian section of a connecting ring to show the outer spherulitic-prismatic layer (sph) and the inner calcified perforate layer (cp) with numerous elongated pores.
× 30.

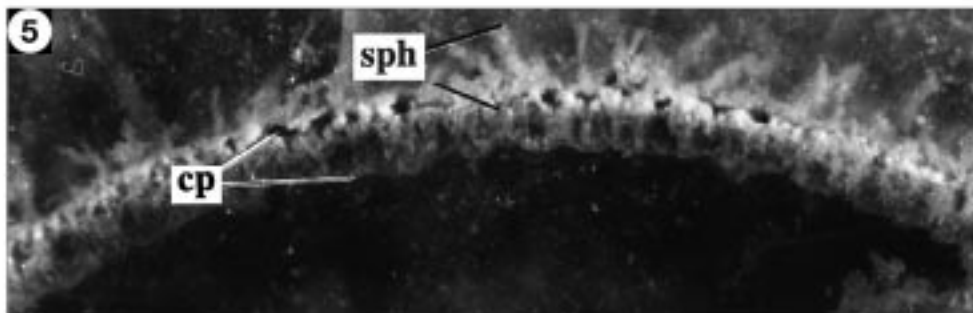
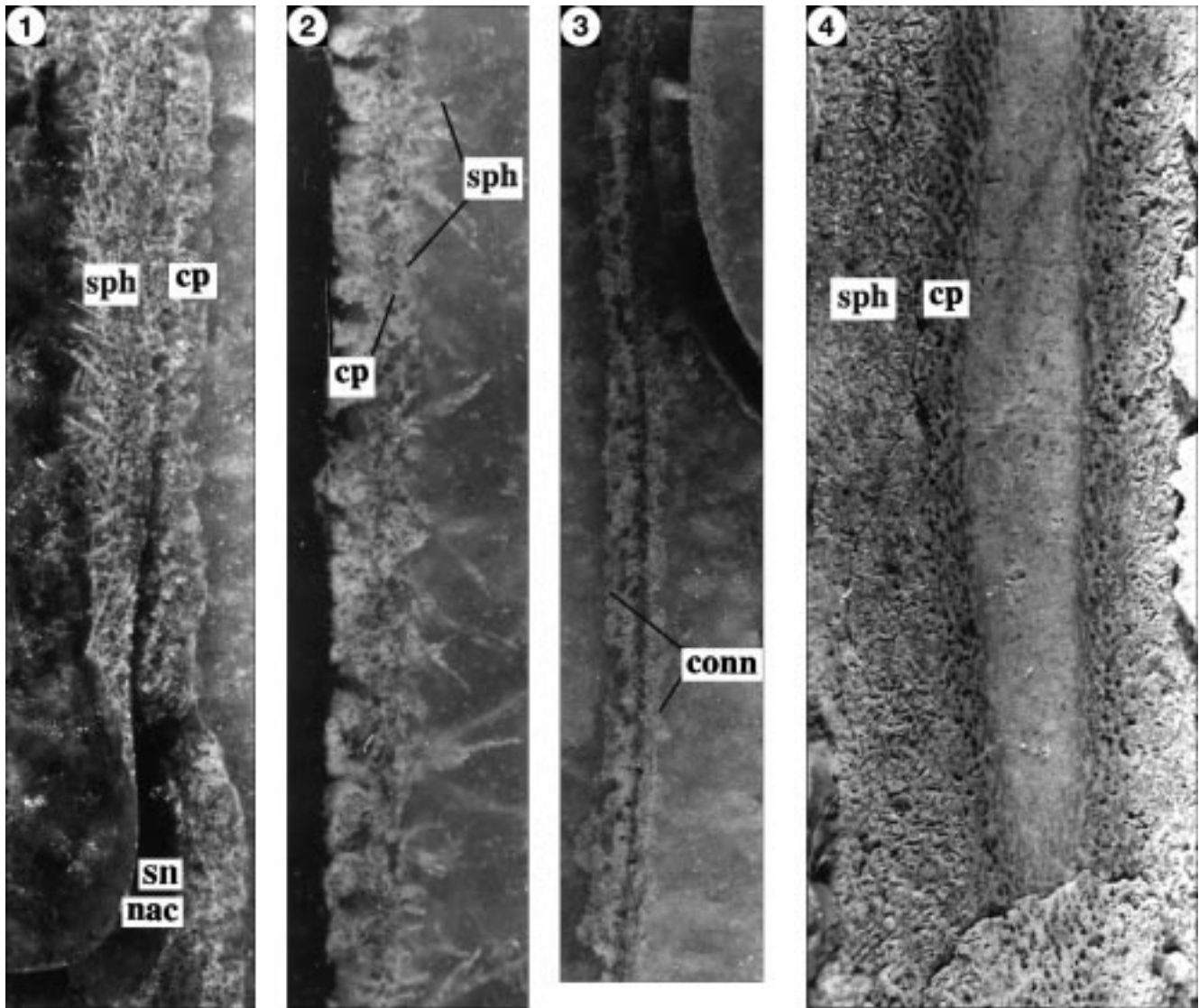


Plate 3

Orthoceratid *Orthoceras regulare*

Fig. 1: Median section of a connecting ring (conn) and a septal neck (sn).
× 20.

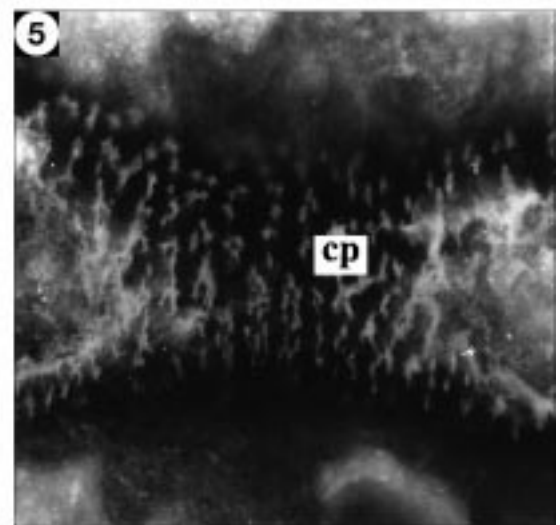
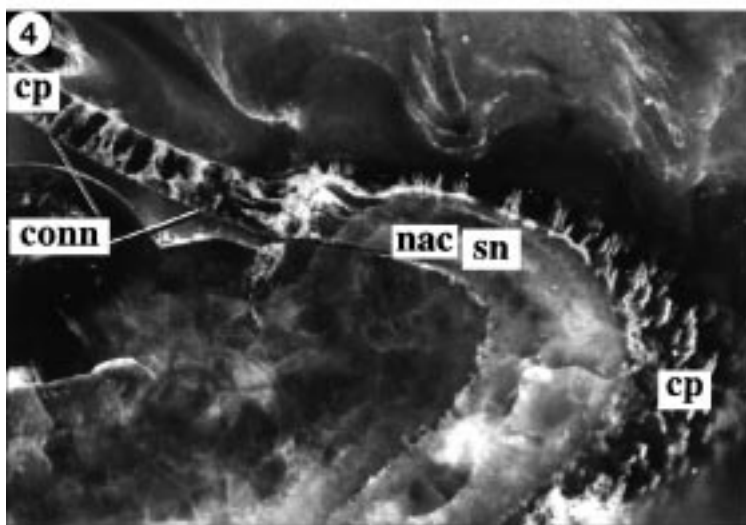
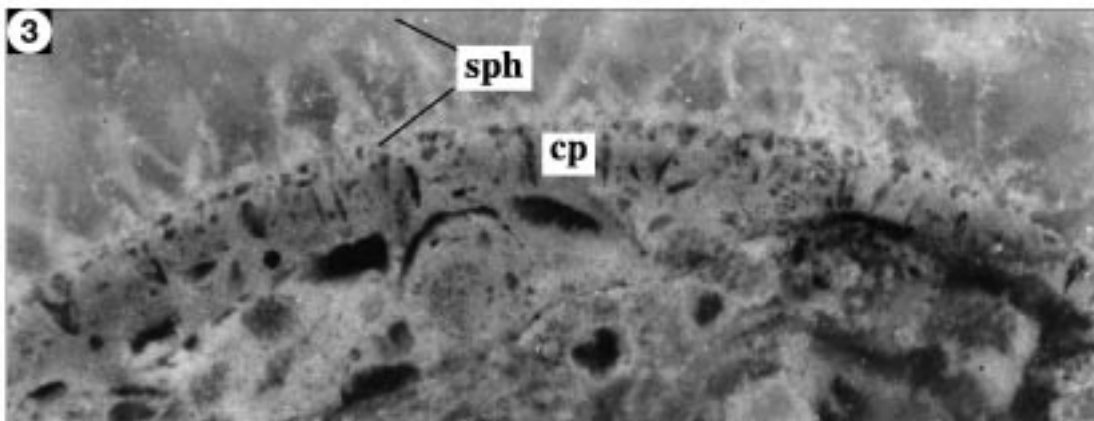
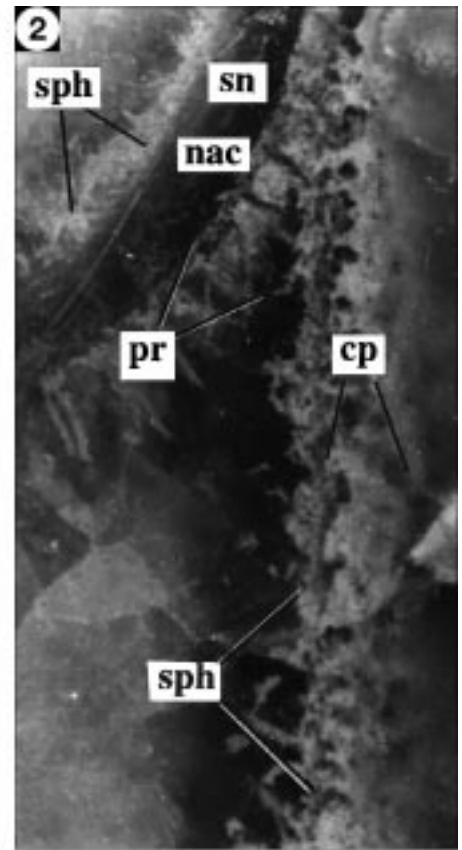
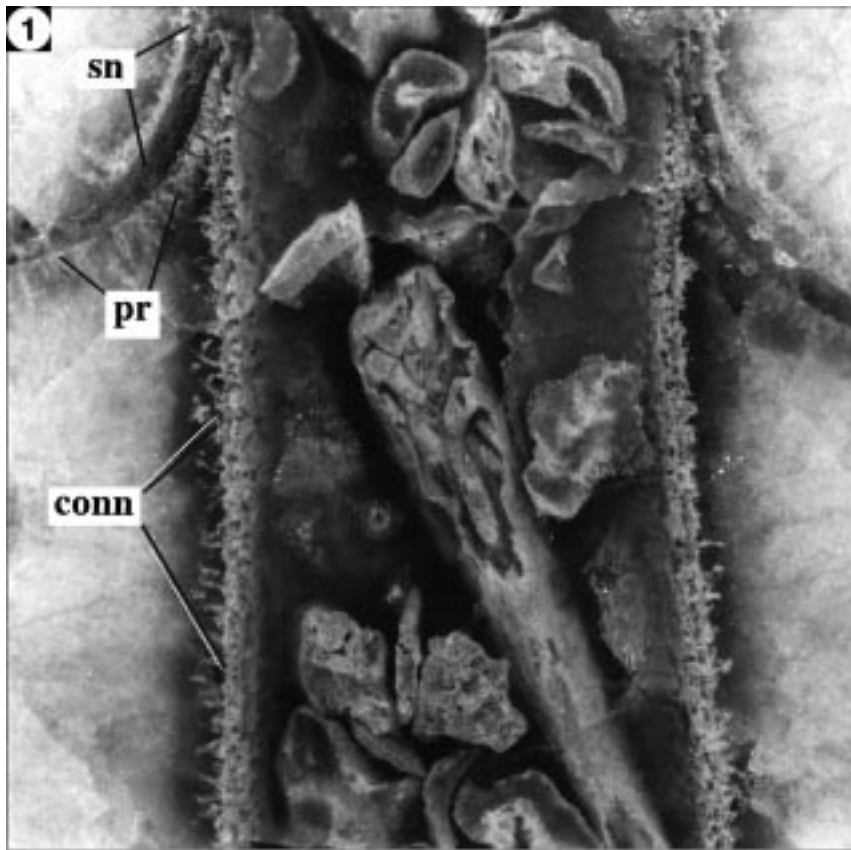
Fig. 2: Detail of Fig. 1 showing three layers of the septal neck (sn): prismatic (pr), nacreous (nac) and spherulitic-prismatic (sph), and two layers in the connecting ring: spherulitic-prismatic (sph) and calcified-perforate (cp) with irregularly arranged pores.
× 50.

Fig. 3: Cross section of a connecting ring with spherulitic-prismatic layer (sph) and calcified-perforate layer (cp); note that in the latter layer the pores have a somewhat irregular course.
× 60.

Actinoceratid *Adamsoceras holmi*

Fig. 4: Median section of a septal neck (sn) and connecting ring (conn) to show that the calcified-perforate layer of the ring (cp) is a structurally modified, direct continuation of the nacreous layer (nac) of the neck.
× 25.

Fig. 5: Paramedian section of the calcified-perforate layer (cp) of a connecting ring to show density and outlines of pores.
× 25.



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