# Revision of Middle Ordovician orthoceratacean nautiloids from Baltoscandia

BJÖRN KRÖGER

Kröger, B. 2004. Revision of Middle Ordovician orthoceratacean nautiloids from Baltoscandia. *Acta Palaeontologica Polonica* 49 (1): 57–74.

The fauna of the Baltoscandic Orthocerataceae is important because it fills a documentary gap between the Lower Ordovician fauna of North America and the upper Middle Ordovician fauna of China and North America. A revision of the Orthoceratidae, Geisonoceratidae, and Arionoceratidae is given on a material of more than 450 specimens. Intraspecific and ontogenetic variations were observed. The following new taxa are erected: *Plagiostomoceras fragile* sp. nov., *Archigeisonoceras repplingense* sp. nov., *Archigeisonoceras picus* sp. nov. *Archigeisonoceras folkeslundense* sp. nov., *Nilssonoceras latisiphonatum* gen. et sp. nov., *Kinnekulloceras kinnekullense* gen. et sp. nov., and *Arionoceras lotskirkense* sp. nov. The genus *Archigeisonoceras* is described for the first time in the Baltoscandic area and the oldest occurrence of the genus *Arionoceras* is documented from the Middle Ordovician of Baltoscandia. It is shown that the endosiphuncular deposits of the Middle Ordovician orthoceratacaceans are highly variable and widespread in the apical parts of the phragmocone.

Key words: Cephalopoda, Nautiloidea, Orthoceratacea, Ordovician, Baltoscandia.

*Björn Kröger [buxcreau@gmx.de], Geologisch-Paläontologisches Institut und Museum, Universität Hamburg, Bundesstr. 55, D-20146 Hamburg, Germany.*

## Introduction

The Baltoscandic Orthoceratite Limestone is a thinly bedded limestone or calcareous shale which is in parts extremely rich in macrofossils. Nautiloids are diverse and common in the limestone. After trilobites they are a dominant element of the preserved macrofauna. The name Orthoceratite Limestone ("Orthoceratitenkalk" of Hisinger 1828), refers to its macrofaunal characteristics. But it refers not to *Orthoceras sensu stricto* but to the term "orthoceraconic", which includes not only *Orthoceras* in its recent restricted meaning but also endoceratids and actinoceratids (see Jaanusson and Mutvei 1955). Orthoceratite Limestone is the autochthon shallow water carbonate of the Baltoscandic Ordovician. It was deposited in an epicontinental area south-east of the Caledonides between the late Tremadoc and the early Caradoc. The average rate of deposition of the limestones and shales was extremely low and the sequences were subdivided by numerous sedimentation breaks, erosion and omission horizons. The deposits rarely exceed a total thickness of more than 150 m (Jaanusson 1982a). The sediments of the Orthoceratite Limestone are exposed in several outcrops in northern Sweden (Jämtland), in central and southern Sweden (Dalarna, Öster-Västergötland, Närke, and Öland), and in the Pleistocene erratics in northern Germany and northern Poland. Detailed studies of the sedimentation history and the micro- and macrofaunal distribution of Jämtland were given by Jaanusson et al. (1982), of Västergötland by Jaanusson (1965a, b), of Öland by Jaanusson (1960), Jaanusson and Mutvei (1982), of the Siljan District of Dalarna by Jaanusson (1965a), and of Östergotland and Närke by Tjernvik (1956). Information on the stratigraphical zonation and origin of the erratics of northern Poland and northern Germany were given by, e.g., Remelé (1883), Gottsche (1877), Jentzsch (1880), Noetling (1882), Neben and Krueger (1971), and Hucke and Voigt (1967). A complex history of stratigraphical division and lithological classification caused usage of different terms for stratigraphical units in Baltoscandia. Fig. 1 gives a comparison of the usual terms of classification of the Orthoceratite Limestone.

Some typical nautiloids of the Orthoceratite Limestone are among the few paleontological objects that were described in pre-Linnéan time. Breynius (1732) used the name *Orthoceras* in his discussion of fossils obtained from glacial boulders near Gdańsk (Poland). Despite the complex and confusing later history of the terms *Orthoceras*, *Orthoceros*, and *Orthoceratites* (see Troedsson 1931; Teichert and Miller 1936; Teichert and Miller 1938; Sweet 1964), and the restricted recent meaning of the type species, *Orthoceras regulare* Schlotheim, 1820, "*Orthoceras*" is the popular synonym for the most characteristic element of the macrofauna of the Orthoceratite Limestone, the orthoconic nautiloids. The interest in these fossils in the 18th and 19th centuries was high. In Sweden, Wahlenberg (1818) and Hisinger (1837) were the first to describe the Ordovician nautiloids. They described and illustrated not single genotypes but form types of typical nautiloids. Some of the material is preserved at the Naturhistoriska Riksmuseet in Stockholm and at the Paleontologiska Institutionen, Uppsala Universitet. The Ordovician fauna of the erratic boulders of Germany and Poland, which originated from the Baltic Orthoceratite Limestone was described by Schlotheim (1820) and Boll (1857). Boll's collection is fortunately preserved at the regional Müritz Museum of Waren / Mecklenburg (Germany).

A second generation of scientists studying fossils of the Orthoceratite Limestone in Sweden were Angelin and Lindström (1880) and Holm (1885, 1891). Their collections are stored for the most part in the Naturhistoriska Riksmuseet in Stockholm. In Germany Dewitz (1879, 1880), Remelé (1880, 1882, 1883), Rüdiger (1889) and others published important studies. A major collection of cephalopods of the Orthoceratite Limestone is preserved at the Naturkundemuseum in Berlin. Barrande (1865–1877) illustrated and mentioned some Baltic cephalopods from what he called "regio asaphorum". Barrande's type species are housed in the Národní Museum in Prague (Czech Republic). In the twentieth century little descriptive work was done on the cephalopods of the Orthoceratite Limestone. Troedsson (1931, 1932) very carefully studied some orthoceratids of the upper parts of the Orthoceratite Limestone. Neben and Krueger (1971) illustrated a collection of some Ordovician cephalopods from the erratic boulders of northern Germany, and Dzik (1984) described and illustrated some Ordovician nautiloids of erratic boulders in Poland. In 1999 King published a short review of the Middle Ordovician nautiloids from Sweden. Recently Mutvei (2002) has studied the structure of the septal neck and connecting ring structures of some Middle Ordovician orthoceratids but did not discuss the status of the material at lower taxonomic levels.

From this short listing of studies on the nautiloids of the Baltoscandic Orthoceratite Limestone it will be evident that the main work on this topic was done in the late 19th century. The taxa appear to be described sufficiently in the excellent publications of that time. But as repeatedly mentioned the taxonomic status of many forms was not clear until now and an extensive revision of the described taxa is required (see e.g., Jaanusson and Mutvei 1955; Dzik 1984; King 1999). In the paleontological collections of institutions in northern Germany (e.g., Paläontologisches Institut und Museum Hamburg, Eiszeitmuseum Schleswig-Holstein, Müritz Museum Waren/ Mecklenburg, Paläontologisches Institut der Universität Greifswald, Naturkundemuseum Berlin) and in Sweden (e.g., Naturhistoriska Riksmuseet, Stockholm) many hundreds of specimens are housed, enough for statistical investigations on the variance of the traits of the stated taxa and to establish new taxa. It is surprising that this work has not been carried out since the late 19th century.

There are several vertically striated or fluted orthoceracones in the Baltoscandic Orthoceratite Limestone. These cephalopods were described in great detail by Troedsson (1932). However, a revision of these taxa regards a revision of the concept of the entire subfamily Kionoceratinae and related groups, which is beyond of the scope of the present work.

| Great Britain | Balto-scandia | Orthoceratite Limestone | | North America |
|---|---|---|---|---|
| Series | Stages | Bio-stratigraphy Moberg 1890 Jaanusson 1960 | Litho-stratigraphy Jaanusson 1960 | Stages |
| Caradoc | Kukruse | | Dalby L. | Chazy |
| | | | Furudal L. | |
| Llanvirn | Uhaku | *Illaenus crassicauda* | Folkeslunda L. | |
| | Lasnamägi | *Illaenus schroeteri* | Seby L. | |
| | Aseri | *Asaphus platyurus* | Skärlöv L. | |
| | | | Segerstad L. | Whiterock |
| | Kunda | *Endoceras vaginatum* | Holen L. | |
| Arenig | Volkhov | *Asaphus lepidurus* | Lanna L. | |
| | | *Ptychopyge limbata* | | |
| | Latorp | *Megalaspis planilimbata* | Latorp L. | Beekmantown |

Fig. 1. Subdivision and stratigraphical correlation of the Orthoceratite Limestone (L., Limestone).

# Material and methods

The investigated nautiloids are housed in the Naturhistoriska Riksmuseet, Stockholm, Sweden (NRM), the Naturkundemuseum Berlin, Germany (NMB), the Geologisch-Paläontologisches Institut und Museum, Univerität Hamburg, Germany (GIH), the Boll collection in the Müritz Museum Waren, Germany (MMW), the Eiszeitmuseum Schleswig-Holstein, Stolpe, Germany (ES), and the Institut für Geologische Wissenschaften, Ernst-Moritz-Arndt-Universität Greifswald, Germany (GIG). The Material of the NRM was repeatedly studied by former students who gave the nautiloids provisional names (*nomina nuda*). But no manuscript was found on the taxonomical attempts on the Orthoceratacea of the Orthoceratite Limestone. Two of the researchers who worked on these specimens were Troedsson and Holm. The Middle Ordovician Orthoceratacea of the Barrandian were studied at the National Museum in Prague in order to compare them with the Baltoscandic cephalopods. Almost 450 orthocerataceans have been investigated. Fifty-seven of them were cut and polished in order to investigate the inner structures of the phragmocone.

The nautiloids were described using some quantitative measurements: (1) The apical angle of the conch (a) is given by the tangents $^{-1}$ of the expansion rate (e). The expansion rate was calculated by dividing the difference between the diameter of the shell at two different points by the distance between them. (2) The relative height of the chambers (ch) is given by dividing the chamber height by the related diameter of the conch. (3) The relative position of the siphuncle (sp) is given by the smaller distance of siphuncle to shell divided by the quotient of the sum of the smaller distance of siphuncle to shell and greater distance of siphuncle to shell.

The statistical values are given as follows: X, mean; S, standard deviation; n, number of specimens/counts.

Completion of the synonymy list was done by using the "Nautiloidea 2000: Data Retrieval System Nautiloidea" by Engeser (Pal. Inst. FU Berlin) and Engeser (2000). All entries in the Data Retrieval System were additionally checked.

# Systematic description

## Order Orthocerida Kuhn, 1940
## Superfamily Orthoceratacea M'Coy, 1844 [nom. transl. Sweet 1964 ex Orthoceratidae M'Coy, 1844]

*Diagnosis*.—The shell of the Orthoceratacea is straight or slightly curved and smooth or ornamented and has a circular cross section. The siphuncle is central or subcentral with ortho- suborthochoanitic and seldom secondarily cyrtochoanitic, septal necks. Endosiphuncular and cameral deposits may occur.

## Family Orthoceratidae M'Coy, 1844

*Diagnosis*.—Ortho- to slightly cyrtoceraconic Orthoceratacea with a shell that is smooth or elaborately ornamented and generally subcircular in cross section. Endosiphuncular deposits are absent or occur only at the most apical parts of the shell.

*Remarks*.—Dzik (1984) included the Michelinoceratidae Flower, 1945, the Geisonoceratidae Zhuravleva, 1959, and the Folioceratidae Collins, 1969 within the Orthoceratidae M'Coy, 1844. He further subdivided the family level only at the generic level. Because of the pure extent and great differences within the species that are included in the family Orthoceratidae it seems necessary to divide the family into subfamilies and to define the Geisonoceratidae as a separate family. The practice of Sweet (1964) and e.g., Zhuravleva (1978), who subdivided the Orthoceratidae into the subfamilies will therefore be followed here. Sweet (1964) and Zhuravleva (1978), however, defined the Orthoceratidae by the absence of endosiphuncular deposits. As can be shown the genus *Orthoceras* developed endosiphuncular deposits in the most apicad parts (see Fig. 2A, B). Consequently, by definition of Sweet (1964) the genus *Orthoceras* is not a part of the Orthoceratidae or the entire family is obsolete. The dilemma is most easily solved by expanding the scope of the Orthoceratidae. Although no clear phylogenetic relationships are visible yet, this expansion should also be a consequence of the general observation of the evolutionary trend (or polarity) of the early Orthocerida in direction of the suppression of endosiphuncular deposits on the one side and of increased differentiation of the endosiphuncular deposits on the other side (Geisonoceratidae, Pseudorthoceratidae).

*Subfamilies included*.—Orthoceratinae M'Coy, 1844, emend. Sweet (1964), Michelinoceratinae Flower, 1945, emend. Ristedt (1968).

## Subfamily Orthoceratinae M'Coy, 1884 [nom. transl. Sweet 1964 ex Orthoceratidae]

*Diagnosis.*—Orthoceratidae with smooth shell, with fine longitudinal or transverse striation or with reticulate shell ornamentation. The shell expanding at a very small angle. 2–5 furrows in the living chamber.

*Remarks*.—In 1956 Balashov established the genus *Bifeovoceras*. The genus was accepted as a valid taxon of the Orthoceratinae by Balashov and Zhuravleva (1962) and Sweet (1964). Dzik (1984), however, regarded it as a junior, subjective synonym of *Orthoceras* Brugière, 1789. The proposal of Dzik (1984) is followed here (see discussion of *Orthoceras bifeovatum* Noetling, 1884).

*Genera included.—Orthoceras* Brugière, 1789, *Ctenoceras* Noetling, 1884

## Genus *Orthoceras* Brugière, 1789

*Type species*: *Orthoceratites regularis* Schlotheim, 1820.

*Diagnosis.*—"Straight orthoconic shells with longitudinal impressions of the living chamber. Exterior sculptured with transverse lines of growth forming a banding somewhat similar to that in *Geisonoceras*, but the bands are composed of densely crowded minute longitudinal ribs, which are especially well shown on a slightly weathered surface. Apertural angle small. Air chambers and siphuncle of medium size; siphuncle central or subcentral." (Troedsson 1931a: 12).

*Remarks*.—Beside the many definitions of the genus *Orthoceras* (e.g., d'Orbigny 1849; Balashov and Zhuravleva 1962; Sweet 1964; Dzik 1984) the diagnosis given by Troedsson (1931a) matches best the observations described herein. Troedsson's definition of the number of longitudinal impressions is not too narrow to include the strong variations of these features (see e.g., *Orthoceras quinquefeovatum* Noetling, 1884, which is shown by Troedsson (1931a) to be a variety of *Orthoceras regulare* with very long impressions) and it gives a certain importance to the shell ornamentation. The sculpture of *O. regulare*, *O. bifeovatum*, and *O. scabridum* is unique among the Baltoscandic orthoceratids.

*Species included.—Orthoceras regulare* Schlotheim, 1820, *Orthoceras bifeovatum* Noetling, 1884, *Orthoceras scabridum* Angelin, 1890.

## *Orthoceras regulare* Schlotheim, 1820

Fig. 2B.

*Orthoceras regulare* Schlotheim; Troedsson 1931: 13–16, 24–29 [cum syn.]

*Material.*—Forty specimens housed in the NRM, NMB, MMW, and GIH (in a large part the material of Troedsson 1931a). Many of these specimens preserve the adult chambers of the phragmocone and the living chamber; sometimes the recrystallized shell is preserved.

*Description.—Orthoceras regulare* was described in great detail by Troedsson (1931). The current description is there-

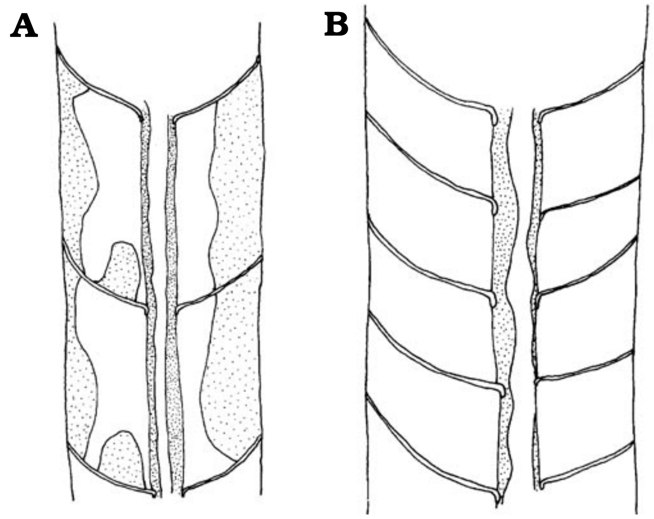



Fig. 2. Longitudinal sections of the apical parts of the phragmocone of *Orthoceras*. **A**. *Orthoceras* sp. from Czerwińsk near Kwidzyn, N Poland, NMB C. 5381, Lasnamägian (apical diameter 3.3 mm). **B**. *Orthoceras regulare* from Bydgoszcz, Poland, NMB C. 5382 (apical diameter 4.5 mm). Endosiphuncular and cameral deposits dotted.

fore mainly an abstract of Troedsson's work supplemented by some new measurements and observations.

*Conch form*: The conch shows a circular cross section. With a maximum diameter: 40 mm, mean diameter of last chamber of the adult phragmocone: 25 mm (max: 29 mm, min: 19 mm) it is the largest *Orthoceras*. The conch shows an apical angle of 1.7–2.9° (mean e: 2.3°).

*Ornamentation*: The shell displays fine, narrowly spaced transverse striae; the elevated space between the striae appear imbricated and flat in nearly mature and mature specimens, and is sharp and acute in the juvenile parts of the shell. In addition to the transverse ornamentation, very minute longitudinal striae form a net-like ornamentation only detectable in well preserved specimens. The transverse banding forms an adapical lobe on the ventral side. The inner part of the shell is smooth, sometimes irregularly punctured. The cast shows a normal line at the ventral side of the phragmocone.

*Phragmocone*: Chambers 0.5 (mean) of the respective diameter in high. Sutures straight and septa concave. Cast of the mural areas displays fine longitudinal lines. Septal necks orthochoanitic. The central to subcentral tubular siphuncle shows a diameter of 0.15 (0.14–0.17) of the respective diameter of the conch. Endosiphuncular lining has been observed in the more apicad parts of the phragmocone (see Fig. 2B). The deposits are more strongly developed in the ventral part of the shell.

*Living chamber*: The long adult living chamber is conical in shape. Three equiangularly arranged longitudinal impressions are found at about one third of the length of the adult living chamber. The impressions vary slightly in general shape but strongly in length (15–50 mm). They form 1–7 mm deep elongated notches in the shell. The conch at the position of the impressions is slightly constricted. The aperture widens rapidly orad of the constriction.

*Distribution*.—*Orthoceras regulare* occurs in the Seby and Folkeslunda Limestone (Lasnamägian) and in the Persnäs Limestone (Uhakuan) of Öland. It is also found in the Upper Grey Limestone (Lasnamägian) of the erratics of northern Germany and Poland.

## *Orthoceras bifoveatum* Noetling, 1884

Fig. 3.

*Orthoceras trochleare* Hisinger; Karsten 1869: 50, pl. 17: 7b.

**Orthoceras bifoveatum* sp. nov.; Noetling 1884: 111–115, pl. 16: 5, 6, pl. 17: 3, 4a, pl. 18: 1, 2.

pars *Orthoceras scabridum* Angelin; Rüdiger 1889: 5–8, pl. 1: 1, 2a, b.

*Orthoceras bifoveatum* Noetling; Troedsson 1931: 16, 29–31, pl. 1: 3–5, pl. 4: 6–10, text-fig. 2.

*Bifoveoceras bifoveatum* (Noetling); Balashov and Zhuravleva 1962: pl. 10: 9–11.

*Bifoveoceras* ("*Orthoceras*") *bifoveatum* (Noetling); Hucke and Voigt 1969: 57, pl. 16: 1.

*Orthoceras bifoveatum* Noetling; Dzik 1984: 95, 105, pl. 22: 8–10, text-figs. 34a, 39.4.

*Material*.—Seventeen specimens available in the NRM, the NMB, and the GIH, most specimens with preserved adult chambers of the phragmocone and living chamber. The shell is generally partly preserved.

*Description*.—*Conch form*: Cross section is slightly compressed or circular. Maximum diameter: 30 mm in the aperture (mean diameter of the aperture 25 mm); mean diameter of last chamber of the adult phragmocone: 21 mm (n = 6). Apical angle of the conch is 2.3–2.9°.

*Ornamentation*: Shell with fine, narrowly spaced transversal striae (< 1 mm). The raised spaces between the striae appear imbricated (see Fig. 6A) in nearly mature and mature growth stages and sharp and acute in juvenile ones. Striae turn apical in the flanks. Striae of the ventral side fall back in comparison to that of the opposite side. Inner shell smooth, sometimes slightly irregularly punctured, as in *Orthoceras regulare*. The cast shows a normal line at the ventral side of the phragmocone.

*Phragmocone*: Chamber height approx. 0.5 (mean) of the respective diameter. Sutures straight. Septa strong by concave. Impression of the mural areas display fine longitudinal

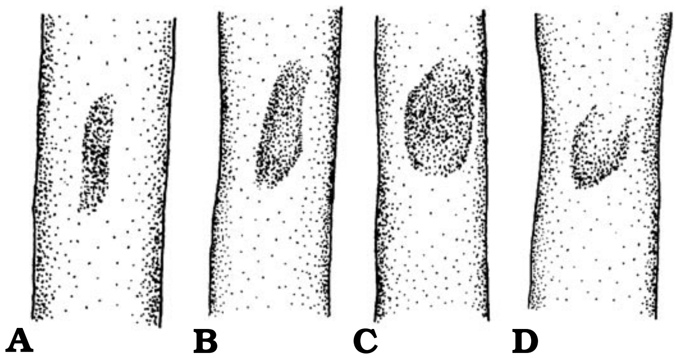



Fig. 3. Variation of the body chamber impressions in adult *Orthoceras bifeovatum* Noetling (right flanks, apex down, × 0.7). **A**. NMB C. 5383, coll. Remelé 1241. **B**. NRM-Mo 154270. **C**. NMB C. 5384, coll. Remelé. **D**. NRM-Mo 154268.

lines. Short orthochoanitic septal necks. Siphuncle subcentral. Siphuncular diameter 0.15–0.2 of the respective diameter of the conch. Hypo- and episeptal and endosiphuncular deposits were observed. Endosiphuncular deposits occur at the most apical parts of the shell (Dzik 1984). Endosiphuncular deposits in form of highly irregular asymmetrical annuli/lining, living chamber long (max. 120 mm).

*Living chamber*: Conical adult living chamber with two, more or less developed (half-moon shaped), lateral impressions in the last quarter. The impressions are highly variable in shape (see Fig. 3), length and depth. Aperture widens rapidly orad of the constriction.

*Remarks*.—The species was described in detail by Noetling (1884) and Troedsson (1931a). The recent observation of a larger amount of material confirms the findings of both authors. Juvenile specimens of the genus *Orthoceras* show a set of features which allow a good differentiation at the species level. Troedsson (1931a) says that "The banding (of *Orthoceras bifoveatum*, the author) [...] is rather similar to that in *Geisonoceras scabridum*..." (Troedsson 1931a: 29), but it is distinctly coarser. The fine longitudinal striation of the shell of *Orthoceras regulare* and the dimension of the siphuncle of *Orthoceras scabridum* are good diagnostic traits for excluding specimens from *Orthoceras bifeovatum*. The adult size of *Orthoceras bifoveatum* is intermediate between *Orthoceras regulare* and *Orthoceras scabridum*.

*Distribution*.—*Orthoceras bifoveatum* occurs in the Seby and Folkeslunda Limestone (Lasnamägian) of Öland and Östergotland and in the Furudal Limestone (Uhakuan) of Dalarna. It is also found the Upper Grey Limestone (Lasnamägian) of the erratics of northern Germany and Poland.

## *Orthoceras scabridum* Angelin, 1880

Figs. 4, 11C.

*Orthoceras regulare* v. Schlotheim; Boll 1857: 69–70, pl. 3: 7a–c.
*Cycloceras trochleare* Hisinger; Eichwald 1860: 1223–1225, pl. 51: 23 a, b.
*Orthoceras regulare* Schlotheim; Karsten 1869: 46, pl. 15: 8a–e (*fide* Angelin, 1880).
*Orthoceras trochleare* (Hisinger); Karsten 1869: pl. 17: 7a, b.
* *Orthoceras scabridum* sp. nov.; Angelin 1880: 4, pl. 4: 6–9, pl. 7: 8–10.
pars *Orthoceras scabridum* Angelin; Rüdiger 1889: 5–8, pl. 1: 1, 2a, b, pl. 2: 9.
*Orthoceras scabridum* Angelin; Holtedahl 1909: 40–42.
*Orthoceras scabridum* Angelin; Yü 1930: 54.
*Geisonoceras scabridum* Angelin; Troedsson 1931: 16–17.
*Geisonoceras constrictum* sp. nov. [*nomen nudum*]; Troedsson 1931: 16.
"*Geisonoceras*" *scabridium* (Angelin) [nom. null.]; Sweet 1958: 9–10.
"*Geisonoceras*" *scabridium* (Angelin) [nom. null.]; Sweet 1959: 296.
*Orthoceras scabridum* Angelin; Hucke and Voigt 1967: 56.
"*Geisonoceras*" *scabridum* (Angelin); Neben and Krüger 1971: pl. 30: 4–6.
*Orthoceras scabridum* Angelin; Dzik 1984: 97, 105, pl. 24: 1, 2, 6–8, text-figs. 35c, d, 39.6.

*Holotype/paratype*: Two specimens illustrated in Angelin (1880): pl. 4: 6, 7, 9 from Öland are housed at the NRM. The adult chambers of the phragmocone, the living chamber and the recrystallized shell are preserved.

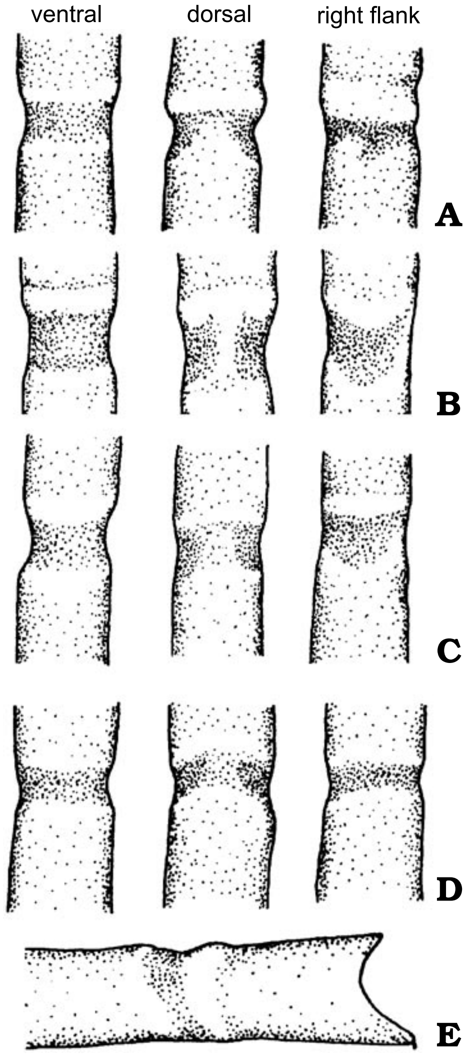



Fig. 4. Variation of the body chamber impressions and aperture in adult *Orthoceras scabridum* Angelin (A–D, × 0.8; E, × 1). **A**. NRM-Mo 3140. **B**. NRM-Mo 155513. **C**. NRM-Mo 155520. **D**. NRM-Mo 154202. **E**. NRM-Mo 155508.

*Material*.—Forty-three specimens housed in the NRM and the NMB, and five specimens at the MMW, most of them with preserved adult chambers of the phragmocone and living chamber. Sometimes the shell is partly preserved.

*Description*.—*Conch form*: Cross section of the conch slightly compressed or circular in juvenile specimens. Maximum diameter: 21 mm in the aperture (mean diameter of the aperture 17 mm). Mean diameter of last chamber of the adult phragmocone: 16 mm. Apical angle of the conch 5.1° (mean). Apical angle of the illustrated types in Angelin (1880): 4°.

*Ornamentation*: Shell with fine, narrowly spaced transversal striae (< 1 mm). The raised spaces between the striae appear imbricated (see Fig. 6A). The striae turn apical at the lateral sides. The striae of the ventral side fall back in comparison to that of the opposite side (see Fig. 4E for shape of the aperture, which resembles the outline of the growth

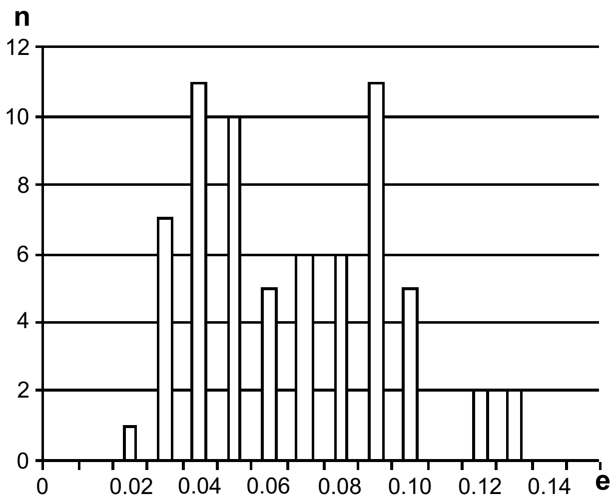



Fig. 5. Histogram of the entire number of observed *Orthoceras* (n = 66) classified by the expansion rate (e). The frequency peak between e = 0.04 (a = 2.3°) – 0.05 (a = 0.9°) represents *O. bifeovatum* Noetling and *O. regulare* Schlotheim, the frequency peak between e = 0.09 (a = 5.1°) – 0.1 (a = 5.7°) represents *O. scabridum* Angelin.

lines.). Inner shell smooth, sometimes irregular, punctured as in *Orthoceras regulare*. The cast shows a normal line at the ventral side of the phragmocone.

*Phragmocone*: Chambers height 0.5 (mean) of the respective diameter, sometimes with strong variations during the whole ontogeny. Sutures straight, septa strongly concave. Impressions of the mural areas display fine longitudinal lines. Short orthochoanitic septal necks. Subcentral siphuncle. Siphuncular diameter 0.1 of the respective diameter of the conch. Cameral and endosiphuncular deposits not observed.

*Living chamber*: Adult living chamber long conical in shape. Adult aperture with lateral openings (see Fig. 4E). Adult living chamber with two, more or less developed (crescent shaped), lateral impressions and a connected constriction at the last third (see Fig. 4). The ventral side of this constriction is slightly flattened, so that a cross section of the adult chamber through the area of the constriction is triangular. Aperture widens rapidly adorally to the constriction.

*Remarks*.—Angelin (1880) gave the first detailed description of *Orthoceras scabridum*. He observed the narrow, lowly elevated and inaequidistant striae of the shell and the impressions of the living chamber: "*Concameratio ultima foveis transversalibus distantibus duabus vel tribus constricta.*" (Angelin 1880: 4). Rüdiger (1889) mentioned many more important details of the shell of *Orthoceras scabridum*. He observed the

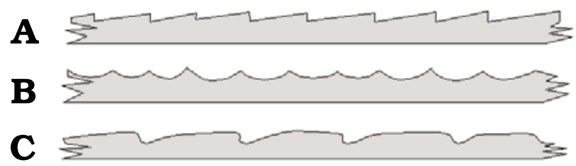



Fig. 6. Schematic sketches of the cross section of the shell. Shell ornamentation of *Orthoceras* (**A**), *Nilssonoceras* (**B**), and *Kinnekulloceras* (**C**) (aperture to the right).

imbricated nature of the many so-called fine "Ringürtel" of the shell. He very carefully described the dorsomyarian muscle attachment scars, which are preserved in many cases in the deepest parts of the living chamber casts in many cases. Furthermore, he mentioned a variation in the typical constrictions/impressions of the living chamber illustrated in Fig. 4. Troedsson (1931a) described an extreme form which occurs in the Seby Limestone of Öland, under the name "*Geisonoceras constrictum*"(*nomen nudum*). The lateral impressions of these variations (see Fig. 4D) are much less or only incipiently developed and only a ring-like furrow is visible. The two specimens examined in the NRM were considered to fall within the variation of *Orthoceras scabridum*. Until now there is no evidence that these specimens belong to a preceding taxon of *Orthoceras scabridum*, because older specimens found in the Segerstad Limestone show the typical shape of the adult living chamber. Instead it is interesting to consider how closely *Orthoceras scabridum* in some cases resembles *Orthoceras bifoveatum* (Fig. 3D). The adult *Orthoceras scabridum* is usually smaller than *Orthoceras bifoveatum*; its relative siphuncle diameter is significantly greater and the apical angle of the shell is clearly smaller (see Fig. 5).

*Distribution.—Orthoceras scabridum* occurs in the Segerstad, Seby, and Folkeslunda Limestone (Aserian–Lasnamägian) of Öland, Dalarna, Västergotland, Östergotland, and in the erratics of northern Germany and Poland. Holtedahl (1909) mentioned it in the *Coelospheridium* Beds (Kukrusian) of the Lake Mjösa district in Norway.

## Genus *Ctenoceras* Noetling, 1884, emend. Sweet (1958)

*Type species*: *Ctenoceras schmidti* Noetling, 1884.

*Diagnosis*.—Slightly cyrtoconic, slightly compressed shell, with prominent sinuous annulations, growth lines, and fine longitudinal costules. Body chamber with two dorsal and one ventral impression. Siphuncle subcentral, exogastric, and nearly tubular with orthochoanitic septal necks.

*Remarks*.—Balashov and Zhuravleva (1962) attributed the genus to Cycloceratinae Hyatt, 1900 as a subfamily of the Orthoceratidae. Sweet (1958) attributed it with reservation to the Stereoplasmoceratidae and later (Sweet 1964) questionably to the subfamily Orthoceratinae. The questionable status of the genus in the 1960s had its reasons in the unknown internal characters. New material from Estonia shows hat the connecting ring of *Ctenoceras schmidti* resembles closely that of *Orthoceras regulare*. The Fig. 11A shows a spherulitic-prismatic outer connecting ring as it is well known in *Orthoceras regulare* and *Orthoceras scabridum*. It must be summarised that *Ctenoceras* shares a lot of characters with typical members of the genus *Orthoceras*: an ornamentation consisting of growth lines, which are rectangular crossed by longitudinal costules, a characteristic structure of the connecting ring, shape of septal necks and typical impressions of the body chamber. *Ctenoceras* is therefore considered to be a close relative of *Orthoceras*.

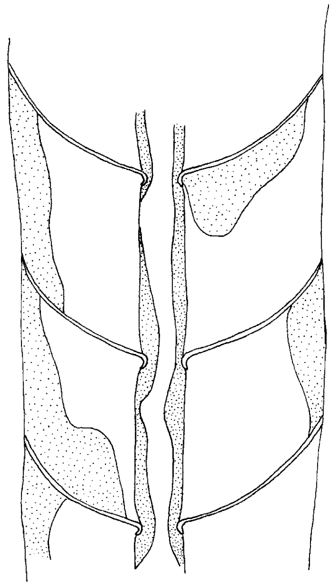


Fig. 7. Longitudinal section of the apical part of the phragmocone of *Archeisonoceras folkeslundense* sp. nov. (NRM-Mo 155476, holotype, diameter of the shell 10 mm).The cameral and endosiphuncular deposits are dotted. Note the short cyrtochoaniticseptal necks.

*Species included.—Ctenoceras schmidti* Noetling, 1884, *Ctenoceras chinense* Lai and Wang, 1981.

## *Ctenoceras schmidti* Noetling, 1884

Fig. 11A.

*Orthoceras undulatum* Sowerby; Schmidt 1858: 197.
*Orthoceras verticillatum* v. Hagenow; Krause 1877: 24–25.
*Cycloceras hisingeri* Boll; Schröder 1880: 63.
* *Ctenoceras schmidti* sp. nov.; Noetling 1884: 116–122, pl. 16: 7, 8, pl. 18: 3–5a.
*Ctenoceras schmidti* Noetling; Troedsson 1931: 16.
*Ctenoceras schmidti* Noetling; Balashov and Zhuravleva 1962: 11: 8.
*Ctenoceras schmidti* Noetling; Sweet 1964: 255, fig. 155: 1a–c.
*Ctenoceras schmidti* Noetling; Neben and Krüger 1971: 17, figs.14–15.
*Ctenoceras schmidti* Noetling; Neben and Krüger 1973: 81, figs.14–17.
*Ctenoceras schmidti* Noetling; Dzik 1984: 97, 105, fig. 39.66.

*Material*.—Four specimens available in the NRM, nine at the NMB and the GIH, most specimens with preserved adult chambers of the phragmocone and living chamber. The shell is generally partly preserved.

*Description.—Conch form*: Slightly cyrtocone. Cross section is slightly compressed. Maximum diameter: 17 mm at aperture; apical angle of conch very low (~ 1°).

*Ornamentation*: Shell annulated (distance of two ribs 2–3 mm) with fine, narrowly spaced transversal growth lines (< 0.5 mm) parallel to the annulations, faint longitudinal costules. Annulation somewhat oblique, describing a lobe on the antisiphuncular side of the conch. Cast with normal line at ventral side of phragmocone.

*Phragmocone*: Chamber height approx. 0.5 (mean) of the respective diameter. Sutures straight. Septa strongly concave. Short orthochoanitic septal necks. Outer part of the connecting ring with a thin spherulitic-prismatic layer. Siphuncle subcentral. Siphuncular diameter about 0.15 mm of the respective diameter of the conch. Hypo-, episeptal, and endosiphuncular deposits not observed.

Living chamber: Conical adult living chamber with two crescent shaped, lateral impressions and a narrow, deep ventral impression at the last third of the living chamber. Length of the living chamber approx. 60 mm. Aperture widens slightly adorally to the constriction.

*Remarks.*—The shell shape and ornamentation is nearly similar to some orthocones of younger beds of the Ordovician and Silurian of the Baltoscandic area (e.g., *Tofangoceras*, *Dawsonoceras*). Especially parts of the phragmocone are indistinguishable from these taxa if only the surface characters are mentioned. This similarity led in the past to a repeated confusion (e.g., Schröder 1881). Possibly the name "schmidti" is borrowed from *Orthoceras schmidti* Boll, 1857 which is a Silurian kionoceratid with very similar ornamentation but different siphuncular shape. The badly preserved *Ctenoceras* sp. B from Sweet (1958) may also be an undescribed kionoceratid (see Dzik 1984: 120).

*Distribution.—Ctenoceras schmidti* occurs in the Upper Red Orthoceratitic Limestone (Lasnamägian) of Öland. It is also found in the Upper Grey Limestone (Lasnamägian) of the erratics of northern Germany and Poland.

## Subfamily Michelinoceratinae Flower, 1945 emend. Sweet (1964), emend. Ristedt (1968)

*Diagnosis.*—Orthoceratidae with a smooth or transversely striated shell, sometimes forming rings. The septal necks are ortho- to suborthochoanitic. Endosiphuncular deposits are not developed. Between the initial chamber and the rest of the conch no constriction is developed.

*Remarks.*—More than twenty genera are assigned to the Michelinoceratinae, but for the most part the shape of their apical parts is unknown. Therefore, it is not clear if these genera belong to the Michelinoceratinae *sensu* Ristedt (1968). Many authors refer to the definition of Sweet (1964), which

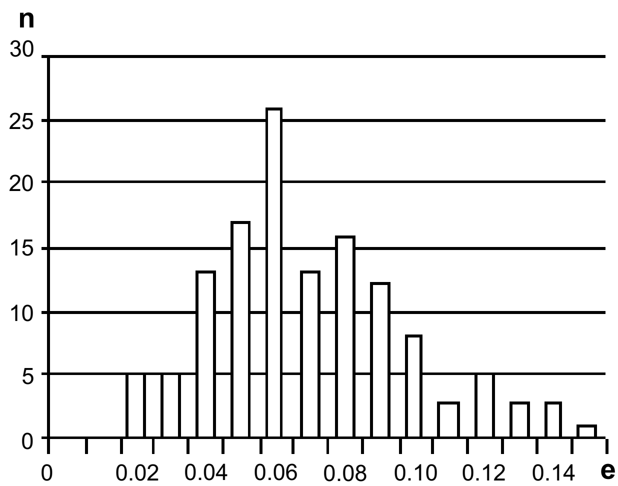



Fig. 8. Histogram of the entire number of observed specimens of *Nilssonoceras nilssoni* (Boll) (n = 130) classified by the expansion rate (e).

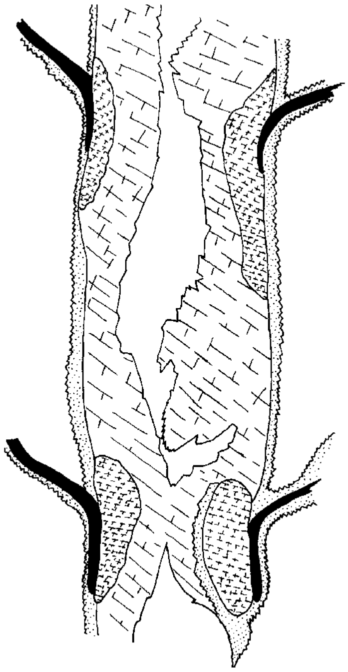


Fig. 9. Longitudinal section of the siphuncle of *Nilssonoceras latisiphonatum* sp. nov., NRM-Mo 158037, holotype (diameter of the siphuncle 10 mm). The siphuncle shows different areas of sparite (dotted: fin grained calcite, medium hatched: medium grained sparite, coarsely hatched: coarse grained sparite) which are interpreted as residues of the spherulitic prismatic layer of the connecting ring (dotted), the endosiphonal annuli (medium hatched) and the endosiphuncular lining (coarsely hatched).

describes the Michelinoceratinae not by the shape of the initial chamber but by the absence of endosiphuncular deposits. But, as can be shown in the case of the Orthoceratidae, the endosiphuncular deposits may be strongly depressed and occur only in the very apical parts of the phragmocone. The apex of the conch in these cases is crucial for defining of the taxon at a (sub-) family level, too. Therefore, the Michelinoceratinae are mostly regarded as a taxonomical wastebasket for all Orthoceridae with a more or less smooth sculpture, without any known siphuncular deposits and without known apical parts.

## Genus *Plagiostomoceras* Teichert and Glenister, 1952

*Type species*: *Orthoceras pleurotomum* Barrande, 1866.

*Diagnosis*.—Michelinoceratinae with a long, slender conch with a slightly compressed cross section. Aperture strongly oblique with a prominent lobe at its antisiphonal side. Surface of the shell covered with weak growth lines.

*Remarks.*—The genus *Plagiostomoceras* is very similar to *Protobactrites* Hyatt, 1900. Differences between the two genera may be the more eccentric siphuncle and the smooth shell in *Protobactrites*. Because no information about the internal characters are given for the latter, it remains a dubious taxon. Therefore, the use of its possible junior synonym (*Plagiostomoceras*) is preferred here. The early growth stages of the type of both *Protobactrites* and *Plagiostomoceras* are unknown. Dzik (1984) placed in the genus two embryonic specimens from the Devonian of the Holy Cross Mountains, which show a globular first chamber. However, by definition of Ristedt (1968) the Michelinoceratinae, in which the genus is grouped herein, are characterised by a shell which did not develop a constriction between the initial chamber and the rest of the conch. Thus, the genus could not be placed in the Michelinoceratinae. The decision of whether or not *Plagiostomoceras* could be placed into the Michelinoceratina must wait until the type species is better known. The two species of *Plagiostomoceras* of the Baltoscandic Orthoceratitic Limestone are the oldest known members of the genus.

### *Plagiostomoceras fragile* sp. nov.

Figs. 11D, 12G, F.

?*Orthoceras* sp. nov. ex aff. *longicameratum* Foord (1888); Teichert 1928: 125, 126.

*Holotype*: The specimen NRM Mo-155529, which shows the last four chambers and the whole living chamber.

*Type locality*: Böda, Stora Mossen of Öland (Sweden).

*Type horizon*: Folkeslunda Limestone (Lasnamägian) of the Orthoceratite Limestone.

*Derivation of the name*: From Latin *fragilis*, fine, breakable: referring to the small size of the adult conchs.

*Material.*—Ten specimens available in the NRM, 5 with preserved adult chambers and living chamber; sometimes the shell is partly preserved.

*Diagnosis.*—A fragile *Plagiostomoceras* (no more than 13 mm in diameter in adult size) with very low apical angle and extremely long chambers.

*Description.—Conch form*: Cross section slightly compressed. Mean diameter of last chamber of the adult phragmocone: 9 mm. Apical angle of the conch very low 1.2–2.4°, mean e: 1.7°.

*Ornamentation*: Shell with very fine, low elevated, narrowly spaced, oblique, transversal striae. Inner shell irregular, punctured as in *Orthoceras regulare*. Mural areas with fine longitudinal lines.

*Phragmocone*: Chamber height 0.7–1.5 of the respective diameter. Sutures straight. Septa strongly concave. Orthochoanitic septal necks. Subcentral siphuncle. Siphuncular diameter 0.09–0.1 of the respective diameter of the conch. Neither cameral or endosiphuncular deposits are observed.

*Living chamber*: Adult living chamber long conical, bulging slightly outwards. Aperture simple, straight with a slight constriction at the very adoral part.

*Comparison.—Plagiostomoceras fragile* can be detected by its small adult size, low apical angle and high chambers. *Orthoceras ariel* Barrande, 1870 and *Orthoceras expectans* Barrande, 1870 show a greater adult diameter, a lower chamber height and a smooth shell. The siphuncle of *Orthoceras expectans* is significantly thinner than that of *Plagiostomoceras fragile*. Parts of the phragmocone differ from the juvenile parts of *Orthoceras regulare* and *Orthoceras bifeovatum* in a thin siphuncle, and from *Orthoceras scabridum* in a weaker sculpture and longer chambers.

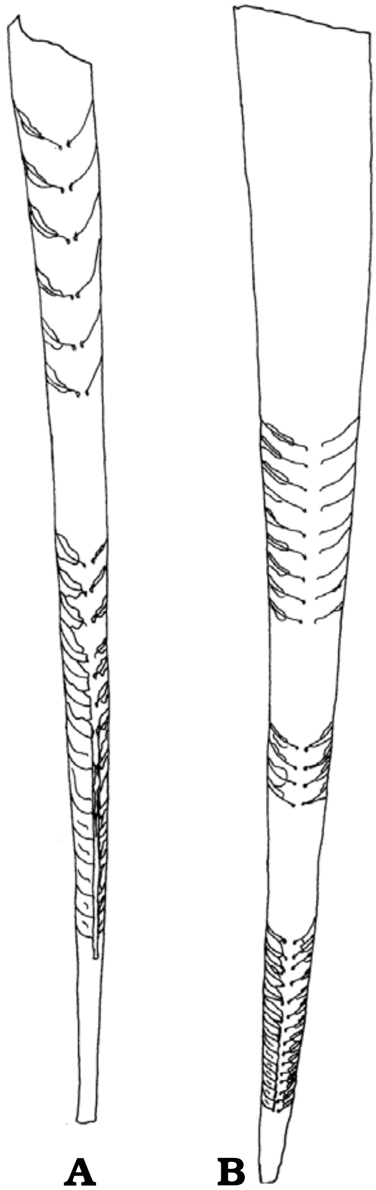



Fig. 10. Longitudinal section of *Archigeisonoceras picus* sp. nov., NRM-Mo 14455, Limbata-Limestone, Resmo (Öland) (**A**) and *Nilssonoceras nilssoni* (Boll, 1857), NRM-Mo 3328, Segerstad-Limestone, Hulsterstadkanalen (Öland) (**B**) showing the development of cameral and endosiphuncular deposits (× 0.55).

*Distribution*.—*Plagiostomoceras fragile* occurs only in the Folkeslunda Limestone of Öland.

## *Plagiostomoceras laevigatum* (Boll, 1857)

Fig. 12A, B.

**Orthoceras laevigatum* sp. nov., non *Orthoceras laevigatum* (McCoy, 1844); Boll 1857: 71–72, pl. 3: 9.

*Orthoceras laevigatum* Boll; Karsten 1869: 47: pl. 16: 2a, b.

?*Orthoceras* aff. *ariel* Barrande, 1868; Rüdiger 1889: 10–11.

*Protobactrites delicatulum* sp. nov.; Troedsson 1932: 32, 33, pl. 2: 5, pl. 4: 3, 4, pl. 7: 1.

*Polygrammoceras delicatulum* Troedsson; Flower 1952: 36.

*Protobactrites delicatulum* Troedsson; Dzik 1984: 105, 106, text-fig. 39.9.

*Paratype*: A small fragment of a phragmocone (length 23 mm, diameter 15–16 mm) from the erratics of the Red Orthoceras Limestone (Aserian?) of northern Germany in the Boll Collection (MMW number) originally labelled by Boll as *Orthoceras laevigatum*. The recrystallized outer shell is preserved.

*Material*.—Two specimens are available in the NMB, one at the MMW and 21 at the NRM (paratypes 154093–96, 14454, 144548).

*Description*.—*Conch form*: Cross section slightly compressed. Maximum diameter: 21 mm. Apical angle of the conch very low being about 1.5–2°.

*Ornamentation*: Shell is smooth with slight irregular slightly oblique growth lines and a faint longitudinal striation which is considerable only in very well preserved specimens. Growth lines forming a sinus at the antisiphonal side of the conch.

*Phragmocone*: Chamber height ~0.5 of the respective diameter. Sutures straight. Septa strongly concave. Orthochoanitic septal necks. Subcentral siphuncle. Siphuncular diameter 0.08 of the respective diameter of the conch. Neither cameral or endosiphuncular depositions observed; living chamber and apical parts of the phragmocone not known.

*Remarks*.—The only two specimens at the MMW, which were originally labelled as *Orthoceras laevigatum* by Boll are badly preserved fragments of (1) a specimen which consist of the mould and parts of the inner shell (which is slightly punctured as in *O. bifeovatum*) and (2) a 28 mm long fragment (diameter 15–16 mm), preserving three chambers of the phragmocone without cameral deposits. The shell of the latter is smooth and its apical angle very low. The central siphuncle is tubular as originally described by Boll. Karsten (1869) described two specimens and mentioned their very low apical angle. Rüdiger (1889) placed *Orthoceras laevigatum* as a synonym of *Orthoceras conicum* Hisinger, which is a *Rhynchorthoceras* (see Dzik 1984: fig. 50), *Rhynchorthoceras conicum* (Hisinger). It should consequently show heavy cameral deposits. But the paratype does not show cameral deposits. Furthermore, the apical angle of the specimen illustrated by Boll (1857: pl. 3: 9) clearly differs from the original description of *O. conicum* Hisinger, 1837. Obviously *Orthoceras laevigatum sensu* Boll is not a *Rhynchorthoceras conicum*. The description of *Orthoceras* aff. *ariel* Barrande by Rüdiger (1889) matches exactly that of the specimens identified here as *Plagiostomoceras laevigatum*, but he does not give an illustration and its original material has not been localised so far. Therefore, no final answer can be given to the question as to whether Rüdiger's *Orthoceras* aff. *ariel* is a synonym of *Plagiostomoceras laevigatum*. But the Silurian *Orthoceras ariel* Barrande shows a clearly higher apical angle than *Plagiostomoceras laevigatum* and yet is another species. Troedsson integrated some nautiloids, which exactly match the description of Boll (1858) into his new species *Protobactrites delicatulum* Troedsson, 1932 (holotype: NRM Mo-14454a). It is therefore regarded as a subjective junior synonym of *P. laevigatum*.

It is noteworthy that the name "*Orthoceras laevigatum*" was wrongly used to label *Cycloceras laevigatum* M'Coy, 1844 by subsequent researchers (e.g., de Koninck 1880). Thus *Orthoceras laevigatum* Boll is clearly the senior homonym and therefore considered a valid taxon.

*Distribution.—Plagiostomoceras laevigatum* occurs in the Red Orthoceratite Limestone (Aserian–Lasnamägian) of Öland, Västergötland and of the erratics of Northern Germany.

## Family Geisonoceratidae Zhuravleva, 1959

*Diagnosis*.—The orthoconic, sometimes slightly cyrtoceraconic conch shows a circular to strongly compressed cross section. The shell is smooth, sometimes sculptured. The suture is straight, simple or slightly undulated. The siphuncle is dorsocentral or ventrocentral. The septal necks are suborthochoanitic to orthochoanitic. The connecting rings are slightly convex or cylindrical. Siphuncular deposits in the form of annuli in the septal foramen may grow anteriorly against the connecting rings or fuse with those of adjacent segments to form continuous siphuncular lining. Cameral deposits are well developed.

*Remarks*.—The Geisonoceratidae include around 20 genera. The family was originally defined by the typical co-occurrence of suborthochoanitic to orthochoanitic septal necks with endosiphuncular deposits forming annuli at the position of the septal foramen. But as showed by Hook and Flower (1977) and Dzik (1984), other orthocerids (e.g., *Orthoceras bifeovatum* Noetling) show endosiphuncular deposits strongly resembling those of the Geisonoceratidae. The crucial point of the differentiation between the Geisonoceratidae and the Orthoceratidae lies in the extent of the endosiphuncular deposits. This seems a rather vague character for the definition of a family. But the endosiphuncular deposits of the Orthoceratinae of the Orthoceratidae are not only highly supressed and occur in the very apicad part of the phragmocone but differ in their highly irregular shape from that of the Geisonoceratidae, which developed clear and distinguishable annuli at the septal foramen in a certain stage of deposition.

## Genus *Archigeisonoceras* Chen, 1984

*Type species*: *Archigeisonoceras elegatum* Chen, 1984.

*Diagnosis*.—Geisonoceratidae with a smooth shell. The suture is straight, the siphuncle slightly eccentric. The septal necks of the juvenile parts of the conch are suborthochoanitic, in later growth stages short orthochoanitic. The connecting ring slightly expands within the chambers. The annulosiphuncular deposits are relatively small and slight. Thin episeptal and hyposeptal deposits occur.

*Remarks*.—Chen et al. (1984) placed the genus in the family Geisonoceridae, which is correct according to Sweet (1964) and Balashov and Zhuravleva (1962). Zou (1988) defined the Early Ordovician genus *Gangshanoceras* Zou as a member of the family *Proteoceratidae* Flower, 1962. *Gangshanoceras* Zou, and *Archigeisonoceras* Chen are virtually identical except for the expansion of the conch and the shift of the siphuncle from the shell wall toward the centre in *Gangshanoceras*. Important is that both genera develop suborthochoanitic septal necks in their juvenile septa but short orthochoanitic ones in the following septa (a feature known from primitive ellesmerocerids). Consequently both genera fall within the Geisonoceridae as well as *Proteoceras* Flower, which is the type genus of the family Proteoceratidae. The family Proteoceratidae is therefore in conflict with the scope of the Geisonoceratidae. Flower (1962) did not accept the family Geisonoceratidae as defined by Zhuravleva (1959) because of the weak definition of the boundary from the family Michelinoceratidae Flower, 1945 (inclusive criterion: tubular siphuncle). Later the originally wide scope of the Michelinoceratidae *sensu* Flower (1945) and Flower (1962) was restricted (e.g., Sweet 1964), and the boundaries of the Geisonoceratidae are defined by exclusion: Pseudorthoceratidae (exclusive cyrtochoanitic necks), Michelinoceratinae (without endosiphuncular deposits). Nevertheless, the early Middle Ordovician *Archigeisonoceras*, *Proteoceras*, and *Gangshanoceras* are intermediate between the Pseudorthoceratidae and the Geisonoceratidae. Chen (1984) illustrated four subadult specimens of *Archigeisonoceras*. The adult living chamber and the apical chambers of *Archigeisonoceras* are known only from the Baltoscandic material. Chen (1984) mentioned that *Archigeisonoceras* differs from *Virgoceras* Flower in its less developed annulosiphuncular deposits. But this difference may be visible only in the certain juvenile parts of the phragmocone, because strong and fusing annulosiphuncular deposits occur in the apical parts of the phragmocone in *A. picus*, *A. folkeslundense*, and *A. repplingense*. *Virgoceras*, which is mainly known from the Middle Silurian of Bohemia, differs from *Archigeisonoceras*, which is known only from the Middle Ordovician, in its stronger inflated siphuncle and in its ornamentation. Distinct growth lines as in *Virgoceras* are not known in *Archigeisonoceras*. It may be concluded that *Archigeisonoceras* and *Gangshanoceras*, which was also found in the late Arenig of Öland (King 1999), are the earliest known Geisonoceratidae.

*Species included*.—*Archigeisonoceras elegatum* Chen, 1984, *Archigeisonoceras robustum* Chen, 1984, *Archigeisonoceras picus* sp. nov., *Archigeisonoceras folkeslundense* sp. nov., *Archigeisonoceras repplingense* sp. nov.

### *Archigeisonoceras repplingense* sp. nov.

Figs. 11E, F, G, 12D, E.

*Geisonoceras* sp. (aff. *O. nilssoni sensu* Angelin, 1880); Dzik 1984: 93, fig. 33, pl. 21: 6, 10.

*Holotype/paratype*: The specimen NRM-Mo 3285 (holotype), which possesses the four last chambers of the phragmocone and the adult chamber. The recrystallized external shell is partly preserved. The specimen NRM-Mo 3284 shows only subadult chambers. The external shell is partly preserved.

*Type locality*: Räpplinge of Öland (Sweden).

*Type horizon*: Lower Grey Orthoceratite Limestone (Volkhovian).

*Derivation of the name*: From Repplingen, a village in Öland.

*Material*.—Fifty-eight specimens available in the NRM (termed *O. repplingense*, *O. promontorii nomen nudum*, and

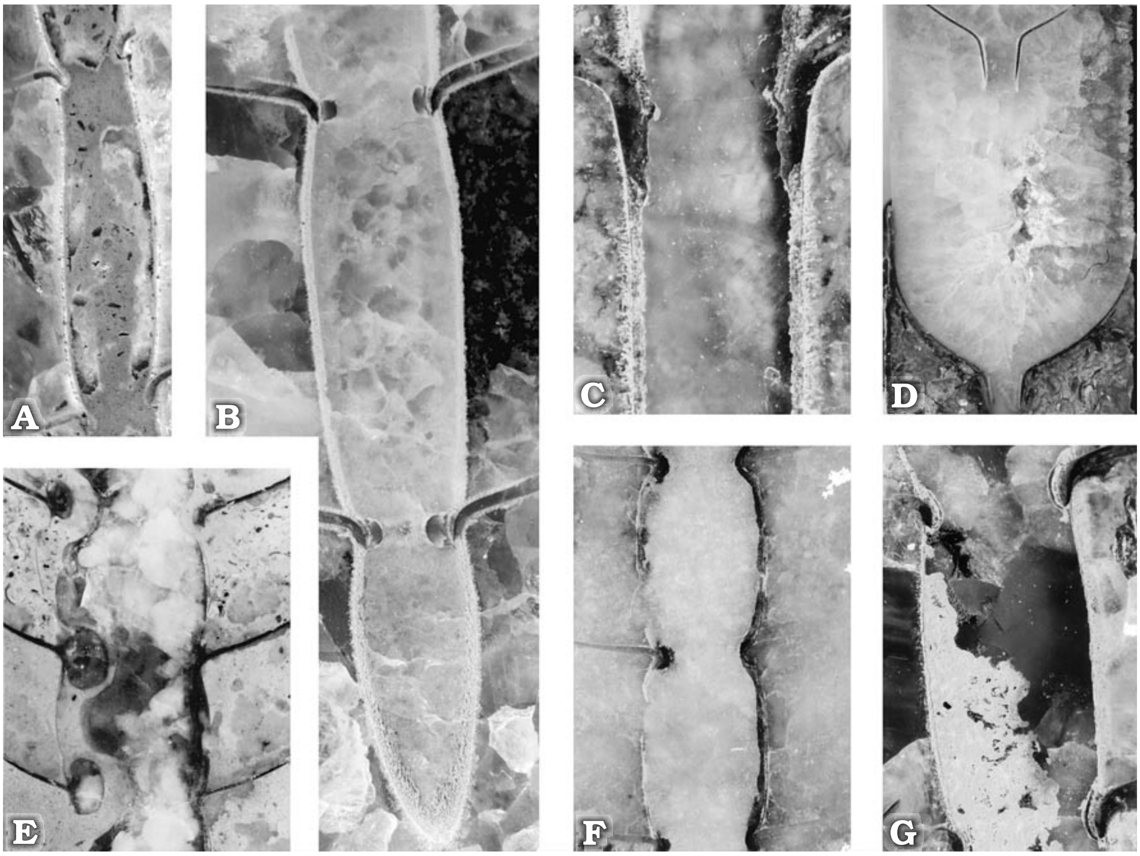



Fig. 11. Polished sections of the siphuncle. **A**. *Ctenoceras schmidti* (Noetling), NRM-Mo 160668b, Kandel (Estonia). Note the calcified connecting ring and the thin lining of a sphaerolitic-prismatic layer at the outer surface of the connecting ring, × 25. **B**. *Archigeisonoceras folkeslundense* sp. nov., NRM-Mo 3223, Källa (Öland). Note the porous structure of the calcified connecting ring and the sphaerolitic-prismatic layer, × 10. **C**. *Orthoceras scabridum* Angelin, NRM-Mo 154771, Södre Bäck (Öland), × 30. **D**. *Plagiostomoceras fragile* sp. nov., NRM-Mo 160559, Gardslösa (Öland), × 6.3. **E**. *Archigeisonoceras repplingense* sp. nov., NRM-Mo 3285 not numbered, Hälludden (Öland), note the asymmetrical development of the endosiphuncular annuli, × 18. **F**. *Archigeisonoceras repplingense*, NRM-Mo 3284, Hälludden (Öland), apical part, × 18. **G**. *Archigeisonoceras repplingense* sp. nov., NRM-Mo 3293, Torp (Öland), note the thin sphaerolithic-prismatic layer of the connecting ring, × 22.

*O. immutabile nomen nudum* by an anonymous former student), 11 specimens from the NMB and one from the ES. Some specimens with preserved adult chambers and living chamber; sometimes the recrystallized shell is partly preserved.

*Diagnosis*.—Small *Archigeisonoceras* (adult diameter approx. 27 mm) with a medium apical angle.

*Description*.—*Conch form*: Conch slightly cyrtoconic. Cross section circular or very slightly compressed. Diameter of the adult living chamber: 26–29 mm. Apical angle of the conch 1.7–21.8°, mean e: 4.6° (n = 56).

*Ornamentation*: External shell smooth.

*Phragmocone*: Chamber height 0.3–0.6 (x = 0.3, n = 35) of the respective diameter. Sutures straight. Septa simple concave. Short orthochoanitic and in apical parts of the conch slightly cyrtochoanitic septal necks. Siphuncle subcentral to central. Siphuncular diameter ca. 0.13 of the respective diameter of the conch. In juvenile chambers hypo- and episeptal deposits (Fig. 11E, F). Small endosiphuncular annuli. Sometimes asymmetrical, thin lining as endosiphuncular deposits (Fig. 11F).

*Living chamber*: Living chamber cylindrical, aperture widens slightly.

*Comparison*.—*Archigeisonoceras repplingense* differs from *Archigeisonoceras folkeslundense* in its smaller adult size, slightly lower chamber height and the shape of the living chamber. It differs from *Archigeisonoceras picus* in the smaller adult size and in the general shape of the conch, from *Archigeisonoceras robustum* in its higher chambers and from *Archigeisonoceras elegatum* in its narrower siphuncle.

*Distribution*.—*Archigeisonoceras repplingense* occurs in the Lanna Limestone (Volkhovian), Holen Limestone (Kundan) of Öland, Östergotland, Västergotland and Närke. Dzik (1984) described *Geisonoceras* sp. (= *Archigeisonoceras repplingense*) from erratics of the Volkhovian (*P. originalis* Zone) of northern Poland.

## *Archigeisonoceras picus* sp. nov.

Figs. 10A, 12B, E, 13I.

*Holotype*: The adult specimen NRM-Mo 14455a–c, which has juvenile as well as adult chambers and parts of the living chamber. The recrystallized external shell is partly preserved.

*Type locality*: Resmo of Öland (Sweden).

*Type horizon*: Limbata Limestone (Volkhovian).

*Derivation of the name:* From Latin *picus*, woodpecker or bird of prey, referring to the shape of the shell.

*Material.*—One specimen available in the NRM (termed *O. picus nomen nudum* by Holm).

*Diagnosis.—Archigeisonoceras* relative cyrtocone, of medium size (maximum diameter: 38 mm) and with high apical angle.

*Description.—Conch form*: Slightly cyrtoconic in cross section, slightly compressed. Apical angle of the conch 6.3°.

*Ornamentation*: External shell smooth with minute, irregular, spaced growthlines.

*Phragmocone*: Chamber height 0.2 of the respective diameter. Sutures straight. Septa simple concave. Short orthochoanitic septal necks in adult parts of the phragmocone, suborthochoanitic in apicad parts. Siphuncle subcentral to central. Siphuncular diameter 0.1 of the respective diameter of the conch. In middle parts of the phragmocone episeptal deposits (Fig. 12E) and well developed endosiphuncular annuli and asymmetric lining in the apical parts of the siphuncle (Fig. 12B).

*Living chamber*: Adult living chamber cylindrical. Aperture not known.

*Comparison.—Archigeisonoceras picus* differs from *Archigeisonoceras repplingense* in its greater adult size, and the lower height of chamber, from *Archigeisonoceras folkeslundense* in its lower chamber height and smaller adult size and from *Archigeisonoceras elegatum* in its narrower siphuncle.

*Distribution.—Archigeisonoceras picus* occurs only in the Limbata Limestone (Volkhov) of Öland.

### *Archigeisonoceras folkeslundense* sp. nov.

Figs. 7, 11B, 12A, 13J, K.

*Holotype*: The adult specimen (two fragments) NRM-Mo 155476, 155477, which preserves juvenile as well as adult chambers and parts of the living chamber. The recrystallized external shell is partly preserved.

*Type locality*: Folkeslunda of Öland (Sweden).

*Type horizon*: Seby Limestone (Lasnamägian).

*Derivation of the name*: From Folkeslunda, a village in Öland.

*Material*.—35 specimens available in the NRM (termed *O. rabrum nomen nudum* and *O. tallbergi nomen nudum* by an anonymous former student), one specimen known from the NMB and one from the ES; some specimens with preserved adult chambers and living chamber, sometimes the recrystallized shell is partly preserved.

*Diagnosis*.—Large *Archigeisonoceras* (maximum diameter: 46 mm) with a medium apical angle and very well developed endosiphuncular annuli.

*Description.—Conch form*: Conch slightly cyrtoconic. Cross section slightly compressed in juvenile specimens and circular in adult ones. Apical angle of the conch 1.7–5.7°, mean e: 4.6° (n = 32).

*Ornamentation*: Shell smooth with slight irregular growth lines.

*Phragmocone*: Chamber height 0.3–0.6 (x = 0.5, n = 24) of the respective diameter. Sutures straight. Septa simple concave. Short orthochoanitic septal necks in adult suborthochoanitic necks in juvenile parts of the phragmocone. Siphuncle subcentral to central. Siphuncular diameter 0.1–0.12 of the respective diameter of the conch. In juvenile chambers hypo- and episeptal deposits (see Fig. 7) and in the apical parts of the siphuncular tube well developed endosiphuncular deposits forming annuli at the septal foramen which fuse apically. Sometimes the episeptal deposits form a horseshoe-shaped thin lining on the concave side of the septa surrounding the area of the siphuncular neck and a tongue toward the ventral mural area (see Fig. 13J).

*Living chamber*: Adult living chamber cylindrical. Aperture not known.

*Comparison.—Archigeisonoceras folkeslundense* differs from *Archigeisonoceras repplingense* in its greater adult size and in the living chamber shape, from *Archigeisonoceras robustum* in its higher chambers, and from *Archigeisonoceras elegatum* in its narrower siphuncle.

*Distribution.—Archigeisonoceras folkeslundense* occurs in the Segerstadt, Seby and Folkeslunda Limestone (Aserian – Lasnamägian) of Östergotland, Västergötland, Öland, and Dalarna and from the Upper Grey Orthoceratite Limestone of the erratics of northern Germany.

## Genus *Nilssonoceras* nov.

*Type species*: *Orthoceras nilssoni* Boll, 1857.

*Diagnosis*.—Orthoceraconic to slightly cyrtoceraconic Geisonoceratidae with a slightly compressed cross section. The shell shows a sharp transversal striation with acute ribs at a distance of around 1 mm or lower. The tubular siphuncle is subcentral to midventral. The septal necks are suborthochoanitic–orthochoanitic. The endosiphonal deposits are highly variable but generally consist of annuli at the septal foramen which may fuse and form an irregular endosiphuncular lining. The cameral and endosiphuncular deposits are more strongly developed at the antisiphonal side of the conch.

*Remarks*.—The genus *Nilssonoceras* differs from all other Geisonoceratidae in its distinct ornamentation. It can be distinguished already by small fragments of the shell. The intraspecific variability of this common Middle Ordovician genus is very high. Especially the endosiphuncular and cameral deposits and the rate of expansion of the conch are strongly variable. So far the genus includes two species: *Nilssonoceras nilssoni* (Boll, 1857) and *Nilssonoceras latisiphonatum* sp. nov.

### *Nilssonoceras nilssoni* (Boll, 1857)

Figs. 10B, 12C, F, 13H, C.

**Orthoceras nilssoni* sp. nov.; Boll 1857: 69, pl. 3: 6.
*Orthoceras wahlenbergii* sp. nov; Boll 1857: 70, pl. 3: 8.
*Orthoceras nilssoni* Boll; Karsten 1869: 46, pl. 16: 1.
*Orthoceras wahlenbergii* Boll; Karsten 1869: 47, pl. 16: 3.
*Orthoceras centrale* Hisinger 1837; Barrande 1874: 694, pl. 438: 6–8.
*Orthoceras tortum* sp. nov.; Angelin 1880: 4–5, pl. 4: 12–15,17, pl. 6: 12, 13.

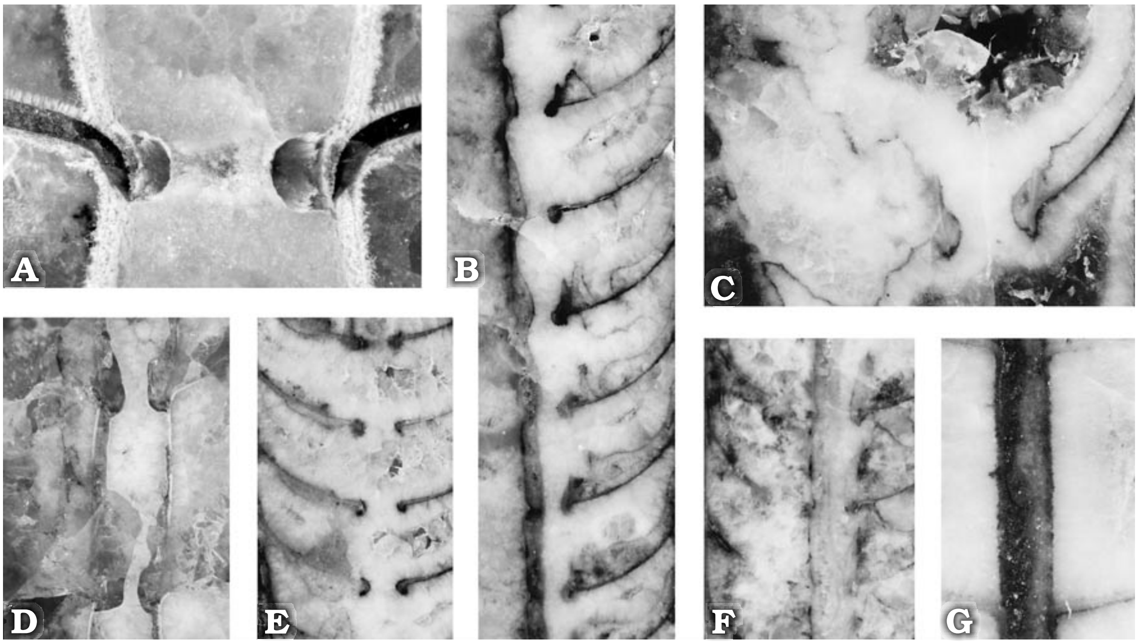



Fig. 12. Polished sections of the siphuncle. **A**. *Archigeisonoceras folkeslundense* sp. nov., NRM-Mo 3223, Källa (Öland), showing the structure of the connectig ring and the layered structure of the endosiphuncular annuli, × 35. **B**. *Archigeisonoceras picus* sp. nov., NRM-Mo 14455, Resmo (Öland), apical part of the phragmocone, × 8. **C**. *Nilssonoceras nilssoni* (Boll), NRM-Mo 3328, Hulterstad Kanalen (Öland), middle part of the phragmocone, × 12. **D**. *Kinnekulloceras kinnekullense* (Foord), NRM-Mo 155245, Utby (Dalarna), × 12. **E**. *Archigeisonoceras picus* sp. nov., NRM-Mo 14455, Resmo (Öland), middle part of the phragmocone, × 8. **F**. *Nilssonoceras nilssoni* (Boll), NRM-Mo 3328, Hulterstad Kanalen (Öland), apical part of the phragmocone with irregular endosiphuncular annuli and lining and strong cameral deposits, × 12. **G**. *Arionoceras lotskirkense* sp. nov., NRM-Mo 3296, Hällar (Öland), × 25.

?*Orthoceras centrale* Hisinger 1880; Angelin: 4, pl. 5: 1–3.
?*Orthoceras centrale* Hisinger; Remelé 1883: 29.
*Orthoceras nilssoni* Boll; Rüdiger 1889:1–3.
*Orthoceras wahlenbergii* Boll; Rüdiger 1889: 8–9.
"*Orthoceros*" *nilssoni* (Boll); Jaanusson and Mutvei 1951: 631, 634.
"*Orthoceros*" *nilssoni* (Boll); Jaanusson 1960: 279.
*Orthoceras nilssoni* Boll; Hucke and Voigt 1967: 56.
"*Geisonoceras*" *nilssoni* (Boll); Neben and Krueger 1971: pl. 15: 12, 13.
"*Orthoceras*" *nilssoni* (Boll); Dzik 1984: 92–95, 97, text-fig. 34, pl. 22: 2.
"*Orthoceras*" *wahlenbergi* (Boll); Dzik 1984: 94, text-fig. 34, pl. 21: 1–8.
*Eosomichelinoceras tortum* (Angelin); King 1999: 147, fig. 5A, B.

*Paratype*: A fragment of a phragmocone (18–24 mm in diameter, 115 mm in length) in the collection of the MMW designated originally by Boll as *Orthoceras nilssoni* from the Red Orthoceratite Limestone (Aserian?) of the erratics of Neubrandenburg / Germany.

*Material*.—One-hundred and thirty-three specimens, mainly from the Remelé Collection in the NMB, where it was labelled as *Orthoceras tortum* or *Orthoceras nilssoni*, and the Holm Collection in the NRM under the name of *Orthoceras nilssoni*. Five specimens came from the collection of erratics in GIH and GIG, three specimens labelled *O. wahlenbergi* and one specimen *Orthoceras nilssoni* from the original Boll Collection in the MMW.

*Description.—Conch form*: Very slightly cyrtoconic conch. Cross section laterally slightly compressed. Apical angle of the conch of the specimen as figured in Boll (1857): 2.3°. Apical angle of the entire material (n = 121) varies greatly: mean 3.4°, with a maximum angle of 8.5° and a minimum rate of 1.7° (see Fig. 8).

*Ornamentation*: Shell transversally striated by sharp, acute striae (Fig. 6B). The distance between the striae strongly varied in the course of the ontogeny of the specimens and between the specimens (0.3–1 mm). Slightly undulating shell in juvenile specimens. Sometimes widely punctured.

*Phragmocone*: Chamber height x: 0.75, max: 1.2, min: 0.25 (n = 95) of the respective diameter. Boll gives a chamber height of 0.83 of the respective diameter. Suture straight. Shape of the septa mammoidal. Mural faces sometimes slightly longitudinal striated. Orthochoanitic septal necks. Ovate septal foramina. Endosiphuncular annuli which are very strong in juvenile chambers and fusing into an intrasiphuncular lining in the apical part of the conch (Fig. 12F). The irregular, bullet-like hypo- and episeptal deposits vary in the 18 cut and polished specimens in their grade of exposition. Sometimes cameral deposits lack also in juvenile chambers, but never in very apical parts of the shell. Sometimes it is difficult to detect the endosiphuncular annuli if the endosiphuncular lining is strong and strongly recrystallized, thus cuts of specimens can show endosiphuncular lining, endosiphuncular annuli and cameral deposits in any variety of these features. The position of the siphuncle is centromarginal to subcentral. A column of measurements (n = 9) gives a mean position of 0.33 (if the centre of the conch is 0.5, the rim 1 or 0) with a minimum of 0.22 and a maximum of 0.4. The thickness of the siphuncle is in the mean 0.14 of the respective diameter of the shell (n = 9, max = 0.17, min = 0.13).

*Living chamber*: The adult living chamber displays a long simple conus: 208 mm at a diameter of 25 mm. The maximum diameter of *Nilssonoceras nilssoni* is 83 mm, although the majority of specimens' fragments are smaller than 10 mm in diameter; *Nilssonoceras nilssoni* therefore after *Kinnekulloceras kinnekullense* is the largest of the Orthocerataceae of the Orthoceratite Limestone.

*Remarks*.—According to Boll (1857) *Orthoceras wahlenbergi* differs from *Orthoceras nilssoni* only in the apical angle. As shown in Fig. 8 the apical angle of *Nilssonoceras* conforms to a simple Gauss distribution with a major peak at a = 3.4, which represents *N. nilssoni sensu stricto*, and a minor peak at 4.6, which represents the values of *Orthoceras wahlenbergii* Boll. There is, however, no reason to split the species according to the apical angle. Dzik (1984) mentioned that "*O. wahlenbergi* and *O. nilssoni* may be merely conspecific morphotypes". This opinion will be followed here and *Orthoceras wahlenbergi* Boll assigned to the species *Nilssonoceras nilssoni* and accepted only as a variation of the latter (*N. nilssoni* var. *wahlenbergi*). Rüdiger (1889) shows that *O. tortum* is a synonym of *N. nilssoni* and the figured specimen in King (1999) exactly illustrates an adoral part of a phragmocone of *N. nilssoni.* Unfortunately the holotype of *O. tortum* Angelin was not found in the collection of the NRM. The only available paratype originally labelled by Angelin as *O. tortum*, does not have the outer shell preserved.

*Comparison*.—*Nilssonoceras nilssoni* differs from *Orthoceras sodale* Barrande, 1870 in its shape of the striae and from *Orthoceras primum* Barrande, 1870 in the cross section of the shell. (The shell of *Orthoceras primum* is additionally to the striation undulated.) *Nilssonoceras nilssoni* differs from *Geisonoceras rivale* (Barrande, 1859) in the shape of the striae and the endosiphuncular deposits, and it differs from *Kinnekulloceras kinnekullense* in different sculpture.

*Distribution*.—The oldest evidence is given by Jaanusson and Mutvei (1951) in the highest Holen Limestone (Kundan) of Dalarna and by King (1999) of Öland. *Nilssonoceras nilssoni* also occurs in the Segerstad, Seby, and Folkeslunda Limestone, and the Furudal Limestone (Aserian–Uhakuan) of Öland, Närke, Dalarna, Västergötland, and Östergotland, and in the erratics of northern Germany and Poland.

## *Nilssonoceras latisiphonatum* sp. nov.

Fig. 9.

*Holotype*: The specimen NRM-Mo 158037, which shows four chambers of a nearly mature specimen.

*Type locality*: Skarlöv of Öland (Sweden).

*Type horizon*: Folkeslunda Limestone (Lasnamägian).

*Derivation of the name:* From Latin *latius*, wide: referring to the large size of the siphuncle.

*Material*.—Six specimens available in the NRM. The recrystallized shell is preserved in all specimens.

*Diagnosis*.—*Nilssonoceras* with a very wide siphuncle (nearly one fourth of the conch diameter) and well developed elongated endosiphuncular annuli.

*Description*.—*Conch form*: Cross section slightly compressed. Maximum diameter: 45 mm. Apical angle of the conch 2.9–5.7°, mean a: 4°.

*Ornamentation*: Shell transversally striated by sharp, acute striae as in *Nilssonoceras nilssoni* (Fig. 6B). Inner shell smooth.

*Phragmocone*: Chamber height 0.3–1.1 (mean 0.8) of the respective diameter. Sutures straight. Shape of the septa tube like, with a septal foramen resembling a mamma (herein called mammoidal). Orthochoanitic septal necks. Siphuncle eccentric to subcentral (sp = 0.33–0.48). Siphuncular diameter 0.25 of the respective diameter of the conch. Elongated endosiphuncular annuli (see Fig. 9). Endosiphuncular lining may occur. Thin hypo- and episeptal cameral deposits. Living chamber and juvenile chambers not known.

*Comparison*.—*Nilssonoceras nilssoni* differs from *Nilssonoceras latisiphonatum* only in the dimension of the siphuncle.

*Distribution*.—*Nilssonoceras latisiphonatum* occurs in the Seby and Folkeslunda Limestone (Lasnamägian) of Öland and the Holen Limestone (Kundan) of Dalarna.

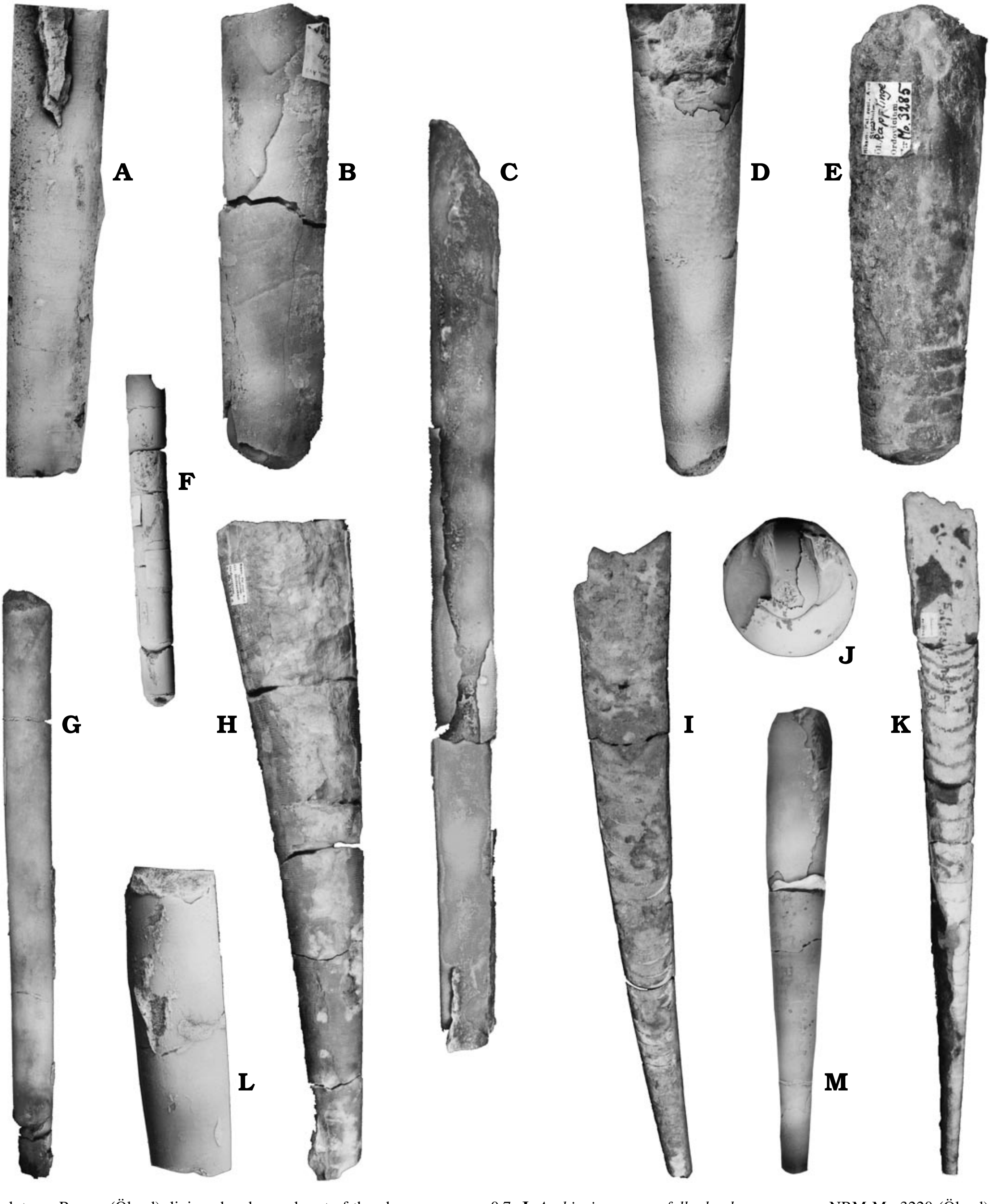
## Genus *Kinnekulloceras* nov.

*Type species*: *Orthoceras kinnekullense* Foord, 1887.

*Diagnosis*.—*Kinnekulloceras* resembles *Nilssonoceras* in most features but strongly differs in its ornamentation. The shell shows a transversal striation with smooth, flat ribs and fine sharp deepened lines in between. The distance apart of the ribs or ribblets is about 1 mm or lower. The relatively wide tubular siphuncle is subcentral to midventral in position. The septal necks are short orthochoanitic – orthochoanitic. The endosiphonal deposits are highly variable but generally consist of annuli at the septal foramen which may fuse and form an irregular endosiphuncular lining. The cameral and endosiphuncular deposits are more strongly developed at the dorsal side of the conch.

*Remarks*.—Like *Nilssonoceras*, the genus *Kinnekulloceras* differs from all other Geisonoceratidae in its distinct ornamentation. The endosiphuncular and cameral deposits are strongly variable. The genus includes only one species: *Kinnekulloceras kinnekullense* (Foord, 1887).

Fig. 13. Shape of the Middle Ordovician Orthoceratacaea. **A**. *Plagiostomoceras laevigatum* (Boll), NMB C. 5385, coll. Patrunky, not numbered, × 0.95. **B**. *Plagiostomoceras laevigatum* (Boll), NRM Mo 31300, Sandby (Öland), note the major sublethal injury at the left flank, × 1. **C**. *Nilssonoceras nilssoni* (Boll), NRM-Mo 3348a, living chamber and part of the phragmocone, × 0.3. **D**. *Archigeisonoceras repplingense* sp. nov., NRM-Mo 3284, Räpplinge (Öland), subadult specimen, × 0.85. **E**. *Archigeisonoceras repplingense* sp. nov., NRM-Mo 3245, Räpplinge (Öland), holotype, living chamber and parts of the phragmocone, × 1. **F**. *Plagiostomoceras fragile* sp. nov., NRM-Mo 160560, part of the phragmocone, × 1. **G**. *Plagiostomoceras fragile* sp. nov., NRM-Mo155529, Böda, Stora Mossen (Öland), holotype, living chamber and last four gas chambers, × 1. **H**. *Nilssonoceras nilssoni* var. *wahlenbergi* (Boll), NRM-Mo 3344, Hulterstad (Öland), living chamber and part of the phragmocone, × 0.5. **I**. *Archigeisonoceras picus* sp. nov. , NRM-Mo 14455a–c, →




holotype, Resmo (Öland), living chamber and part of the phragmocone, × 0.7. **J**. *Archigeisonoceras folkeslundense* sp. nov., NRM-Mo 3220 (Öland), conve× side of the septum with thin horseshoe-like hyposeptal deposits leaving a tongue-like space between siphuncle and shell rim, × 1.1. **K**. *Archigeisonoceras folkeslundense* sp. nov., NRM-Mo 155476, 155477, holotype, Folkeslunda (Öland) adult specimen with preserved parts of the living chamber and the phragmocone, × 0.3. **L**. *Arionoceras lotskirkense* sp. nov., NRM-Mo 154080, Löts Kirka (Öland), part of the living chamber, × 1.4. **M**. *Arionoceras lotskirkense* sp. nov., NRM-Mo 154079, Löts Kirka (Öland), living chamber and part of the phragmocone, × 1.

### *Kinnekulloceras kinnekullense* (Foord, 1887)

Fig. 12D.

* *Orthoceras kinnekullense* sp. nov.; Foord 1887: 400, fig. 2a–c.
*Orthoceras kinnekullense* Foord; Foord 1888: 2, fig. 1a–c.
*Orthoceras kinnekullense* Foord; Crick 1898: 85.
*Orthoceras kinnekullense* Foord; Phillips 1982: 38.
*Orthoceras kinnekullense* Foord; Hughes 1985: 178, fig. 3A, E.
*Orthoceras kinnekullense* Foord; Phillips 1987: 81.
"*Geisonoceras*" *kinnekullense* (Foord); King 1999: 147, fig. 5C, D.

*Material*.—Seventeen specimens from the collection of the NRM were considered; most specimens are testiferous, some with preserved body chamber.

*Description*.—*Conch form*: Cross section nearly circular. Apical angle of the conch of the specimen figured in Foord (1888): 6.3°. Mean apical angle of the entire material (n = 12): 4.6°, with a maximum apical angle of 6.3° and a minimum angle of 1.7°.

*Ornamentation*: Shell transversally striated. In between the striae smooth, flat raised lirae (Fig. 6C) (called "ribblets" by Foord 1888). The distance of the lirae varies in the course of the ontogeny of the specimens and between the specimens (mean ca. 0. 5 mm).

*Phragmocone*: Chamber height with x: 0.73 (n = 9) varies strongly between the observed specimens as well as in the ontogeny between max: 0.9 and min: 0.2 of the respective diameter. Foord (1888) gives a chamber height of 0.33 of the respective diameter. Sutures straight. Shape of the septa mammoidal. Orthochoanitic septal necks. Connecting ring bulging slightly outwards. Irregular endosiphuncular annuli are sometimes very well developed and may fuse to form an endosiphuncular lining (Fig. 12D). Irregular, bullet-like, hypo- and episeptal deposits vary in their grade of exposition. The cameral deposits of the antisiphonal part of the phragmocone are generally strongly developed as in *Nilssonoceras nilssoni*, thus cutt specimens could show endosiphuncular lining, endosiphuncular annuli, and cameral deposits in any variety. The position of the siphuncle is subcentral (sp = 0.42). The thickness of the siphuncle is ca. 0.1 of the respective shell diameter.

*Living chamber*: Not known. The maximum known diameter of *Kinnekulloceras kinnekullense* is 82 mm, but most fragments of the shell show diameters lower than 10 mm.

*Comparison*.—*Kinnekulloceras kinnekullense* differs from *Nilssonoceras nilssoni* in its different ornamentation.

*Distribution*.—*Kinnekulloceras kinnekullense* occurs in the Folkeslunda Limestone (Lasnamägian) of Öland, Västergötland, Östergotland, and Dalarna.

## Family Arionoceratidae Dzik, 1984, emend. Gnoli (1998)

*Diagnosis*.—Orthoceratidae with a relative short straight to slightly cyrtoconic (most commonly endogastric) shell. The cross section of the shell is circular. The narrow cylindrical siphuncle is central with "suborthochoanitic, terminally very acuminate, and short septal necks" (Gnoli 1998). The connecting rings slightly expanding within chambers. A big protoconch usually more than 2 mm in length, ogive-like in shape is crossed by a long caecum linked apicad to the beginning of the conch by a short prosiphon (see Gnoli 1998).

*Remarks*.—The family is common in the Ludlow of Bohemia, e.g., *Arionoceras arion* (Barrande) and the Wenlock of Sardinia, e.g., *Arionoceras submiliforme* (Meneghini). The earliest representative known so far is *Arionoceras gyratum* (Miagkowa) from the Llandovery of Siberia (Miagkowa 1967). *Arionoceras lotskirkense* sp. nov., described herein, is of Middle Ordovician age.

## Genus *Arionoceras* Barskov, 1966

*Type species*: *Orthoceras arion* Barrande, 1868.

*Diagnosis*.—The orthoceraconic or slightly cyrtoceraconic *Arionoceras* shows a relatively high apical angle. The cross section of the shell is circular. The surface of the shell is smooth or shows a weak transverse sculpture. The siphuncle is central. The septal necks are suborthochoanitic, very short, and acuminate. Their length is less than the diameter of the septal foramen. The connecting ring is cylindrical. The protoconch is large, pointed apically, ogival in shape, and bent ventrally. Cameral deposits developed in the apical chambers of adult specimens (slightly modified from Serpagli and Gnoli 1977).

*Remarks*.—A definitive placing of a specimen in the genus is possible only if the protoconch is known. But the specific shape of the nearly adult conch and siphuncular tube is considered as a valuable criterion for determination. The Ordovician *Arionoceras* differs significantly from all other known Baltic cephalopods in even these specific features of the nearly mature shell. As pointed out by Gnoli (1998), the genera *Caliceras* Kolebaba and *Psilorthoceras* Ristedt represent synonyms of *Arionoceras* Barskov. Regarding the type species of the Arionoceratidae it must be mentioned that *Orthoceras affine* Meneghini, 1857 is a senior synonym of *Orthoceras arion* Barrande, 1868 (see Serpagli and Gnoli 1977). The name *Orthoceras affine*, however, was preoccupied by *O. affine* Portlock, 1843 which is a *Mithortoceras* (Histon, 1998). Consequently, *O. arion* Barrande, 1868 is the only valid name of the type species of the *Arionoceratidae*.

### *Arionoceras lotskirkense* sp. nov.

Figs. 12G, 13L, M.

*Holotype*: The specimen NRM-Mo 154079. Adult chamber and nearly mature parts of the phragmocone, recrystallized shell well preserved.

*Type locality*: Löts Kyrka of Öland (Sweden).

*Type horizon*: Folkeslunda Limestone (Lasnamägian).

*Derivation of the name*: From the locality of Löts Kyrka in Öland.

*Material*.—Fifteen specimens available in the NRM (termed *O. schmalensei nomen nudum* by an anonymous former student). One specimen is housed at the MMW, and 3 specimens available at the NMB. Some specimens with preserved adult chambers and living chamber.

*Diagnosis*.—Small, smooth Orthoceratacea with a maximum diameter of no more than 12–13 mm and a length of approx.

140 mm. Very short suborthochoanitic septal necks and a thin tubular siphuncle.

*Description.—Conch form*: Slightly cyrtoconic conch. Cross section very slightly compressed. Mean apical angle of the conch 5.1°.

*Ornamentation*: Shell smooth. Very minute inaequidistant growth lines, which are ventrally slightly bent forward.

*Phragmocone*: Mean chamber height 0.5 of the respective diameter. Sutures straight. Septa simple, concave. Very short suborthochoanitic septal necks. Subcentral siphuncle. Siphuncular diameter ca. 0.08 of the respective diameter of the conch. No cameral and siphuncular deposits are known (only relatively adoral chambers are observed, Fig. 12G).

*Living chamber*: Adult living chamber cylindrical and compressed. Aperture widens with a thickening of the shell in the most adoral part, forming a slight constriction on the cast.

*Comparison.—Arionoceras ariel* (Barrande, 1866) and *Arionoceras valens* (Barrande, 1866) are clearly larger than *Arionoceras lotskirkense*. *Arionoceras gyratum* (Miagkowa, 1967) shows a larger adult diameter and a higher apical angle.

*Distribution.—Arionoceras lotskirkense* occurs in the Segerstad (Aserian), Seby and Folkeslunda Limestone (Lasnamägian) of Öland and Dalarna, and in the Upper Red and Grey Orthoceratite Limestone (Aserian–Lasnamägian) of the erratics of northern Germany.

# Acknowledgements

I wish to thank Anette Günther of the Müritz Museum Waren for providing the material of Boll, Dr. Mike Reich of the Paläontologisch-Geologischen Institut of the Universität Greifswald, Dr. Harry Mutvei of the Naturhistoriska Riksmuseet (Stockholm), Dr. Vojtech Turek and Ivan Kolebaba of the Národní Museum (Prague), Dr. Thomas Becker of the Museum für Naturkunde Berlin, Universität Münster for cooperation, Dr. Jerzy Dzik of the Instytut Paleobiologii PAN (Warsaw) for early reviewing the manuscript and fruitful discussion and Michael Turnbull (Berlin) for English correction. I am also deeply indebted to Dr. Mauritio Gnoli of the Università degli Studi di Modena e Reggio Emilia (Modena), Dr. Kathleen Histon, Geologische Bundesanstalt (Vienna) and Dr. Charles H. Holland, Trinity College (Dublin) for critical comments on the manuscript and discussion. The study was supported by the Deutche Forschungsgemeinschaft (DFG).

# References

Angelin, N.P. and Lindström, G. 1880. *Fragmenta Silurica*. 66 pp. Samson & Wallin, Stockholm.

Barrande, J. 1865. *Système Silurien du centre de la Bohëme*, I. Première partie: Recherches Paléontologiques, vol. II, Classe de Mollusques, Ordre des Céphalopodes, 1865: ser. 6, pls. 1–107; 1866: ser. 7, pls. 108–244; 1867: ser.1, 712 pp.; 1868: ser. 8, pls. 245–350; 1870: ser. 2, 266 pp., ser. 9, pls. 351–460; 1874: ser. 3, 804 pp.; 1877: ser. 4, 742 pp., ser. 5, 743 pp., supplement 1, 297 pp., supplement 2, pls. 461–544. Prague.

Balashov, Z.G. [Balašov, Z.G.] 1956. On the systematic position and stratigraphic distribution of the genus *Orthoceras* [in Russian]. *Ežegodnik Vsesoûznogo Paleontologičeskogo Obŝestva* 15: 223–247.

Balashov, Z.G. [Balašov, Z.G.] and Zhuravleva, F.A. [Žuravleva, F.A.] 1962. Otrâd Orthoceratida. *In:* J.A. Orlov (ed.), *Mollûski Golovonogie I, Osnovy Paleontologii*, 82–93. Akademiâ Nauk SSSR, Moskva.

Barskov, I.S. 1966. *Golovonogie pozdnego ordovika i silura Kazahstana i Srednej Azji*. 200 pp. Autoreferat Dissertatcii na soiskanie učenoj stepni kandidata geologo-mineralogiyh nauk. Izdatel'stvo Moskovskogo Universiteta, Moskva.

Boll, E. 1857. Beitrag zur Kenntnis der silurischen Cephalopoden im norddeutschen Diluvium und den angrenzenden Lagern Schwedens. *Archiv des Vereins der Freunde der Naturgeschichte in Mecklenburg* 11: 58–96.

Breynius, J.Ph. 1732. *Dissertatio physica de polythalamiis*. 64 pp. Benghem, Gedania [Gdańsk].

Brugière, J.G. 1789. *Histoire naturelle des vers*. vol. 1, pt. 1, *Encyclopedie methodique* 6, 757 pp. Panckoucke, Paris.

Chen T. 1984. The Ordovician cephalopod fauna and the subdivision of Ordovician from southern Xizang (Tibet). *Acta Palaeontologica Sinica* 23: 452–468 [English abstract, 468–471].

Crick, G.C. 1898. *List of the Types and Figured Specimens of Fossil Cephalopoda in the British Museum (Natural History)*. 103 pp. British Museum Natural History, London.

Dewitz, H.H. 1879. Beiträge zur Kenntnis der in ostpreussischen Silurgeschieben vorkommenden Cephalopoden. *Schriften der physikalisch-ökonomischen Gesellschaft zu Königsberg* 20: 162–180.

Dewitz, H.H. 1880. Ueber einige ostprussische Silurcephalopoden. *Zeitschrift der Deutschen geologischen Gesellschaft* 32: 371–393.

Dzik, J. 1984. Phylogeny of the Nautiloidea. *Palaeontologia Polonica* 45: 1–219.

Engeser, T. 2001. *Fossil Nautiloidea Page*. [online] www.userpage.fu-berlin.de/~palaeont.

Eichwald, E. 1860. *Lethaea Rossica ou Paléontologie de la Russie*. 1654 pp. Schweizerbart, Stuttgart.

Flower, R.H. 1945. Classification of Devonian nautiloids. *American Midland Naturalist* 33: 675–724.

Flower, R.H. 1962. Part 1: Revision of *Buttsoceras*, Part 2, Notes on the Michelinoceratida. *New Mexico Institute of Mining and Technology, State Bureau of Mines and Mineral Resources, Memoir* 10: 1–40.

Foord, A.H. 1887. On "*Orthoceras* (*Endoceras*) *duplex*" Wahlenberg et auct., with descriptions of three new species of *Endoceras* from the Ordovician of Sweden and Russia contained in the British Museum (Natural History). *Annals and Magazine of Natural History* 5 (20): 393–403.

Foord, A.H. 1888. *Catalogue of the fossil Cephalopoda in the British Museum* (Natural History). Part 1, London (British Museum).

Frey, R.C. 1995. Middle and Upper Ordovician Cephalopods of the Cincinnati Region of Kentucky, Indiana, and Ohio. *United States Geological Survey Professional Paper* 1066P: 1–119.

Gottsche, C. 1877. *Die Sedimentär-Geschiebe der Provinz Schleswig-Holstein*. 65 pp. Lévy & Salabelle, Yokohama.

Gnoli, M. 1998. *Some remarks and emendation of the family Arionoceratidae Dzik 1984 (Cephalopoda, Nautiloidea)*. http://palaeo-electronica.org/1998_2/gnoli/issue2.htm

Hisinger, W. 1828. Geognostik karta öfver en dal av Skaraborgslä. *Anteckningar i Physik och Geognosie* 4. 260 pp. Stockholm.

Hisinger, W. 1837. Lethaea suecica seu setrificata sveciae, iconibus t characteribus illustrata. *Holmiae*. 36 pp. Norstedt.

Histon, K. 1998. Nautiloid species from the Carboniferous of Ireland. *Irish Journal of Earth Sciences* 16: 45–60.

Holm, G. 1885. Ueber die innere Organisation einiger silurischer Cephalopoden. *Palaeontologische Abhandlungen* 3: 1–27.

Holm, G, 1891. Om mynningen hos *Lituites* Breyn. *Geologiska Föreningens i Stockholm Förhandlingar* 132 (7): 736–781.

Holtedahl, O. 1909. Studien über die Etage 4 des norwegischen Silursystems beim Mjösen. *Videnskabs-Selskapets Skrifter* I Mat.-Nat. Kl. 1909 (7): 1–76.

Hook, S.C. and Flower, R.H. 1977. Late Canadian (Zones J, K) cephalopod faunas from southwestern United States. *New Mexico Bureau of Mines and Mineral Resources Memoir* 32: 1–56.

Hughes, W.W. 1985. Planetary rotation and invertebrate skeletal patterns: prospects for extant taxa. *Geophysical Survey* 7: 169–183.

Hucke, K. and Voigt, E. 1967. Einführung in die Geschiebeforschung (Sedimentärgeschiebe). *Nederlandse Geologische Vereniging*. 132 pp. Oldenzaal.

Jaanusson, V. 1960. The Viruan (Middle Ordovician) of Öland. *Bulletin of the Geological Institutions of the Univerity of Uppsala* 38 (3): 207–288.

Jaanusson, V. 1965a. Lower and Middle Viruan (Middle Ordovician) of the

Siljan District. *Bulletin of the Geological Institutions of the Univerity of Uppsala* 42 (3): 1–41.

Jaanusson, V. 1965b. The Viruan (Middle Ordovician) of Kinnekulle and northern Billingen. *Bulletin of the Geological Institutions of the Univerity of Uppsala* 43 (1–3): 1–74.

Jaanusson, V. 1982a. Introduction to the Ordovician of Sweden. *In:* D.L. Bruton and S.H. Williams (eds.), IV International Symposium on the Ordovician System. Field Excursion Guide. *Paläontological Contributions from the University of Oslo* 279: 1–9.

Jaanusson, V. 1982b. The Ordovician in Västergotland. *In:* D.L. Bruton and S.H. Williams (eds.), IV International Symposium on the Ordovician System.Field Excursion Guide. *Paläontological Contributions from the University of Oslo* 279: 164–183.

Jaanusson, V., Larsson, K., and Karis, L. 1982. The sequence in the autochthon of Jämtland. *In:* D.L. Bruton and S.H. Williams (eds.), IV International Symposium on the Ordovician System. Field Excursion Guide. *Paläontological Contributions from the University of Oslo* 279: 47–54.

Jaanusson, V. and Mutvei, H. 1951. Ein Profil durch den Vaginatum-Kalkstein im Siljan-Gebiet, Dalarna. *Geologiska Föreningens i Stockholm Förhandlingar* 73 (4): 630–636.

Jaanusson, V. and Mutvei, H. 1955. Stratigraphie und Lithologie der unterordovizischen *Platyurus*-Stufe im Siljan-Gebiet, Dalarna. *Bulletin of the Geological Institutions of the Univerity of Uppsala* 35: 7–34.

Jaannusson, V. and Mutvei, H. 1982. Ordovician of Öland. Guide to Excursions. *IV International Symposium on the Ordovician System*, 23 pp. Swedish Museum of Natural History, Stockholm, Oslo.

Jentzsch, A. 1880. Übersicht der silurischen Geschiebe Ost und Westpreussens. *Zeitschrift der Deutschen Geologischen Gesellschaft* 1880: 623–630.

Karsten, G. 1869. Die Versteinerungen des Uebergangsgebirges in den Geröllen der Herzogthümer Schleswig und Holstein. *Beiträge zur Landeskunde der Herzogthümer Schleswig und Holstein*, Reihe 1, Heft 1, 85 pp. Ernst Homann, Kiel.

King, A.H. 1999. A review of Volkhovian and Kundan (Arenig–Llanvirn) Nautiloids from Sweden. *In*: F. Olóriz and F.J. Rodríguez-Tovar (eds.), *Advancing Research on Living Fossil Cephalopods.*, 137–159. Kluwer Academic/Plenum, New York.

Koninck, L.G., de 1880. Faune de calcaire carbonifère de la Belgique, 2[e] partie, *Gyroceras Cyrtoceras*, *Gomphoceras*, *Orthoceras*, *Subclymenia* et *Goniatites*. *Annales du Musée Royal d'Histoire naturelle de Belgique* 5: 1–133.

Krause, A. 1877. Die Fauna der sogen. Beyrichien- oder Choneten-Kalke des norddeutschen Diluviums. *Zeitschrift der Deutschen Geologischen Gesellschaft* 12: 15–49.

Kuhn, O. 1940. *Paläozoologie in Tabellen*. 50 pp. Fischer, Jena.

McCoy, F. 1844. *A Synopsis of the Characters of the Carboniferous Limestone Fossils of Ireland*. 207 pp. University Press, Dublin.

Miagkowa, E.I. [Miagkova, E.I.] 1967. *Silurskie Nautiloidei Sibirskoj Platformy. Llandoverijskie Orthoceratida, Discosorida i Oncocerida*. 54 pp. Nauka, Moskva.

Moberg, J.C. 1890. Anteckningar om Ölands ortocerkalk. *Sveriges Geologiska Undersökning C* 109: 11–22.

Mutvei, H. 2002. Connecting ring structure and ist significance for classification of the orthoceratid cephalopods. *Acta Palaeontologica Polonica* 47 (1): 157–168.

Neben, W. and Krueger, H.H. 1971. Fossilien ordovizischer Geschiebe. *Staringia* 1: 1–55.

Noetling, F. 1882. Ueber *Lituites lituus*. *Zeitschrift der Deutschen Geologischen Gesellschaft* 34: 156–193.

Noetling, F. 1883. Die Cambrischen und Silurischen Geschiebe der Provinzen Ost- und West-Preussen. *Jahrbuch der Königlich Preussischen geologischen Landesanstalt und Bergakademie zu Berlin* 1882: 261–324.

Noetling, F. 1884. Beiträge zur Kenntniss der Cephalopoden aus Silurgeschieben der Provinz Ost-Preussen. *Jahrbuch der Königlich Preussischen Geologischen Landesanstalt und Bergakademie zu Berlin* 1883: 101–135.

Orbigny, A.D., d' 1849. *Cours élémentaire de Paléontologie et de géologie stratigraphiques. Tome 1.* 299 pp. Victor Masson, Paris.

Phillips, D. 1982. *Catalogue of the Type and Figured Specimens of Fossil Cephalopoda (excluding Mesozoic Ammonoidea) in the British Museum (Natural History)*. 94 pp. British Museum Natural History, London.

Phillips, D. 1987. *Additions to the Catalogues of Type and Figured Fossil Cephalopoda in the British Museum (Natural History).* 155 pp. British Museum Natural History, London.

Remelé, A. 1880. Über einige neue oder seltene Versteinerungen aus silurischen Diluvialgeschieben der Gegend von Eberswalde. *Festschrift für die Fünfzigjährige Jubelfeier der Forstakademie Eberswalde*, 179–252.

Remelé, A. 1882. Über einige gekrümmte untersilurische Cephalopoden. *Zeitschrift der Deutschen Geologischen Gesellschaft* 34: 116–138.

Remelé, A. 1883. *Untersuchungen über die versteinerungsführenden Diluvialgeschiebe des norddeutschen Flachlandes mit besonderer Berücksichtigung der Mark Brandenburg*. 1. Stück Allgemeine Einleitung nebst Uebersicht der älteren baltischen Sedimentgebilde, Untersilurische Cephalopoden. 108 pp. Springer, Berlin.

Ristedt, H. 1968. Zur Revision der Orthoceratidae. *Akademie der Wissenschaften und Literatur in Mainz, Abhandlungen der mathematisch-naturwissenschaftlichen Klasse* 1968: 211–287.

Rüdiger, H. 1889. *Ueber die Silur-Cephalopoden au den Diluvialgeschieben*. 86 pp. Michael and Schuster, Güstrow.

Saladzius, V. 1966. Mollusc fauna of the Silurian deposits of the South of the East Baltic territory. *Paleontology and Stratigraphy of the Baltic and Byelorussia* 1: 31–73.

Serpagli, E. and Gnoli, M. 1977. Upper Silurian cephalopods from southwestern Sardinia. *Bollettino della Società Paleontologica Italiana* 16 (2): 153–196.

Schlotheim, E.F., von 1820. *Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Tier- und Pflanzenreichs der Vorwelt erläutert.* 437 pp. Gotha.

Schmidt, F. 1861. Untersuchungen über die Silurische Formation von Ehstland, Nord Livland und Ösel. *Archiv für die Naturkunde Liv-, Ehst- und Kurlands, 1. Serie (Mineralogische Wissenschaften, nebst Chemie, Physik und Erdbeschreibung)* 2: 1–248.

Schröder, H. 1882. Beiträge zur Kenntniss der in ost- und westpreussischen Diluvialgeschieben gefundenen Silurcephalopoden. *Schriften der Physikalisch-ökonomischen Gesellschaft zu Königsberg i. Pr.* 22: 54–96.

Sweet, W.C. 1958. The Middle Ordovician of the Oslo region of Norway. 10. Nautiloid cephalopods. *Norsk geolisk Tidsskrift* 3 (1): 1–178.

Sweet, W.C. 1959. Muscle attachment impressions of some Paleozoic nautiloid cephalopods. *Journal of Paleontology* 33: 293–305.

Sweet, W.C. 1964. *Nautiloidea-Orthocerida. In:* R.C. Moore (ed.), *Treatise on Invertebrate Paleontology*, Part K, *Mollusca* 3, *Cephalopoda*, K277–K319. Geological Society of America and the University of Kansas Press, Kansas.

Teichert, C. 1928. Über *Orthoceras regulare* Schlotheim und verwandte Formen. *Zeitschrift für Geschiebeforschung* 4 (3): 115–126.

Teichert, C. and Miller A.K. 1936. What is *Orthoceras*? *American Journal of Science* 31: 352–362.

Teichert, C. and Miller A.K. 1938. The earliest use of the name *Orthoceras* for cephalopods. *American Journal of Science* 35: 143–144.

Teichert, C. and Glenister, B.F. 1952. Fossil nautiloid faunas from Australia. *Journal of Paleontology* 26: 730–752.

Tjernvik, T.E. 1956. On the Early Ordovician of Sweden. Stratigraphy and fauna. *Bulletin of the Geological Institutions of the Univerity of Uppsala* 36 (2–3): 80–109.

Troedsson, G.T. 1931. Studies on Baltic fossil cephalopods. 1. On the nautiloid genus *Orthoceras*. *Lunds Universitets Årsskrift, NF* 2, 27 (16): 1–34.

Troedsson, G.T. 1932. Studies on Baltic fossil cephalopods. 1. Vertically striated or fluted orthoceracones in the Orthoceras Limestone. *Lunds Universitets Årsskrift, NF* 2, 28 (6): 1–38.

Wahlenberg,G. 1818. Petrificia Telluris Svecanea. *Nova Acta Regiae Societatis Scientarum Upsaliensis* 8: 1–116.

Yü, C.C. 1930. The Ordovician Cephalopoda of Central China. *Palaeontologica Sinica B* 1 (2): 1–101.

Zhuravleva, F.A. [Žuravleva, F.A.] 1959. On the family Michelinoceratidae [in Russian]. *Materialy k Osnovam Paleontologii* 3: 47–48.

Zhuravleva, F.A. [Žuravleva, F.A.] 1978. Devonskie Orthoceratoidea [in Russian]. *Trudy paleontologičeskogo Instituta* 168: 1–224.

Zou X. 1988. Ordovician nautiloid faunas from Lunshan, Jurong, Jiangsu. *Acta Palaeontologica Sinica* 27: 309–330.