A New Genus of Middle Tremadocian Orthoceratoids and the Early Ordovician Origin of Orthoceratoid Cephalopods

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A new genus of middle Tremadocian orthoceratoids and the Early Ordovician origin of orthoceratoid cephalopods

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The cephalopods of the subclass Orthoceratoidea, which are termed "orthoceratoids" herein, are a group that remains "the last unexplored wilderness in the Cephalopoda" (Flower 1962: 23). After 45 years this statement still holds true because phylogeny reconstructions are hindered by their morphological simplicity, numerous homeomorphies and iterative evolution. The Orthocerida, straight cephalopods that are characterised by a wide chamber spacing, a thin tubular siphuncle and a small spherical initial chamber, lacking a cicatrix (Kröger 2006) were the ancestors of bactritoids, ammonoids, and coleoids (Engeser 1996). The origin of the Orthocerida is poorly understood. The earliest unequivocal Orthocerida are known from the Floian (Early Ordovician). A number of poorly known possible Orthocerida and/or stem group Orthocerida are known from the Tremadocian. Here, I reassign the long known middle Tremadocian "*Orthoceras attavus*" to the new genus *Slemmestadoceras* belonging to a group of worldwide distributed orthoceratoids. The presence of *Slemmestadoceras* with a thin, probable tubular siphuncle and small initial chambers in the middle Tremadocian suggests that the Orthocerida may have originated already at that time. The comparison of *Slemmestadoceras* with following late Tremadocian and Floian orthoceratoids demonstrates that a higher level taxon comprising these forms, such as the subclass Orthoceratoidea may constitute a paraphylum.

The Orthoceratoidae comprise a wide range of orthocones with short septal necks and tubular or expanded siphuncles of the orders Ascocerida, Dissidocerida, Lituitida, Orthocerida, and Pseudorthocerida (Sweet 1964; Dzik 1984; Zhuravleva 1994; Kröger et al. 2007). Two main groups are recognisable within the Orthoceratoidae, orthocones with a conical apex, having a cicatrix (Ascocerida, Pseudorthocerida) and orthocones with small spherical apex lacking a cicatrix (Lituitida, Orthocerida). The Ascocerida and Lituitida are very characteristic orders that appear in the Middle Ordovician (Furnish and Glenister 1964; Dzik 1984). The Dissidocerida include orthocones with slightly expanded tubular siphuncles and rod-like endosiphuncular deposits known from the Silurian Dissidoceratidae and several Early Ordovician families (Zhuravleva 1994; Evans 2005). The Orthocerida was emended by Kröger and Isakar (2006: 143) and comprises now only orthoceratoids with a spherical apex and a simple siphuncle. By contrast, the Orthocerida sensu Sweet (1964: K223) comprise a wide range of orthoceratoids classified today within the Orthocerida, Pseudorthocerida, and Dissidocerida. Herein I always refer to the emended order Orthocerida sensu Kröger and Isakar, 2006 as orthocerids. The origin of the Orthocerida and Pseudorthocerida is poorly understood. In the Early Ordovician a number of orthocones occurred that are either poorly known proper members of these latter orders or stem group members, respectively.

Classically the origin of Orthocerida was sought within the middle Floian (Flower 1962; Hook and Flower 1977) when the first straight orthocerids with wide chamber spacing and a central, narrow, empty siphuncle appear. Recently, Evans (2005) described the new genus *Semiannuloceras* from the early Floian (Moridunian) of Wales and classified it within the orthocerid family Baltoceratidae. Furthermore, Evans (2005) formulated a scenario of the early evolution of orthoceratoid cephalopods and the origin of Orthocerida, in which he suggests an ancestry of the Orthocerida from the Troedssonellidae and/or Polymeridae,

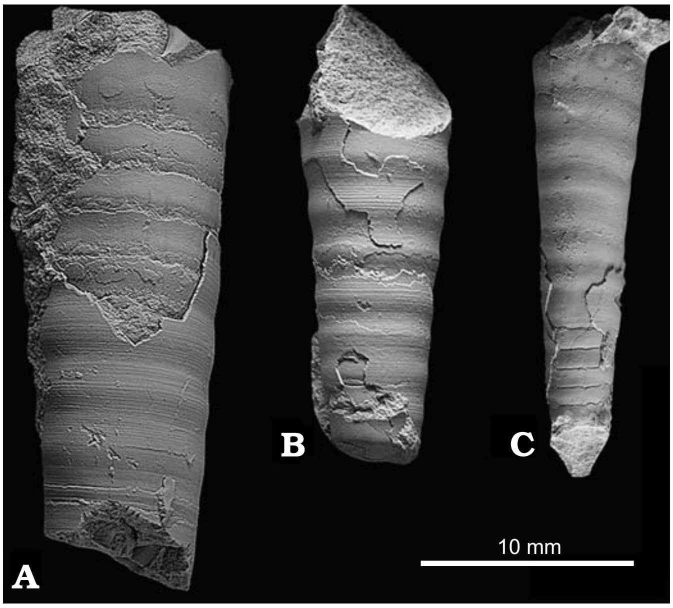

Fig. 1. Orthoceratoid cephalopod *Slemmestadoceras attavus* (Brøgger, 1882) from Black nodule layer at base of Bjørkåsholmen Formation (*Bienvillia angelini* bed), *Paltodus deltifer* Conodont Zone, Timeslice 1b of Webby et al. (2004), Tremadocian, Lower Ordovician; Oslo Region, Norway. **A**. PMO 1870b, lateral view of largest known specimen. **B**. PMO1219b, antisiphuncular? view. **C**. PMO 1219a, lateral view, note the long body chamber and the slightly oblique septa.

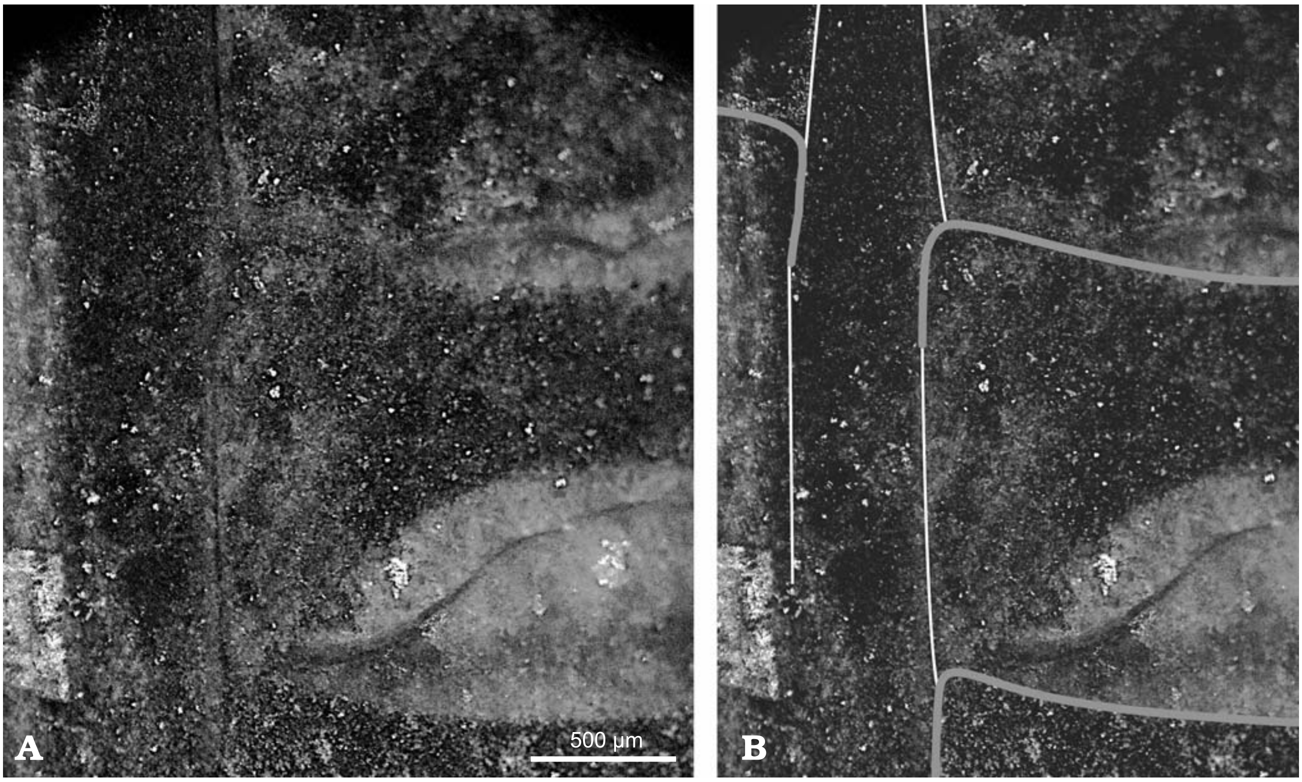

Fig. 2. Details of the median section of detail of siphuncle and septa of *Slemmestadoceras attavus* (Brøgger, 1882), PMO 1219a, from Black nodule layer at base of Bjørkåsholmen Formation, Tremadocian, Lower Ordovician; Slemmestad, Oslo Region, Norway. Apex downward. Note the tubular siphuncle at left. Grey areas at right show traces of upward bent septa. **A**. Original photograph. **B**. Intepretation of the visible structures. Septa and septal necks dark grey, Connecting ring white line.

which occurred in the earliest Moridunian (earliest Floian). The latter two groups are orthocones with a wide marginal or eccentric siphuncle with characteristic endosiphuncular deposits. This may suggest an ancestry of the Orthocerida from vacuosiphonate Protocycloceratidae of the Ellesmerocerida by narrowing of the siphuncle and simultaneously widening of septal spacing in the Floian.

The monotypic new genus *Slemmestadoceras* from the middle Tremadocian (Stairsian equivalent) Bjørkåsholmen Formation of Norway possesses a narrow marginal siphuncle, orthochoanitic septal necks, and straight sutures, which are typical characters of the Orthocerida (Figs. 1, 2). In *Slemmestadoceras*, the connecting ring is poorly preserved and it is difficult to decide if the ring was slightly concave or tubular (Fig. 2). The slender, straight shell, and the nearly tubular, thin connecting ring are characters that occur in a number of cephalopods of similar and slightly younger age. In *Kyminoceras forresti* Teichert and Glenister, 1954 from the Emanuel Creek limestone, of Western Australia the rings also appear tubular or only slightly concave. *K. forresti* is considered of mid-Tremadocian (equivalent with the Rochdale Formation, compare Kröger and Landing 2008) by Glenister (1952), but Zhen et al. (2001) correlate the lowermost Emmanuel Limestone with earliest Floian. A third genus of this group of slender orthocones with thin tubular, or slightly concave connecting rings is *Vassaroceras* (Ulrich et al. 1944), from the Stairsian Rochdale Formation of New York, USA. In *Vassaroceras* the connecting ring is unusually thin and tubular, or slightly concave (Kröger and Landing 2008).

Therefore, together with *Slemmestadoceas attavus*, which is described herein, one or two other middle Tremadocian species are known, comprising slender orthoconic shells and thin nearly tubular connecting rings. These middle Tremadocian forms are transitional to the Orthocerida of the Floian. However, because the available data on the connecting ring shape are equivocal and data on apex morphology are lacking, a classification at the order level is impossible.

An additional enigmatic form is "*Ellesmeroceras elongatum* Kobayashi", described by Balashov (1955) from the Tremadocian Ustkutsk Regional Stage of Siberia, which is externally very similar to *Ellesmeroceras* but internally differs in having an eccentric tubular siphuncle.

In an attempt to resolve the early phylogeny of the early orthoceratoids I compiled a character matrix of several Tremadocian and Floian taxa (Table 1). This compilation includes key taxa of early orthoceratoids of the families Baltoceratidae, Polymeridae, Troedssonellidae, and of orthocone ellesmerocerids belonging to the Cyptendoceratidae, Ellesmeroceratidae, and Protocycloceratidae, and representatives of the Orthoceratidae. The genus *Rioceras* was included as representative of a group of slender ellesmerocerids, which are falsely assigned to the Baltoceratidae since Flower (1964) and are often referred to as "vacuosiphonate Baltoceratidae" (compare Evans 2005: text-fig. 10). Regrettably, with the current data no resolution is possible that would support

Table 1. Character matrix for typical Tremadocian and Floian orthoceratoid cephalopods and straight annulated Ellesmerocerida. Cross section: 1, compressed, 2, circular, 3 depressed. Ornamentation: 1, annulated; 2, smooth. Siphuncle position: 1, marginal; 2, eccentric; 3, central-subcentral. Siphuncle diameter relative to conch cross section: 1, narrow (≤ 0.1); 2, medium (> 0.1 ≤0.3); 3, large (> 0.3). Connecting ring shape: 1, concave; 2, tubular; 3, convex. Septal distance given as number of chambers per distance similar to conch cross section: 1, narrow (≥ 8); 2, medium (> 8 ≥ 5); 3, wide (< 5). Suture shape: 1, lobate; 2, straight. No sufficient resolution results in a consensus tree of the parsimony analysis, consequently no equivocal grouping and phylogenetic scenario can be constructed.

Species	cross section	ornamentation	siphuncle position	siphuncle diameter	siphuncular deposits	connecting ring shape	septal distance	suture shape
Belloceras milleri Cecioni, 1971	3	1	1	3	1	3	2	2
Buttsoceras adamsi (Butts, 1926)	3	2	3	2	3	2	3	2
Cyptendoceras ruedemanni Ulrich and Foerste, 1936	3	2	1	3	4	1	1	2
"*Ellesmeroceras elongatum* Kobayashi" in Balashov (1955)	1	2	2	1	1	2	1	2
Kyminoceras forresti Teichert and Glenister, 1954	2	1	1	2	1	2	2	1
Moridunoceras castelli Evans, 2005	2	2	2	2	3	3	3	2
Palorthoceras kayseri Kröger, Beresi, and Landing, 2007	2	2	3	1	1	2	3	2
Polymeres demetarum Murchison, 1839	2	2	1	3	3	3	1	2
Protocycloceras lamarcki (Billings, 1859)	2	1	1	2	1	1	2	2
"*Protocycloceras*" cf. *lamarcki* in Balashov (1955)	2	1	2	2	1	2	2	2
"*Protocycloceras*" *angustisiphonatum* (Ying, 1989)	2	1	3	1	1	2	3	2
"*Protocycloceras*" *hupehense* (Shimizu and Obata, 1936)	2	1	3	2	1	2	3	2
"*Protocycloceras*" *stefanini* (Cecioni, 1953)	3	1	1	3	4	2	2	2
Rhabdiferoceras annuliferum Flower, 1964	3	2	1	3	4	3	3	2
Rudolfoceras cornuoryx (Whitfield, 1886)	1	1	2	1	1	1	1	1
Semiannuloceras abbeyense Evans, 2005	2	1	1	2	1	2	3	2
Slemmestadoceras attavus (Brøgger, 1882)	2	1	1	1	1	2	2	1
Vassaroceras henrietta (Dwight, 1884)	1	1	1	1	1	2	1	1
Walcottoceras monsensis (Walcott, 1924)	1	1	1	1	1	1	1	1

the unequivocal placing of one of these families in a monophyletic clade supporting the Orthoceratoidea. Even the introduction of directionality of the siphuncle shape gives no satisfactory results as it produces more than hundred similar parsimonious trees and the consensus tree is not resolved. Several very different phylogenetical scenarios are possible and the paraphyly of the Dissidocerida cannot be ruled out with the current data (Fig. 3).

Therefore, the new genus *Slemmestadoceras* cannot be unequivocally placed within any higher taxon. Moreover, the placing of the genus within the Orthoceratoidea is problematical because there is no cladistic support for this subclass. However, the presence of *Slemmestadoceras* shows that the earliest potential Orthoceratida appeared already in the middle Tremadocian, (Timeslice 1b; Webby et al. 2004; Stairsian and equivalent beds). The beginning of the Floian, roughly six million years later, when a large number of new orthoceratoid morphologies appeared almost simultaneously, marks the start of the Palaeozoic story of orthoceratoid success.

Institutional abbreviation.—PMO, Paleontological Museum Oslo, Norway.

Systematic palaeontology

Subclass Orthoceratoidea McCoy, 1844

Order and Family uncertain

Genus *Slemmestadoceras* nov.

Etymology: From Slemmestad, Oslo Region Norway, the small harbour next to the type locality of the Bjørkåsholmen Formation (Owen et al. 1990).

Type species: *Orthoceras attavus* Brøgger, 1882, from the base of Bjørkåsholmen Formation, Vestfossen, Norway, by monotypy.

Diagnosis.—Orthoconic longicones similar to *Kyminoceras* and *Protocycloceras* with respect to the apical angle of approximately 6°, and a number of four rounded annulations per distance similar to the conch diameter. In contrast to *Kyminoceras* septa are straight, sloping slightly adapically in direction of prosiphuncular conch side and instead of five, only four chambers occur at a distance similar to the conch cross section. Siphuncle marginal and nearly half as wide as in *Kyminoceras* with diameter 0.1 of conch cross section. Connecting ring tubular, septal necks orthochoanitic.

Remarks.—The new genus is based on the unique combination of straight sutures and a comparatively wide tubular siphuncle. *Protocycloceras* differs in having a siphuncle with concave segments and *Semiannuloceras* Evans, 2005 in having a wider apical angle and an annulation that fades out during growth.

Stratigraphic and geographic range.—Black nodule layer at the base of the Bjørkåsholmen Formation (*Bienvillia angelini* bed), *Paltodus deltifer* Conodont Zone, Timeslice 1b of Webby et al. (2004), Tremadocian, Lower Ordovician; Oslo Region, Norway.

Slemmestadoceras attavus (Brøgger, 1882)

Figs. 1, 2.

1882 *Orthoceras attavus* sp. nov.; Brøgger 1882: 53, 54, pl. 4: 9, 10, 17; pl. 10: 16.

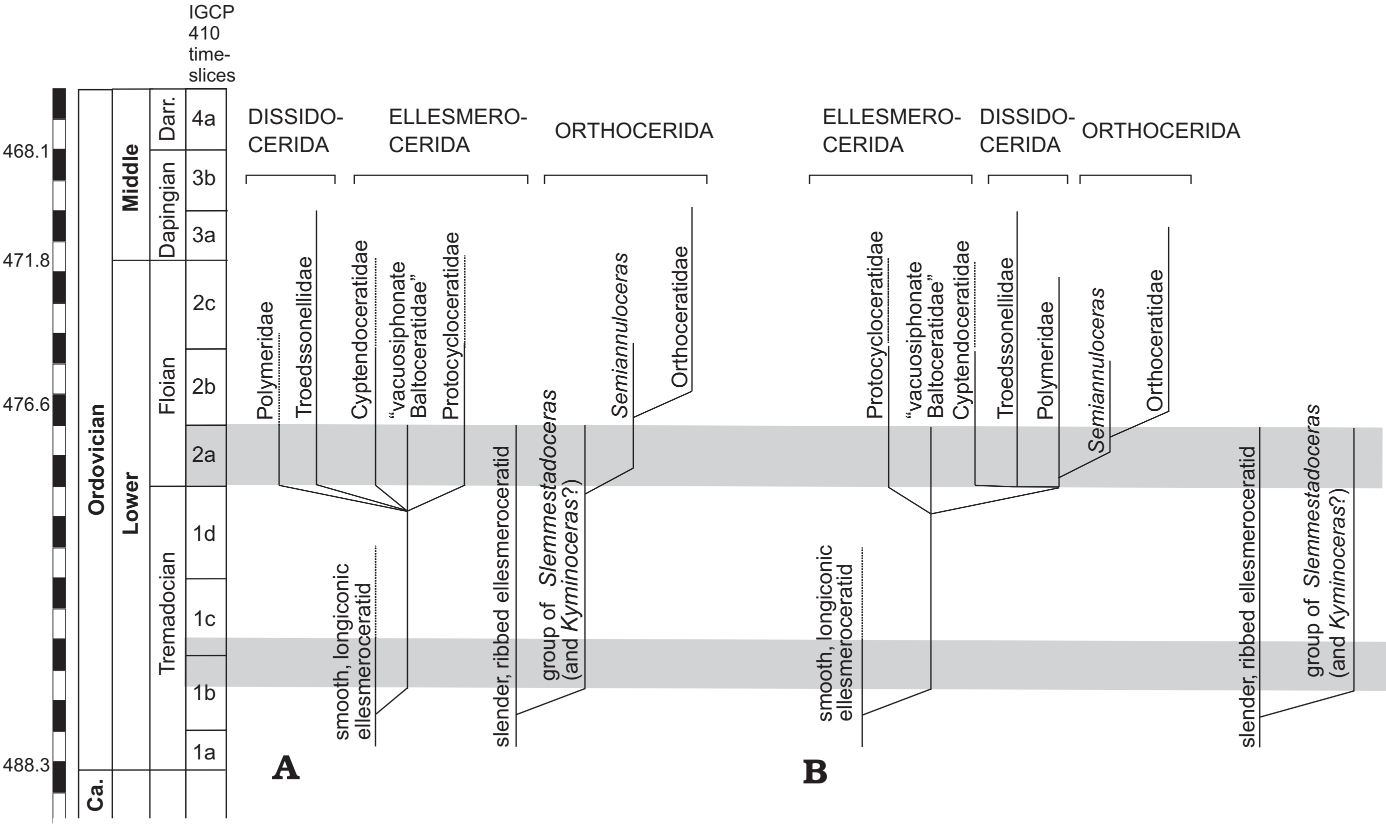

Fig. 3. Two possible phylogenetical trees of the early evolution of Orthoceratoidea. Based on the cladistic analysis (see text) several alternative trees are possible. **A**. Tree with Dissidocerida and Orthocerida independently evolving and a paraphyletic Orthoceratoidea origin, suggesting *Slemmestadoceras* gen. nov. may be an ancestal orthocerid. **B**. Tree concurrent with Evans (2005: text-fig. 10), suggesting an ancestry of the Orthocerida from vacuosiphonate Protocycloceratidae of the Ellesmerocerida by narrowing of the siphuncle and simultaneously widening of septal spacing in the Floian. Stratigraphic occurrences corrected based on Ordovician stratigraphic chart of Webby et al. (2004: fig. 2.1–2). Grey intervals mark main radiation events in the Stairsian and equivalent beds and earliest Floian. Abbreviations: Ca., Cambrian; Darr., Darrivillian.

1931 *Orthoceras attavus* Brøgger; Foerste (1931): 280.
1953 *Protocycloceras attavus* (Brøgger); Balashov (1953): 212.
1999 *Orthoceras attavus* Brøgger; Ebbestad (1999): 17.

Material.—Nine specimens from PMO. Impression of specimen PMO I 0001(the specimen itself is lost) in a nodule of black limestone from the Bjørkåsholmen Formation, labelled as paratype and originally figured in Brøgger (1882: pl. 4: 9), specimen PMO I 0004 (labelled as lectotype by unknown person) and figured in Brøgger (1882: pl. 10: 16) both from the base of the Bjørkåsholmen Formation, Vestfossen, Norway. PMO I 1875–1876, from Odden north of Slemmestad. Specimens PMO 1219a, 1220a from Bjørkåsholmen, Slemmestad, Norway, and PMO 58710a–c from a nodule of the Bjørkåsholmen Formation of unknown locality, collected by Lars Størmer in 1915 and 1936 respectively. Specimen PMO 1219a designated as lectotype herein.

Diagnosis.—Same as for genus.

Description.—Largest specimen PMO 1876 with conch cross section 9 mm. Angle of expansion approximately 0.11 (mean 0.11, n = 5). Cross section subcircular, very slightly compressed. Ornamented with regularly spaced wide transverse shallow undulations. Undulations form shallow ventral lobes, and at a distance equivalent to conch cross section diameter three rounded ridges occur. Depth of valley between ridges of undulation about 0.1 mm at conch cross section 6 mm. In specimen PMO I 0004 four ridges occur at distance similar to conch height. Conspicuous growth lines parallel to undulations, at specimen PMO 1876 approximately ten growth lines per millimetre. Shell thickness at conch cross section 9 mm 0.2 mm at PMO 1876. Septa nearly straight, sloping slightly adapically in direction of prosiphuncular conch side. Septal distance 2 mm at specimen PMO 1876. Conch straight or only very faintly bent. Siphuncle marginal. Long body chamber in juvenile growth stages. At specimen PMO 58710a conch diameter at base of body chamber 5.4 mm, body chamber length 16 mm, there apically five phragmocone chambers are preserved with septal distance 0.8 mm. Specimen very slightly bent with siphuncle at concave side of conch curvature.

Sutures straight and directly transverse. Siphuncle marginal, tubular with diameter 0.5 mm at conch cross section 5 mm. Septa in specimen PMO 1219a strongly recrystallized but orthochoanitic septal necks visible. Connecting ring preserved only as dark seam.

Remarks.—A small slender apex of *Slemmestadoceras*, similar to that of known Baltoceridae (e.g., Evans 2005: pl. 3: 15; pl. 4: 16) can be assumed by the slender conch fragments of the smallest preserved specimen, which are approximately 2 mm in diameter. However, it is not known if the apex is spherical or conical.

All known specimens from the Bjørkåsholmen Formation are from dark limestone nodules ("schwarze Kalksteinellipsoide" Brøgger 1882: 16) from a layer in the lowermost part of the formation. This level can be traced throughout the entire Bjørkåsholmen Formation in the Oslo Region; it contains abundantly the trilobite *Bienvillia angelini* (Linnarsson, 1869) as well as other trilobites and mollusks. Ebbestad (1999) supposed a depositional setting well below a normal storm wave base or even below a storm wave base. Beneath *Slemmestadoceas attavus* undescribed specimens of *Ellesmeroceras* sp. co-occur in the same horizon that are in the collection of the PMO. Lamansky (1905: 27) described "*Orthoceras attavus*" from the Billingen Regional Stage (B_1beta) of Popovka, St. Petersburg Oblast, Russia. Lamansky's original specimen at the Palaeontological museum of the VSEGEI at St. Petersburg (Nr. 122/222) shows surface characters similar to *S. attavus*. However, similar ornamented orthocerids are very common in the Early Ordovician, making a definite species and genus designation impossible and it remains questionable if this specimen is a *Slemmestadoceras*.

Stratigraphic and geographic range.—Same as for genus.

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