The cephalopods of the Kullsberg Limestone Formation, Upper Ordovician, central Sweden and the effects of reef diversification on cephalopod diversity

Björn Kröger[a] and Martina Aubrechtová[b*]

[a]Finnish Museum of Natural History, University of Helsinki, Pohjoinen Rautatiekatu 13, Helsinki, Finland, bjorn.kroger@helsinki.fi, [b]Institute of Geology and Palaeontology, Faculty of Science, Charles University in Prague, Albertov 6, 128 43 Praha 2, Czech Republic, aubrechm@gmail.com [corresponding author]

Abstract: The cephalopods collected from the mud-mounds of the Kullsberg Limestone Formation, late Sandbian–earliest Katian(?), south central Sweden, are highly diverse and comprise 26 identifiable species of 12 families and six orders in a sample of c. 180 specimens. The assemblage is strongly dominated by orthocerids in abundance and diversity. In contrast, the time equivalent assemblage of the reef limestone of the Vasalemma Formation of Estonia is dominated by actinocerids and less diverse. Only one third of the species co-occur in the two palaeogeographically relatively close assemblages, respectively. The taxonomic composition of the Kullsberg assemblage is on the order level more similar to that of the late Katian–early Hirnantian Boda Limestone Formation of south central Sweden, which represents a similar relatively deep depositional environment. The high local differentiation of cephalopod reef faunas exemplifies the importance of the emergent Baltic reef habitats in the diversification processes during early Late Ordovician. Of the described taxa, the following are new: *Beloitoceras thorslundi* sp. nov., *Cameroceras motsognir* sp. nov., *Clothoceras thornquisti* gen. *et* sp. nov., *Danoceras skalbergensis* sp. nov., *Discoceras amtjaernense* sp. nov., *D. nilssoni* sp. nov., *Endoceras naekki* sp. nov., *Furudaloceras tomtei* gen. *et* sp. nov., *Isbergoceras consobrinum* gen. *et* sp. nov., *I. niger* gen. *et* sp. nov., *Isorthoceras nikwis* sp. nov., *I. sylphide* sp. nov., *I. urdr* sp. nov., *I. verdandi* sp. nov., *Kullsbergoceras nissei* gen. *et* sp. nov., *Ordogeisonoceras uppsalaensis* sp. nov., *Valkyrioceras dalecarlia* gen *et* sp. nov.

Keywords: Great Ordovician Biodiversification Event (GOBE), bioherm, palaeogeography, Sandbian Stage, Katian Stage, GICE

Introduction

This faunal analysis is the last of a series of three papers, all of them outline fossil cephalopod assemblages within Late Ordovician reef settings of Baltoscandia, and none of the assemblages was described before in its entirety. The first of these analyses monographically covered the cephalopod assemblage of the Boda Limestone Formation, late Katian–Hirnantian stages, of central Sweden (Kröger 2013) and the second paper is a description of the cephalopods of the Vasalemma Formation, late Sandbian Stage, of northern Estonia (Kröger & Aubrechtová 2017). The cephalopods of the Kullsberg Limestone Formation, described herein, connect the two former assemblages stratigraphically and geographically, and this triangle allows for the distinction of global evolutionary trends and local habitat pattern.

The carbonates of the Kullsberg Limestone, like that of the Boda Limestone, are exposed in the Siljan impact structure of central Sweden (Fig. 1). They are associated with the oldest mud mound generation of the area (Jaanusson 1982; Ebbestad & Högström 2007; Calner *et al.* 2010). More generally, the Kullsberg Limestone represents the time interval of the oldest extensive reef and mound formation across the Baltic Basin and Baltoscandia (Kröger *et al.* 2016). Mud mounds and reefs of the late Sandbian stage are known from Norway (Steinvika and Mjøsa limestones, Harland 1981), from the subsurface of the Baltic sea (e.g. Flodén 1980) and from Estonia (Vasalemma Formation, Kröger *et al.* 2014a, b; Fig. 2). These reefs and mounds mark the beginning of a prolonged Ordovician and Silurian evolution of bioherms and the onset of a pronounced facies differentiation across the area (see review in Kröger *et al.* 2016). At the same time the late Sandbian locally and globally marks the early climax of the Great Ordovician Biodiversification Event (GOBE, e.g. Hints *et al.* 2010; Servais *et al.* 2010; Kröger & Lintulaakso 2017, and references therein).

The reef evolution is a central aspect of the GOBE (e.g. Webby 2002; Adachi *et al.* 2011; Kröger *et al.* 2016, and references therein), but it remains poorly explored how the diversification of swimming and mobile potential reef dwellers, such as cephalopods, was affected by the expansion and diversification of reefs during the Ordovician. Did the establishing of a widespread reef and mound habitat affect the in-between habitat diversity (β diversity) of cephalopods and did during the Late Ordovician a reef-related cephalopod fauna appear? These are the questions which we addressed here based on the existing framework of taxonomic studies (Kröger 2013; Kröger & Aubrechtová 2017).

Studied Material and Geological Setting

Abbreviations

NRM RMo: Swedish Museum of Natural History, Stockholm, Sweden; **PMU**: Museum of Evolution, Uppsala University, Uppsala, Sweden.

Studied material

The studied material exclusively came from previously existing museum collections and no new material was collected by the authors. Most of the available specimens were collected in the first half of the 20th century by Swedish geologists Orvar Isberg (1884–1950), and Elsa Warburg (1886–1953). The collections comprise more than 160 cephalopod conch fragments of all size classes, spanning such with a diameter of <1 mm to large phragmocones with diameters of more than 100 mm. The presence of many poorly preserved small orthocerid fragments indicates that the collection is not biased towards nicely preserved or rare species or specimens.

Geological Setting and Stratigraphy

The Palaeozoic sediments in the Siljan area, Dalarna, central Sweden, occur in the circular, c. 75 km wide Siljan ring graben. This impact structure of Middle Devonian age (Reimold *et al.* 2005) prevented stratigraphically older Palaeozoic sediments from subsequent erosion. The impact caused some tectonic disturbance of the bedding with a generally strong, large scale (> tens of meters to kilometers) fracturing and folding. Nevertheless, the Ordovician succession is remarkably complete and diagenetically little altered (see review in Ebbestad & Högström 2007).

In the Siljan ring structure, peculiar, several hundred meter wide, geographically isolated bodies of limestone occur. Traditionally these often brachiopod-rich limestone bodies were subsumed under the "*Leptaena* Limestone". In the early 20th century, it became obvious that the *Leptaena* Limestone represents two stratigraphically distinct mud-mound generations (see e.g. Warburg 1925). The lithostratigraphic term Kullsberg Limestone was introduced by Troedsson (1928) and comprises the stratigraphically older generation of the mud-mound carbonates. The stratigraphically younger mound generation is contained within the Boda Limestone Formation (see review in Ebbestad *et al.* 2015; Kröger *et al.* 2016).

A number of nine distinct Kullsberg Limestone mounds are known with reported diameters of between 300–350 m and thicknesses of about 40–50 m. This contrasts with the Boda Limestone with more than 20 known individual mounds with diameters of up to 1 km and thicknesses of up to 90 m (Ebbestad & Högström 2007 and references therein).

A high-resolution stratigraphical correlation of the Kullsberg Limestone is not trivial because of the lack of diagnostic fossils such as conodonts (e.g. Bergström 2007). However, the relative age can be well constrained because the Kullsberg Limestone overlies the Kinnekulle K-bentonite which has been dated with an absolute age of c. 455 Ma (Bauert *et al.* 2014 and references therein) and because it records the onset of the Guttenberg Carbon Isotope Excursion (GICE, Calner *et al.* 2010; Bergström *et al.* 2011). The onset of the GICE is well documented from many Baltoscandian sections (e.g. Ainsaar *et al.* 2010; Bergström *et al.* 2011, 2016). In a recent review, Kröger *et al.* (2016) argued that the shallow water reefs of the Norwegian Mjøsa and Steinvika Limestone formations and of the Estonian Vasalemma Formation are nearly time equivalent to the Kullsberg Limestone Formation. The reefal part of the Vasalemma Limestone (except for the stratigraphically younger Saku Member) was interpreted as exclusively latest Sandbian (Kröger & Aubrechtová 2017). The termination of the Kullsberg mound growth probably occurred slightly later, but the exact timing is difficult to determine because currently, the correlation with the inter-mound facies is not fully resolved (Calner *et al.* 2010).

Methods

The specimens were studied using a stereoscopic microscope Olympus SZX7 (ACH 1x) and a stereoscopic microscope Olympus SZX16 (0.5xPF) with attached camera. The measurements were taken either by a caliper, or calibrated measure inserted into the microscope. Polished median sections of selected specimens were prepared and photographed. For photographing of surficial structures, selected specimens were coated with ammonium chloride. Nikon D5300 and Canon EOS 6D cameras were used for photographing. The photographs were finished with CorelDRAW X5 and Photoshop CS5. The morphological terms for the description of the cephalopod shell are adopted from Kröger (2004) and Kröger & Isakar (2006). The terminology of the septal necks with terms such as orthochoanitic, suborthochoanitic, cyrtochoanitic and loxochoanitic is not always unambiguous when the septal neck is very short. This can create some cursory conflicts between existing genus and species diagnoses and specific descriptions. For a discussion of this problem see Kröger & Isakar (2006: 140, 153).
Six descriptive indices are used: The whorl expansion rate (WER) adopted from Korn & Klug (2003) is used for the description of coiled specimens. The whorl expansion rate is calculated as WER = $(dm_1/dm_2)^2$ where dm_1 is the diameter of the conch and dm_2 the diameter

360° preceding dm_l. The whorl width index (WWI) is the whorl width divided by the whorl height. The siphuncular position ratio (SPR) and siphuncle segment compression ratio (SCR) are adopted from Frey (1995) and are calculated as the minimum distance of the connecting ring from the conch margin divided by the corresponding conch height, and as siphuncle segment length divided by siphuncle segment height, respectively. The relative chamber length (RCL) is the chamber length divided by the corresponding conch diameter, and the relative siphuncular diameter (RSD) is the diameter of the siphuncle divided by the corresponding conch diameter.

The diversity measures and the measures of evenness are calculated 1.) based on subsampled richness after the shareholder quorum subsampling method of Alroy (2010) using R and the functions of the version 3.3 provided by John Alroy in 2011 (http://bio.mq.edu.au/~jalroy/SQS.html); and 2.) based on extrapolated Hill numbers using the method of Chao *et al.* (2014) and the R Package iNext (Hsieh *et al.* 2016). The taxonomic distinctness (Clarke & Warwick 1999) was calculated with a step length of 1. This is justified in the case of Palaeozoic cephalopods because in all taxa, a fixed scheme of species, genus, family, order is used (see e.g. Moore 1964). The multivariate analyses were executed with the R functions of Vegan (Oksanen *et al.* 2013). A correspondence analysis as implemented in the function cca (all cephalopod orders are the variables of the analysis) of vegan was preferred herein as ordination method because it results in a relative ordering of the assemblages (see Oksanen *et al.* 2013). The data for the comparison of the cephalopod assemblages are compiled from the literature (see Kröger & Aubrechtová 2017, Data Supplement 3).

Systematic palaeontology

Order **Tarphycerida** Flower in Flower & Kummel, 1950

Family **Trocholitidae** Chapman, 1857

Genus ***Discoceras*** Barrande, 1867

Type species. *Clymenia antiquissima* Eichwald, 1842, Kärdla, Island of Hiiumaa, Estonia, Nabala to Pirgu regional stages, late Katian Stage.

Diagnosis (after Furnish & Glenister 1964). Gradually expanding conchs with a ribbed or smooth shell surface, characterized by a slight to moderate whorl overlap, circular to subquadrate whorl cross-section, central position of siphuncle in initial half-volution, marginodorsal in succeeding 1.5 to 2 whorls, subdorsal at maturity, and thick, layered connecting rings.

Discoceras amtjaernense sp. nov.

(Figs 3A–B, 4A–B, 5A, C)

Holotype. Specimen PMU #D736, herein figured at Figs 4A, B.

Derivation of name. Referring to the type locality.

Diagnosis. *Discoceras* with a slightly depressed to slightly compressed ovoid whorl cross-section, WWI decreases with increasing shell diameter from 0.85 to < 1.17, WER varies between c. 1.7–2.7, UWI between 0.3–0.5, growth gyroconic in latest growth stage; ornamented with faint irregularly spaced lirae with deep hyponomic sinus and with shallow irregularly spaced ribs in latest growth stages.

Material. Holotype and an additional number of 17 specimens at the NRM and PMU, from localities Amtjärn (8), and Kullsberg (9), Dalarna, central Sweden, Kullsberg Limestone Formation (see Data Supplement 1).

Type locality and horizon. Amtjärn, central Sweden, Kullsberg Limestone Formation.

Occurrence. Kullsberg Limestone Formation, central Sweden, late Sandbian Stage.

Description. The holotype is a fragment of a phragmocone and a body chamber, with three whorls with a maximum diameter of 47 mm. The preserved body chamber has a length of c. 70°. At its maximum diameter, the specimen has a whorl width of 18.5 mm and a whorl height of 17 mm; the umbilicus has a diameter of 19.6 mm. The specimen is ornamented with pronounced growth lines or transverse lirae that form a deep hyponomic sinus (Fig. 4B). Additionally, in latest growth stages, very shallow, irregularly spaced ribs are apparent (Fig. 4A). In the whorl cross section (see also Fig. 3A), the venter is shallowly rounded, convex and the imprint zone is very shallow.

The specimens included within this species reveal a relatively high variability in WER, varying between 1.7–2.7 (median 2.23, n = 16), with no ontogenetic trend (Fig. 6A). The WWI is more constrained, varying between 0.86–1.17 (median 0.99, n = 13), with a clear decreasing trend during ontogeny (Fig. 6B).

The largest specimen in the collections has a diameter of 66 mm (PMU #D1378), but it is not clear, if this specimen reached adult size. Gyroconic growth stages are reached during late ontogeny at different conch sizes (at diameters 36 mm in PMU #D1368; 40 mm in PMU #D1367, and PMU #D1384; 58 mm in PMU #D1381; 66 mm in PMU #D1378). This variability in coiling pattern is also reflected in a relatively high variability of the UWI (0.3–0.47, median 0.39, n = 16), especially during later growth stages.

Remarks. With respect to its oval conch cross section and ornamentation, this species of *Discoceras* is most similar to *D. fleischeri* Sweet, 1958 from the late Sandbian–earliest Katian Steinvika Formation of the Oslo Region and to *D. roemeri* Strand, 1934 from the latest Katian Husbergøya Formation of the Oslo Region. Both latter species differ from *D. amtjaernense* sp. nov. in having more depressed whorls, especially during late growth stages (see Fig. 6B). *D. roemeri* additionally differs from *D. amtjaernense* sp. nov. in having a more pronounced dorsal imprint zone. The Estonian *D. vasalemmense* (Balashov, 1953) (see description in Kröger & Aubrechtová 2017) differs in having a heart-shaped conch cross section and longitudinal ornamentation elements.

Five specimens of *D. amtjaernense* sp. nov. show a detached adult whorl. The detachment is preserved in three of the five specimens at a diameter of c. 40 mm or less and in two specimens at a diameter of c. 60 mm or more (see above). Possibly, this represents sexual dimorphism or some other type of variation.

The specimen RMo 125682 is preserved with a distinct longitudinal colour mark on both flanks of the conch (Fig. 5A, C). This colour mark is also visible in the ornament as a low longitudinal ridge. The specimen´s morphology is well within the variability of other specimens assigned to *D. amtjaernense* sp. nov., herein. Based on this single specimen, it is impossible to decide, if the colour mark is characteristic for *D. amtjaernense* sp. nov. or, alternatively, if specimen RMo 125682 should be treated as a separate species. Herein, we place this specimen within *D. amtjaernense* sp. nov. until more data are available.

Discoceras nilssoni sp. nov.

(Figs 3C, 4C)

Holotype. Specimen RMo 141723–141724, by monotypy.

Derivation of name. Referring to R. Nilsson, the collector of the holotype.

Diagnosis. *Discoceras* with a slightly compressed trapezoidal whorl cross-section, with greatest whorl width near venter; venter and flanks in cross section convex, rounded; WWI decreasing with increasing shell diameter from 1.25 to 1.1; WER 2.2; shallow dorsal imprint zone; ornamented with fine, irregularly spaced growth lines and widely irregularly spaced shallow ribs that form deep hyponomic sinus.

Material. Holotype, only.

Type locality and horizon. Furudal, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.

Occurrence. Known from the type locality and type horizon only.

Description. The holotype and single specimen is a nearly complete specimen with a diameter of 43 mm, a maximum whorl width of 16 mm, a maximum whorl height of 14.3 mm, and with 2.5 volutions; 180° of the body chamber are preserved. The conch cross section (Fig. 3C) is rounded, trapezoidal, with largest width near the venter and convex margins at flanks and venter. The imprint zone is very shallow, less than one mm at the diameter of 43 mm. The siphuncle is near (0.5 mm from) the dorsal conch margin and almost 2 mm wide at a whorl width of 12.5 mm. The conch surface is ornamented (Fig. 4C) with pronounced irregularly spaced growth lines and irregularly spaced (distance c. 30°) shallow ribs. The ribs are more pronounced in later growth stages. The growth lines and ribs are parallel and form a deep and wide hyponomic sinus on the venter.

Remarks. *Discoceras nilssoni* sp. nov. belongs to the group of species of *Discoceras* with subrectangular to trapezoidal conch cross sections. *D. hyatti* Strand, 1934 from the late Katian Husbergøya Formation in the Oslo Region and *D. ievense* Balashov, 1953 from the Jõhvi Regional Stage of northern Estonia are most similar to the new species. *D. nilssoni* sp. nov. differs from these two species in having more pronounced, rounded flanks and venter. It expands faster than *D. hyatti* (WER in *D. hyatti*: 1.9) and has more depressed whorls than *D. ievense* (WWI in *D. ievense*: 0.97).

Order **Discosorida** Flower in Flower & Kummel, 1950

Family **Cyrtogomphoceratidae** Flower, 1940

Genus ***Furudaloceras*** gen. nov.

Type species. *Furudaloceras tomtei* sp. nov., Dalarna, central Sweden, Kullsberg Limestone Formation, latest Sandbian Stage.

Diagnosis. Small cyrtogomphoceritid with relatively slender, slightly curved conch, elliptically compressed conch cross section with width/height-ratio of 0.75, and nearly perfect elliptical conch cross section; adult conch c. 20 mm in height; conch curvature nearly straight at concave side of curvature except earliest growth stages; ornamented with very shallow, irregularly spaced ribs and faint, transverse lirae or growth lines, ornamentation nearly directly transverse with shallow sinus on pro-siphuncular side; sutures form shallow lateral sinus; siphuncle positioned near conch margin at concave side of conch curvature, siphuncle strongly expanded with diameter of c. 0.19 of conch height.

Derivation of name. Referring to the type locality of the type species.

Occurrence. As for the type species, by monotypy.

Remarks. *Furudaloceras* gen. nov. is a compressed cyrtogomphoceratid with similarity to

Kiaeroceras Strand, 1934, and *Strandoceras* Flower, 1946. The two latter genera have a compressed conch cross section with a more narrowly rounded pro-siphuncular side. *Furudaloceras* gen. nov. differs from *Kiaeroceras* in being much smaller in conch height (the adult height of species of *Kiaeroceras* is 60–80 mm) and in having a shorter body chamber without a pronounced adult constriction. *Strandoceras* differs in having a stronger conch curvature with a concave curvature at the pro-siphuncular side of the conch throughout growth, except for the adult body chamber.

Furudaloceras tomtei gen. nov. *et* sp. nov.

(Figs 7A, 8F, 9D)

Holotype. Specimen PMU #D1392, herein figured at Fig. 7A.

Diagnosis. As for the genus, by monotypy.

Derivation of name. Referring to the Tomte, a dwarf in the Scandinavian folklore, because of its small size and the dwarf cap-like conch form.

Material. Holotype and an additional number of 16 specimens from Amtjärn (1), Furudal (14), and Kullsberg (1), all Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages (see Data Supplement 1).

Type locality and horizon. Furudal, Kullsberg Limestone Formation, central Sweden, late Sandbian Stage.

Description. The holotype is a 26 mm long fragment of a phragmocone with parts of a body chamber with a conch height of 5.3–16.2 mm and a conch width of 3.9–12.6 mm; an angle of expansion of 23° and a relative conch width of 0.77–0.78. The relative distance between two adjacent septa (RCL) is c. 0.153. The sutures form a shallow lateral lobe. In lateral view, the concave side of the conch is nearly straight. The conch is slightly undulated. The conch surface is nearly smooth with faint transverse striae or growth lines (Fig. 7A). The sculpture forms a distinct but shallow sinus at the pro-siphuncular side of the conch. The conch cross section is elliptically compressed, with narrowly rounded pro- and anti-siphuncular sides. The largest specimen known from this species is RMo 141705, a fragment with no internal characters preserved, with a length of 37 mm, an angle of expansion of 21°, and with a maximum conch height of 20 mm. The conch laterally expands throughout its entire length, but its width remains constant at 14 mm at its adoral 10 mm. The siphuncle in specimen RMo 141718 is near the concave margin of the shell curvature, it has a diameter of 1.4 mm at a corresponding conch height of 7.8 mm. The siphuncular segments are strongly expanded (see also Figs 8F, 9D) with a SCR of c. 2.15.

Remarks. Based on the growth features of the largest known specimen, an adult conch height of not much more than 20 mm is assumed in this species.

Genus ***Kullsbergoceras*** gen. nov.

Type species. *Kullsbergoceras nissei* gen. *et* sp. nov., Furudal, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.

Diagnosis. Strongly compressed cyrtocones, with ovate elliptical cross section, with narrowly rounded antisiphuncular side; siphuncle positioned near conch margin at concave side of conch curvature; sutures with shallow lateral lobe and acute saddle at pro-siphuncular side; septal necks short cyrtochoanitic; siphuncular segments strongly expanded within chambers; aperture open with shallow peristomal saddle at flanks.

Derivation of name. Referring to the Kullsberg locality, from which most of the specimens of the type species are known.

Occurrence. As for the type species, by monotypy.

Remarks. *Kullsbergoceras* gen. nov. resembles the Silurian *Protophragmoceras* Hyatt in Zittel, 1900, from which it differs in being less curved, more compressed, and in lacking a pronounced hyponomic sinus. The otherwise similar *Strandoceras* Flower, 1946 differs in having a stronger conch curvature and a narrowly rounded pro-siphuncular side of the conch cross section.

Kullsbergoceras nissei sp. nov.

(Figs 7B–E, 8A, 10A–B)

Holotype. Specimen RMo 141708, herein figured at Figs 7D–E.

Diagnosis. As for the genus, by monotypy.

Derivation of name. Referring to the nisse, a dwarf in the Scandinavian folklore, because of its small size and the cap-like conch form.

Material. Holotype and an additional number of 11 specimens from Furudal (3), and Kullsberg (8), all Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages (see Data Supplement 1).

Type locality and horizon. Furudal, Kullsberg Limestone Formation, central Sweden, late Sandbian Stage.

Description. The holotype is a fragment of a phragmocone and part of a body chamber, with a total conch length of 17 mm, a conch height of 9.5–15.7 mm, and a conch width of 4.5–14.0 mm. The angle of expansion is 20° and the relative conch width is 0.74–0.76. The distance between two adjacent septa is c. 1 mm at a conch height of 10.5 mm. The sutures form a shallow lateral lobe. In lateral view, the convex side of the conch is more curved than the concave side. The shell is slightly undulated. The preserved part of the body chamber has a length of c. 11 mm. The conch surface is nearly smooth, with faint transverse striae or growth lines (Figs 7D–E). Conch cross section ovate, elliptical, with the more narrow edge on the anti-siphuncular side of the conch (see also Figs 10A–B).

Specimen RMo 125655 represents the largest, and probably adult, specimen known from *Kullsbergoceras nissei* sp. nov.. It is a fragment of a phragmocone with a complete (?) body chamber. The total conch length is 18 mm, the conch height is 14.1–18.0 mm, and the conch width is 10.7–13.0 mm. A relative conch width is 0.72–0.76. An angle of expansion is 12°. The relatively low value of the angle of expansion is an effect of an adult lateral contraction of the body chamber. The body chamber has a length of 13 mm. The conch surface of this specimen is well preserved, with fine, directly transverse growth lines and a shallow irregular undulation of the shell. A hyponomic sinus is not developed. The siphuncle is nearly marginal in specimens RMo 125644 and 125645 and positioned at the concave side of the conch curvature. The diameter of the siphuncle is 2.2 mm at a conch height of 13 mm (in specimen RMo 125644), siphuncular segments are strongly expanded (see also Fig. 8A) with a SCR of c. 2.3.

Order **Oncocerida** Flower in Flower & Kummel, 1950

Family **Oncoceratidae** Hyatt, 1884

Genus ***Beloitoceras*** Foerste, 1924

Type species. *Oncoceras pandion* Hall, 1861, from the Black River Formation, Sandbian Stage, by original designation.

Diagnosis (after Frey 1995). Shell strongly curved and breviconic, circular to compressed in cross section. Inflation of shell occurs in the adoral part of the phragmocone. Sutures straight and transverse, adapically, sloping through ontogeny to the concave side of the shell curvature. Phragmocone chambers short (five to eight relative to shell diameter), increasing through ontogeny. Living chamber short, compressed. Muscle-scars ventromyarian. Surface smooth or with fine, raised transverse lirae. Siphuncle on the convex side of the shell curvature. Siphuncular segments subtubular adapically, expanded and elongate ovate adorally. Septal necks short, adapically, suborthochoanitic, more recurved and cyrtochoanitic through ontogeny. Connecting rings thin, homogeneous. Endosiphuncular deposits not present. Cameral deposits may be present.

Beloitoceras thorslundi sp. nov.

(Figs 10D, 11H–I)

Holotype. Specimen PMU 28981, by monotypy.

Diagnosis. *Beloitoceras* with a relatively slender and only slightly gibbous conch; anti-siphuncular side of conch curvature concave throughout its length; adult diameter c. 28 mm.

Derivation of name. Referring to Per Thorslund (1900–1981), a geologist of the Sveriges Geologiska Undersökning, Uppsala, the finder of the holotype.

Material. Known from holotype, only.

Type locality and horizon. Skålberget, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.

Description. The holotype and single specimen is a 43 mm long fragment of a phragmocone with parts of a body chamber, with a conch height of 16.3–28 mm and a conch width of 13.6–24.5 mm. The conch cross section is elliptically compressed, the relative conch width is 0.66 (Fig. 10D). The angle of expansion is 15°. The greatest conch width and height is reached at a distance of c. 10 mm from the adult aperture. The adoral 5 mm of the conch are contracting strongly by 5 mm. In lateral view, the concave side of the conch curvature is curved throughout the entire length. The conch surface (Fig. 11H–I) is ornamented with directly transverse lirae, c. 2 occur per millimeter. The lirae form a distinct, shallow hyponomic sinus on the convex side of the conch curvature. The siphuncle is submarginally positioned and relatively thin, with a septal perforation of c. 2 mm at a conch height of 16.3 mm. The siphuncle is positioned with a distance of c. 1 mm from the conch margin at a conch height of 17.8 mm, and circular in cross section.

Remarks. This slender species of *Beloitoceras* resembles *Lyckholmoceras norvegiae* Strand, 1934 in general growth form, but differs in having a hyponomic sinus and siphuncle on the convex side of the conch curvature; its growth form is unique within *Beloitoceras*.

Beloitoceras stoermeri Sweet, 1958

(Figs 11A–B)

1958 *Beloitoceras stoermeri* Sweet: 81, pl. 5, fig. 1, pl. 17, fig. 1, pl. 21, fig. 7.

1984 *Beloitoceras stoermeri* Sweet, 1958, Dzik: 60, fig. 17.18.

Material. One specimen, RMo 125653, from Kullsberg, Dalarna, central Sweden, Kullsberg

Limestone Formation, late Sandbian–early Katian(?) stages.

Occurence. Arnestad Formation, and Kullsberg Limestone Formation, late Sandbian –early Katian(?) stages, Norway and Sweden.

Type locality and horizon. Bratterud, Ringerike district, Norway, Arnestad Formation (Lower *Chasmops* Shale), late Sandbian Stage.

Diagnosis (after Sweet 1958). *Beloitoceras* characterized by an only slightly gibbous conch and a dorsum, which is concave throughout its length. The species belongs to the form-group typified by *B. clochense* Foerste, but is larger (with adult conch diameter of c. 15 mm) and somewhat less strongly compressed than previously described representatives of this form-group.

Description. Specimen RMo 125653 is a 47 mm long fragment of a phragmocone with parts of an adult body chamber, with a nearly circular conch cross section and with conch diameters of 14–21 mm. In the longitudinal view, the conch is curved on anti-siphuncular and pro-siphuncular sides throughout growth. In cross section, the pro-siphuncular side is more rounded than the anti-siphuncular side. The greatest conch diameter is reached at a distance of c. 20 mm from the adult aperture.

The siphuncular perforation has a diameter of c. 1.2 mm at a conch diameter of 14 mm. It is positioned at 2.3 mm from the conch margin at the convex side of conch curvature. The conch surface is ornamented with fine, irregularly spaced, directly transverse lirae, rugae, and growth lines, c. 2–4 lirae occur per millimeter. No hyponomic sinus occurs.

Family **Diestoceratidae** Foerste, 1926

Genus ***Danoceras*** Troedsson, 1926

Type species. *Danoceras ravni* Troedsson, 1926, from the Cape Calhoun Series, Upper Ordovician, Cape Calhoun, northern Greenland, by original designation.

Diagnosis (after Sweet 1964). Diestoceratid with conch slightly contracted at aperture; septal necks cyrtochoantic, recumbent; segments elongate, sub-trapezoidal in longitudinal section; thin annulosiphonate rings in septal foramen produce distinctive irregular linear process extending adapically and adorally, but not forming rays continuous from segment to segment.

Danoceras skalbergensis sp. nov.

(Figs 8B, 9G, 11F–G)

Holotype. Specimen PMU 28980, by monotypy.

Diagnosis. Slender *Danoceras* with a maximum conch height of c. 60 mm, an angle of expansion of c. 18° and 25 mm deep contracted adult peristome, conch ornamented with directly transverse irregular annuli and striae, which are more pronounced during earlier growth stages, and with shallow hyponomic sinus at pro-siphuncular side.

Derivation of name. Refers to the type locality.

Material. Known from the holotype, only.

Type locality and horizon. Skålberget, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.

Description. The holotype and single specimen is an orthoconic fragment of parts of a phragmocone and an adult body chamber, with the adult peristome partly preserved. The conch has a compressed elliptical cross section. It has a maximum height of 60 mm and a maximum width of 56 mm (relative width 0.93) at a position c. 20 mm adorally from the base of the body chamber. The distance from the last suture towards the adult peristome is c. 45 mm. The adoral 25 mm of the body chamber are contracted towards a height of 53 mm. The adoralmost 30 mm of the shell wall are strongly thickened, with a thickness of 3 mm against a thickness of c. 1 mm at the base of the body chamber. The adapical part of the conch constantly expands with an angle of 18°. The conch cross section appears to be more compressed at the more apical parts of the conch, but because of the fragmentary character of the specimen, the exact rate of compression cannot be determined.

The conch surface is ornamented (Fig. 11F–G) with directly transverse, irregularly spaced, shallow undulations or ribs and striae. At the adoral part of the body chamber, the distance between these ribs is c. 1 mm. At the adapical part, at a conch height of less than 37 mm, the ribs are more deeply pronounced and more widely spaced with a distance of c. 2–2.5 mm. Additionally, fine growth lines run parallel to the ribs and striae. The ornament forms a shallow and narrow hyponomic sinus at the pro-siphuncular side of the conch. The phragmocone is collapsed and only parts of the septa are preserved (Fig. 8B). The distance between the adoral three septa is 5.5 mm, 4 mm respectively (RCL 0.08–0.11). The septal perforation is close to the conch margin (5.4 mm from conch margin) and has a diameter of 1.3 mm at a corresponding conch height of 48 mm. The septal necks (Figs 8B, 9G) are cyrtochoanitic and probably adnate towards the septa. The connecting rings (Figs 8B, 9G) are strongly expanded within chambers and adnate at the septa. The maximum siphuncle diameter is c. 5 mm, where the septal perforation is 1.3 mm (Fig. 8B). The area of the septal necks is strongly recrystallized but the general appearance is very similar to the annular endosiphuncular thickenings known from the genotype of *Danoceras* (Troedsson 1926).

Remarks. This species is most similar to *Danoceras broeggeri* Strand, 1934 from the late

Katian Stage of the Oslo area, from which it differs in being less compressed (relative width 0.7 in *D. broeggeri*), and in having a strictly straight lateral outline of the phragmocone. The Cincinnatian species of *Danoceras* and the late Katian *Danoceras scandinavicum* Strand, 1934 are smaller (< 40 mm in maximum conch diameter) (Flower 1946).

Family **Graciloceratidae** Flower in Flower & Kummel, 1950

Genus ***Isbergoceras*** gen. nov.

Type species. *Isbergoceras niger* gen. *et* sp. nov., Stavnestangen, Ringerike, Norway, Gastropod Limestone, late Katian Stage; by original designation.

Diagnosis. Slender cyrtocones with nearly circular conch cross section; adult aperture slightly constricted; sutures directly transverse; siphuncle positioned at convex side of conch curvature, at some distance from conch margin; septal necks suborthochoanitic; siphuncular segments nearly tubular with distinct constrictions at septal perforation.

Derivation of name. In the honor of Orvar Isberg (1884–1950), a Swedish palaeontologist, who published an extensive monograph on the Boda and Kullsberg Limestone bivalves (Isberg 1934).

Occurrence. As for the type species.

Remarks. *Isbergoceras* gen. nov. superficially resembles the nearly time equivalent Norwegian *Broeggeroceras* Sweet, 1958 in general conch shape, but differs in having a more sharply constricted adult peristome, a clearly larger adult size (adult diameter in *B. contractum* Sweet, 1958 = 44 mm; in *I. niger* gen. *et* sp. nov. = 26 mm), and a westonoceratid-like expanded siphuncle with cyrtochoanitic septal necks. The oncocerid *Oonoceras* Hyatt, 1884 is another brevicone, which is superficially very similar to *Isbergoceras* gen. nov., but it differs from the latter in having a more marginally positioned siphuncle, with more expanded siphuncular segments and cyrtochoanitic septal necks. *Oonoceras* is in need of a revision. It is possible that, e.g., some of the internally inappropriately known species from the Cynthiana Limestone (early Katian Stage, Kentucky, USA) described in Flower (1942) are closely related to *Isbergoceras* gen. nov.

Isbergoceras niger sp. nov.

(Figs 8E, 11D–E)

Holotype. Specimen RMo 125652, by monotypy.

Diagnosis. *Isbergoceras* with an adult size of c. 26 mm, an angle of expansion of c. 9°, ornamented with transverse, irregularly spaced lirae, rugae and growth lines.

Derivation of name. From Latin, black, referring to the color of the holotype.
Material. Known from the holotype, only.
Type locality and horizon. Kullsberg, Kullsberg Limestone Formation, central Sweden, late Sandbian Stage.
Description. The holotype and single specimen is a c. 65 mm long fragment of a phragmocone, with a nearly complete adult body chamber, with a circular conch cross section and a diameter of 15–26 mm (angle of expansion c. 9°). The preserved part of the body chamber has a length of 28 mm and has its maximum diameter at its mid-length with 26 mm. The adult peristome is not preserved. The distance between two adjacent septa is c. 6 mm at a conch diameter of 19 mm (RCL = 0.32). The sutures are directly transverse. In lateral view, the concave side of the conch curvature is concave throughout the entire length of the fragment. The conch surface (Fig. 11D–E) is ornamented with transverse, irregularly spaced lirae, rugae and growth lines; c. 1–3 lirae occur per millimeter. The lirae form a shallow, broad hyponomic sinus on the convex side of the conch curvature. The siphuncle (Fig. 8E) is positioned at a distance of 3 mm from the convex margin of the conch curvature. It has a diameter of 2 mm at a conch diameter of 23 mm. The siphuncular segments (Fig. 8E) are ovate, moderately expanded within the chambers, with constrictions at the position of the septal perforation.

Isbergoceras consobrinum sp. nov.

(Figs 10C, 11C)

Holotype. Specimen RMo 125654, by monotypy.
Diagnosis. As for the genus.
Derivation of name. From Latin, cousin, because it is currently the only other known species of *Isbergoceras* gen. nov.
Material. Known from the holotype, only.
Type locality and horizon. Kullsberg, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.
Description. The holotype and single specimen is a c. 42 mm long fragment of a phragmocone with a part of an adult body chamber. The conch is circular in cross section (Fig. 10C), the diameter is 17–22 mm (angle of expansion c. 7°). The preserved part of the body chamber is 19 mm long and nearly tubular. The conch is faintly constricted at c. midlength of the specimen. The adult peristome is not preserved but a beginning part of a constriction indicates near adult size of the specimen. The distance between two adjacent

septa is c. 4 mm at a conch diameter of 21.5 mm (RCL = 0.19). The sutures form a very shallow lateral lobe. In lateral view, the concave side of the conch curvature is concave throughout the entire length of the fragment. The conch surface has irregularly spaced thickenings and shallow, directly transverse constrictions. The conch is ornamented (Fig. 11C) with transverse, irregularly spaced lirae, rugae and growth lines, c. 1–3 lirae occur per millimeter. The lirae form a very shallow, broad hyponomic sinus on the convex side of the conch curvature. The siphuncle is positioned at a distance of 2.5 mm from the convex side of the conch curvature, where the conch diameter is 17 mm, and where the siphuncular perforation has a diameter of 1.3 mm (RSD =0.08).

Remarks. *I. consobrinum* gen. *et* sp. nov. differs from the genotype in being smaller in adult size and more slender. The adult body chamber appears to be more curved in *I. consobrinum* gen. *et* sp. nov., but this is questionable, because of the fragmentary character of the specimen.

Family **Valcouroceratidae** Flower, 1946

Genus ***Valkyrioceras*** gen. nov.

Type species. *Valkyrioceras dalecarlia* gen. *et* sp. nov., Kullsberg, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.

Diagnosis. Slender, very slightly fusiform cyrtocones with nearly circular juvenile and compressed adult conch cross section, with flattened anti-siphuncular side at concave side of conch curvature; ornamented with faint, narrowly spaced, rounded transverse lirae, which form shallow hyponomic sinus at concave side of conch curvature. Siphuncle slightly eccentric towards convex side of conch curvature, with barrel-shaped siphuncular segments and with cyrtochoanitic septal necks.

Derivation of name. From Valkyria, a female figure in the Norse mythology.

Occurrence. As for the type species.

Remarks. Endosiphuncular deposits are not known from the four specimens assigned to this new genus, but assignment to the Valcouroceratidae is justified by the unique combination of conch shape, siphuncular position and siphuncular segment shape. The otherwise similar Tripteroceratidae Flower, 1941 differ mainly in having a flattened pro-siphuncular side and no actionosiphuncular deposits. *Valkyrioceras* gen. nov. is most similar to *Augustoceras* Flower, 1946 with regards to the conch cross section, but differs from the latter in having a more slender, less curved conch.

Valkyrioceras dalecarlia sp. nov.

(Figs 8C, 9F, 12C, 13F, 16E)

Holotype. Specimen RMo 125640, herein figured at Fig. 12C.

Diagnosis. As for the genus.

Derivation of name. From Latin, Dalecarlia, the type region of this species.

Material. Holotype and three additional specimens; RMo 9066, 9067, and 125624 from Kullsberg , Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages (see Data Supplement 1).

Type locality and horizon. Kullsberg, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.

Description. The holotype is the most complete specimen; it represents a 105 mm long, weakly curved fragment of a phragmocone with a width of 12–33 mm, and a height of 11.5–28.5 mm (width/height ratio 1.04–1.16). The conch cross section is slightly compressed or nearly circular during early growth stages. During later growth stages, it is depressed and flattened at the anti-siphuncular side (= concave side of conch curvature) (see also Fig. 13F, specimen RMo 9067). The maximum conch width occurs at a mid-height of the cross section. The surface is ornamented with faint, narrowly spaced, rounded transverse lirae (distance c. 2–3 per one mm), which form a shallow hyponomic sinus at the concave side of conch curvature. The sutures form a shallow saddle on lateral sides of the conch. The chamber distance is c. 5.5 mm at a conch height of 20 mm (conch width 23 mm) (RCL 0.25). The siphuncle is slightly subcentral at the convex side of conch curvature. In specimen RMo 9066, the center of the septal perforation is c. 8 mm from the conch margin at the convex side of the conch curvature (= pro-siphuncular side), where the conch height is 18.2 mm, and the septal perforation has a diameter of 1.5 mm (SPR 0.44), respectively. In specimen RMo 9066 (Fig. 16E), siphuncular segments are barrel-shaped and moderately expanded within the chambers (ratio of septal perforation / maximum siphuncular width = 0.75). The septal necks in specimen RMo 125624 are cyrtochoanitic (Figs 8C, 9F). Endosiphuncular deposits are not present in the two cut specimens (RMo 9066 and 9067), which have conch diameters of 15–20 mm, respectively.

Order **Endocerida** Hyatt in Zittel, 1990

Family **Endoceratidae** Hyatt, 1884

Genus ***Cameroceras*** Conrad, 1842

Type species. *Cameroceras trentonense* Conrad, 1842, Middleville, New York, USA, Trenton Limestone, early Katian Stage; by original designation.

Diagnosis (adopted from Teichert 1964). Slender, large orthocones with circular or somewhat depressed cross section; sutures simple and straight, or with very slight ventral lobe; siphuncle up to 0.5 of corresponding conch cross section in diameter; mostly marginally positioned; septal necks holochoanitic; endocones simple; endosiphuncular tube narrow, situated in half of siphuncle that is closer to conch margin.

Cameroceras motsognir sp. nov.

(Figs 14A–E)

Holotype. Specimen RMo 9281C–D, herein figured at Fig. 14A.

Diagnosis. *Cameroceras* with nearly straight adult and curved juvenile conch, with an angle of expansion of up to 10° in juvenile growth stage, decreasing in later growth stages. Cross section circular. Conch slightly irregularly undulated. Surface ornamented with shallow, rounded, slightly oblique transverse lirae, which form shallow hyponomic sinus on pro-siphuncular side of conch, with distance of c. 1–2 mm. Sutures directly transverse, with distance (cameral depth) varying from 0.15 to 0.2 of the corresponding conch cross section. Siphuncle nearly marginal, on concave side of conch curvature, with diameter of c. 0.4 of corresponding conch diameter. Siphuncular segments shallow, concavo-convex in longitudinal section. Septal necks holochoanitic. Embryonic shell large, conical, slightly compressed, with angle of expansion of c. 60°, a maximum diameter of 17 mm and a length of c. 30 mm.

Derivation of name. Referring to Motsognir, the father of dwarfs in the northern mythology.

Material. Holotype and three additional specimens RMo 9281A, PMU D#1400, #1401 from Kullsberg, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages (see Data Supplement 1).

Type locality and horizon. Furudal, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.

Description. The holotype is a c. 170 mm long fragment of a phragmocone with a diameter c. 17–38 mm. The phragmocone is curved, with the siphuncle at the concave side of the conch curvature. The conch is ornamented with shallow, rounded lirae (distance c. 1–2 mm), which ran nearly directly transverse in the apical part of the conch. At the pro-siphuncular side at the adoral part of the holotype, the lirae are slightly oblique and form a shallow hyponomic sinus. Additionally, the adoral part of the shell is shallowly undulated at an irregular distance. The most adapical 5 mm of the holotype are distinguished from the rest of the specimen with straight longitudinal lirae, grooves and wrinkles and a distinct constriction (Fig. 14A). Adorally of this constriction, the conch is for c. 20 mm of its length nearly tubular and the characteristic transverse ornamentation and undulation begins.

Two specimens PMU D#1400 (Fig. 14D–E) and #1401 (Fig. 14B–C) have the apex preserved and show that the most apical part is a straight cone with an angle of expansion of c. 60° and a slightly compressed cross section (width 10.3 mm/height 11.1 mm in PMU D#1400, and width 9.3 mm/height 11.7 mm in PMU D#1401). The apex is ornamented with characteristic longitudinally wrinkled striae and grooves and with irregularly spaced, directly transverse constrictions. Internal details of the apical parts are not known.

The chamber distance is c. 0.23 of the corresponding diameter in the holotype (at diameter of 17 mm) and 0.16 and 0.18 of the corresponding diameter in specimen RMo 9281A (at diameters of 43 mm and 34 mm, respectively). The siphuncle is not strictly marginal, but positioned very close to the margin at the concave side of the conch curvature in the holotype, and in all other specimens. The diameter of the siphuncle is c. 13 mm at the adoral part of the holotype (c. 0.37 of the corresponding conch diameter) and 18 mm in specimen RMo 9281A (c. 0.42 of the corresponding conch diameter). Siphuncular segments are concavo-convex in longitudinal view and the septal necks are holochoanitic. Details of the endosiphuncular deposits are not known.

Remarks. *Cameroceras motsognir* sp. nov. is similar to *Cameroceras turrisoides* Kröger, 2013 from the late Katian–Hirnantian Boda Limestone Formation of Dalarna, but the former has a more curved early ontogenetic stage, and a smaller and more compact apex (apex of *C. turrisoides* is c. 50 mm long with an angle of expansion of c. 25°)

Cameroceras spp.

Material. Five specimens: PMU D#153, #154 from Amtjärn; PMU D#151, RMo 161232 from Kullsberg; PMU D#152 from Skalberget, all Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages (see Data Supplement 1).

Description. All four specimens are small fragments of phragmocones with a circular conch cross section and with diameters of 42 mm (PMU D#151), 48 mm (PMU D#152), 60 mm (PMU D#154) and 65 mm (PMU D#153). The conch surface is smooth and the relative chamber distance varies between 0.2 (PMU D#151), 0.23 (PMU D#153), and 0.27 (PMU D#152). The siphuncle is marginal or very close to the conch margin in all specimens. The relative siphuncle diameter varies between 0.26 (PMU D#153, D#154), 0.33 (PMU D#152), and 0.38 (PMU D#151).

Remarks. These specimens are all relatively small fragments, which do not allow reliable calculation of the angle of expansion. They all lack endosiphuncular deposits. Hence, a determination at the species level is not possible. The fragments are probably related to *Cameroceras aluverense* Balashov, 1968, *Cameroceras kegelense* Balashov, 1968, *Cameroceras rakverense* Balashov, 1968, and / or *Cameroceras vertebrale* (Eichwald, 1860). All of these species have a marginal siphuncle, with a relative diameter of approximately 0.3. They differ mostly in the angle of expansion and details of sutural shape. The species are, however, in need of a revision, which would include an analysis of the intraspecific variation of main conch characteristics, which is beyond the scope of this paper.

Genus ***Endoceras*** Hall, 1847

Type species. *Endoceras annulatum* Hall, 1847, Watertown, New York, USA, Trenton Limestone, early Katian Stage; by original designation.

Diagnosis (adopted from Teichert 1964 and Balashov 1968). Slender, large orthocones similar to *Cameroceras*, but with annulation; cross section circular or slightly depressed; sutures simple and straight; siphuncle large; marginally or submarginally positioned; septal necks holochoanitic; endocones simple subcircular; endosiphuncular tube narrow, situated in half of siphuncle that is closer to conch margin.

Endoceras naekki sp. nov.

(Figs 14F–H)

Holotype. Specimen PMU D#1389, herein figured at Fig. 14F.

Diagnosis. *Endoceras* with low angle of expansion (< 5°). Cross section circular. Conch ornamented with narrowly and irregularly spaced (1–2 per millimeter), slightly oblique annuli, which form shallow hyponomic sinus and with fine, irregularly spaced longitudinal striae, and shallow irregular undulations. Annuli with sharp ridges during earlier growth stages and more rounded in later growth stages. Sutures directly transverse, with distance (cameral depth) of c. 0.2 of the corresponding conch cross section. Siphuncle submarginal, with distance from conch margin of 0.1–0.17 of corresponding conch diameter. Siphuncular diameter of c. 0.4 of corresponding conch diameter. Siphuncular segments shallow concave in longitudinal section. Septal necks holochoanitic. Endocones simple.

Derivation of name. Referring to Näkk, or Näkki, a shape shifting water spirit in the Scandinavian folklore. Referring to the change in the annulation shape during growth.

Material. Holotype and two additional specimens PMU D#1394, and RMo 161229, from

Kullsberg , Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages (see Data Supplement 1).

Type locality and horizon. Skålberg, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.

Description. The holotype is a c. 74 mm long fragment of a phragmocone, with a diameter of 21–26 mm (angle of expansion 3.9°) and with a circular conch cross section. The adapical two thirds of the holotype are ornamented with distinct annuli with sharp ridges and rounded valleys (Fig. 14F). The annulation gradually but rapidly changes at the adoral third of the holotype into more narrowly spaced and more rounded annuli. Additionally, a fine longitudinal liration occurs at the adapical two thirds of the specimen. The annuli are slightly oblique and form a shallow, indistinct hyponomic sinus at the pro-siphuncular side of the conch. The chamber distance is 5 mm at a conch diameter of 22 mm (c. 0.23 of corresponding conch diameter). The siphuncle is by 2.5 mm shifted from the conch margin, where the conch diameter is 24.5 mm and where the siphuncular diameter is 8.7 mm. The septal necks are holochoanitic and form slightly concave siphuncular segments in the longitudinal section. Endosiphuncular deposits form a thin endosiphuncular cone.

Specimen PMU D#1394 (Figs 14G–H) is 67 mm in diameter and represents three chambers of the phragmocone. The conch is ornamented with fine, irregularly spaced annuli and transverse lirae, and rugose growth lines. The annuli and lirae are slightly oblique, forming a shallow hyponomic sinus at the pro-siphuncular side of the conch. The sutures have a distance of 16 mm (relative chamber height 0.24) and the siphuncle is 27 mm in diameter (RSD 0.4). The siphuncle is positioned at a distance of c. 11 mm from the conch margin (SPR 0.17). Siphuncular segments are slightly concave in longitudinal section. Septal necks are holochoanitic.

Remarks. The species is unique within *Endoceras* with regard to its sharp, and not rounded annuli during early growth stages and with regard to its uneven annulation.

Order **Actinocerida** Teichert, 1933

Family **Gonioceratidae** Hyatt, 1884

Genus ***Hoeloceras*** Sweet, 1958

Type species. *Hoeloceras helgoeyense* Sweet, 1958, from the Elnes Formation, late Darriwilian–early Sandbian stages, Nes-Hamar district, Oslo region, Norway; by original designation.

Diagnosis (after Sweet 1958). Shell orthoconic or curved in shape, depressed (but not flattened) in cross-section. Sutures either straight or bearing dorsal and ventral lobes and lateral saddles. Septal necks short cyrtochoanitic. Connecting rings broadly expanded, recumbent adapically, not recumbent adorally. Endosiphuncular deposits present. Surface smooth or with fine transverse lirae.

Hoeloceras muroni Kröger & Aubrechtová, 2017

(Figs 8D, 12D, 13D–E)

2017 *Hoeloceras muroni* Kröger & Aubrechtová: p. 16, Figs 16A, 17D.

Material. Four specimens: PMU#100 from Amtjärn, PMU#5(16), #103, and RMo 161249 from Kullsberg, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages (see Data Supplement 1).

Occurence. Vasalemma Formation, Estonia and Kullsberg Limestone Formation, central Sweden, late Sandbian–early Katian (?) stages.

Type locality and horizon. Rummu Quarry, northern Estonia, Vasalemma Formation, Keila Regional Stage, late Sandbian Stage.

Diagnosis (emended)**.** *Hoeloceras* with a smooth, slightly curved shell, angle of expansion of up to 13°, and nearly straight, transverse sutures.

Description. Specimen PMU #5(16) is the largest of the three specimens (Figs 12D, 13E), and the largest specimen assigned to this species. It is a short fragment of a phragmocone with a width of 39 mm and a height of 31.7 mm. The conch surface is smooth. The specimen has seven phragmocone chambers at a conch length of 28 mm (RCL c. 0.125). The adoralmost chamber is significantly shortened and probably indicates adult size. The septal perforation occurs in a distance of c. 5 mm from the conch margin (SPR 0.16) and is less than 2 mm in diameter. Siphuncular segments are strongly expanded within the chambers, with a maximum diameter of 8 mm (Fig. 8D).

Specimen PMU #103 (Fig. 13D) has a height of 10.4–12.9 mm, a width of 12.5–16.3 mm, and a length of 11.5 mm. It expands laterally with an angle of 19° and dorso-ventrally with an angle of 13°. The septal perforation is at a position of 2 mm from the conch margin at the adapical end of the specimen (SPR 0.19).

Remarks. The species was formerly known only from the holotype, a 57 mm long fragment with diameters of 9–20 mm. The two specimens from the Kullsberg Limestone are considerably larger than the type specimen (up to a conch width of 39 mm) but agree with the latter in general conch features and form and position of the siphuncle. This general similarity suggests that ontogenetic changes of the conch cross section are minor (Fig. 15). The angle of expansion varies between the Kullsberg Limestone specimens and in-between the Kullsberg and Vasalemma Limestone specimens from 7–13°. This variation is now included into the emended diagnosis of the species.

Order **Orthocerida** Kuhn, 1940

Family **Orthoceratidae** McCoy, 1844

Genus ***Pleurorthoceras*** Flower, 1962

Type species. *Orthoceras clarksvillense* Foerste, 1924, Waynesville Formation, Richmondian Regional Stage, Ohio, USA, by subsequent designation (Flower 1962).

Diagnosis (after Frey 1995). Slender, orthoconic, longiconic orthoceratids with circular shell cross-section, straight and transverse sutures and chamber heights from one-third to one-half the diameter of the shell, body chamber long, tubular; conch surface smooth; siphuncle slightly subcentral in position, narrow, almost tubular; septal necks short, suborthochoanitic; connecting rings thin, homogeneous, only slightly expanded; endosiphuncular deposits unknown, cameral deposits initially mural, during ontogeny mural–episeptal and thickened ventrally.

Pleurorthoceras clarksvillense (Foerste, 1924)

(Figs 9H, 16C)

1924 *Orthoceras clarksvillense* Foerste: 220, pl. 42, figs 1A–B.

1995 *Pleurorthoceras clarksvillense* (Foerste), Frey: P37–P38, pl. 2, figs 10–15 (cum. syn.).

2017 *Pleurorthoceras organi* Kröger & Aubrechtová: p. 26, Figs 20E–F, 21I, 22B.

Diagnosis (compiled from Frey 1995). Slightly curved *Pleurorthoceras* with chamber distance of less than 0.3 to 0.5 of corresponding conch diameter, with narrow siphuncle, nearly centrally positioned during early growth stages and subcentral in later growth stages.

Material. Three specimens, from Amtjärn (PMU #9(16)) and Kullsberg (PMU #10(16), PMU #107), all Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages (see Data Supplement 1).

Occurrence. Waynesville and Liberty formations, eastern USA; Vasalemma Formation, Estonia and Kullsberg Limestone Formation, central Sweden, late Sandbian–late Katian stages.

Description. The most complete specimen, PMU#10(16), is a portion of a phragmocone with a length of 68 mm and a diameter of 52–58 mm. The distance of septa is c. 20 mm. The distance of the siphuncle from the conch margin is 19 mm and the diameter of the septal perforation is 5.2 mm at a conch diameter of 58 mm.

The two other specimens have diameters of 50 mm, and 58 mm and corresponding septal distances of 17 mm, and 26 mm, respectively. Their siphuncle is 18 mm and 16 mm from the conch margin, respectively, and the diameter of the septal perforation is c. 0.1 of the conch diameter. The connecting ring of specimen PMU #107 is tubular and septal necks are short orthochoanitic to suborthochoanitic (Figs 9H, 16C).

Remarks. *P. clarksvillense* was described in detail by Frey (1995) on the basis of 23 specimens and distinguished from *P. selkirkense* (Whiteaves, 1891) by its relatively narrow septal spacing. The specimens of *P. clarksvillense* described by Frey (1995) and previous authors have diameters of c. 15–30 mm. But none of the figured and described specimens can be interpreted as an adult, based on features such as septal spacing or adult body chamber modifications. Hence, the adult size of this species is not known. Kröger & Aubrechtová (2017) described a new species, *P. organi*, from the Vasalemma Formation Formation, which in turn was only known from fragments of juvenile specimens with maximum diameters of less than 11 mm. The authors distinguished this species from *P. clarksvillense* mainly based on the lower angle of expansion of the former. Our new material from the Kullsberg Limestone comprises three non-adult specimens with diameters of 50–58 mm. A diagrammatic comparison of the three size classes (type region: 15–30 mm; Vasalemma Limestone: 7–10 mm; Kullsberg Limestone: >50 mm, respectively), reveals a trend of an increasing angle of expansion and septal distance, and a decreasing relative siphuncle distance (Fig. 17). Unfortunately, from the three collections, no overlapping size classes are known and no adult specimens are described. Hence, the available material can be interpreted as representing three distinct species or, alternatively, as representing different size classes of a single species. Our decision to assign all specimens within *P. clarksvillense* is based on Frey's (1995) observation of a shifting siphuncular position from more central towards more marginal during ontogeny in the type material. This trend is in agreement with smaller and larger specimens from the Vasalemma and Kullsberg Limestone formations (Fig. 17).

P. chinense Chen, 1987 differs from *P. clarksvillense* in having a higher diameter of the siphuncle (0.17 of the corresponding conch diameter).

Genus ***Striatocycloceras*** Kröger & Isakar, 2006

Type species. *Orthoceras undulostriatum* Hall, 1847, Middleville, New York, USA, Trenton Limestone, early Katian Stage; by subsequent designation (Kröger & Isakar 2006).

Diagnosis (after Kröger & Isakar 2006). Slender, circular or slightly compressed orthocones with asymmetrically curved septa and straight transverse or slightly oblique sutures. Sutures parallel, or nearly so, to the annulations. Annulations slightly irregularly spaced, with fine transverse ornament. Siphuncle eccentric, narrow, tubular or slightly expanded within the chambers. Septal necks orthochoanitic. Cameral and endosiphuncular deposits not known.

Remarks. The captions of the figures of the species of *Striatocycloceras* in Kröger & Isakar (2006) are erroneous and misleading (see also Kröger 2013). The errors must be corrected as follows: *Striatocycloceras obliquum* (Teichert, 1930) is figured in Kröger & Isakar (2006: figs 7K, O, 8D, 11), as correctly stated in the text, and *Striatocycloceras undulostriatum* (Hall, 1847) is also correctly figured (Kröger & Isakar 2006: figs 7L 8E, 10A); other species shown are *Striatocycloceras romingeri* (Foerste, 1932) (Kröger & Isakar 2006: figs 7P, 8R-T) and *Striatocycloceras foerstei* (Teichert, 1930) Kröger & Isakar (2006: figs 7Q, 10H).

Striatocycloceras undulostriatum (Hall, 1847)

(Fig. 18I)

1847 *Orthoceras undulostriatum* Hall: 202, pl. 43, fig. 7.

1928 *Cycloceras undulostriatum* (Hall), Foerste: 176, pl. 40, figs 1A–D.

2006 *Striatocycloceras undulostriatum* (Hall), Kröger & Isakar: 150, figs 7L, 8E, 10A (cum syn.).

2017 *Striatocycloceras undulostriatum* (Hall), Kröger & Aubrechtová: Data Supplements 1–2.

Diagnosis (after Kröger & Isakar 2006**)**. Slightly curved, slightly compressed *Striatocycloceras* with very low apical angle of approximately 2°. Adult dorsoventral diameter approximately more than 30 mm, with four to six annulations at a distance that equates the corresponding shell diameter in an adult. Annulations slightly oblique, irregularly spaced, with faint lobe at the side in opposition of the siphuncle. Distinct growth lines, 10–12 per cycle of annulations, one or two cycles of annulations per chamber. Suture lines run slightly oblique in relation to annulations forming a slight sinus at the side opposite to the siphuncle. Siphuncle subcentral. Short, orthochoanitic septal necks.

Material. A total of 23 specimens from Amtjärn (1) and Kullsberg (22), all Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages (see Data Supplement 1).

Occurrence. Black River Group and Trenton Limestone, eastern USA; Haljala to Vormsi regional stages, Estonia and Baltic Pleistocene erratic boulders, Sandbian to Katian stages.

Description. The specimens at PMU are fragments of phragmocones of relatively early growth stages, with diameters of 13.5–14.9 mm (PMU#29–30), 20.5–23.5 mm (PMU#28), 20.4–23.6 mm (PMU#1382), and an angle of expansion of 1.7°, 4.2° and 4°. In all four specimens from PMU, the distance of the annuli varies from 4.5–5 per corresponding diametre. Additionally, 9–11 lirae (or distinct growth lines) occur, which run parallel to the annulations.

Remarks. The species was described in detail by Kröger & Isakar (2006). It is the second most common species in the Vasalemma Limestone of northern Estonia (see Kröger & Aubrechtová 2017). The description herein adds some details on the variability of the ornamentation and angle of expansion. As noted already in Kröger & Isakar (2006), the apical angle varies in *S. undulostriatum* and is generally higher in earlier growth stages and lower (conch nearly tubular) during late ontogeny. The measurements of the PMU specimens vary in the angle of expansion with maximum values of above 4°. We consider this as an artefact of measurement, which sometimes gives diameters from the valleys of annulations and sometimes values from the ridges of annulations. This effect should be taken into account when comparing published angles of expansion of this species.

Family **Geisonoceratidae** Zhuravleva, 1959

Genus ***Ordogeisonoceras*** Frey, 1995

Type species. *Orthoceras amplicameratum* Hall, 1847, from the Trenton Limestone, latest Katian Stage, Middleville, New York, USA, by original designation.

Diagnosis (adapted after Frey 1995). Shell is straight, longiconic, circular in cross-section. Sutures are straight, transverse. Phragmocone chambers are as high as one-half the diameter of the shell. Living chamber is long and tubular. Surface ornamented with fine longitudinal or transverse striae. Siphuncle situated close to the dorsal margin later in ontogeny, more central earlier in ontogeny. Siphuncular segments are elongate, depressed. Septal necks are suborthochoanitic. The connecting rings are thin, homogeneous, and slightly expanded. Small annulosiphonate deposits are developed adapically. Cameral deposits are developed adapically. Hyposeptal and episeptal cameral deposits are developed ventrally and episeptal dorsally.

***Ordogeisonoceras*? *uppsalaensis* sp. nov.**

(Figs 9I, 16D, 19)

Holotype. Specimen PMU #8(16), herein figured at Fig. 19.

Diagnosis. Large orthocones with straight shell, with angle of expansion of up to 9°, ornamented with imbricated transverse lirae (with c. 1 mm distance at conch diameter of 70 mm); conch cross section circular; siphuncle subcentrally positioned (SPR c. 0.4), with diameter of c. 0.1 of corresponding conch diameter; siphuncular segments slightly expanded, fusiform; septal necks suborthocoanitic.

Derivation of name. Referring to Uppsala, the city of the PMU, the collection of the holotype.

Material. Holotype and one additional specimen, PMU#7(16), from Amtjärn, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.

Type locality and horizon. Kullsberg, Kullsberg Limestone Formation, central Sweden, late Sandbian Stage.

Description. The holotype is a portion of a phragmocone and a part of the body chamber, with a length of 212 mm and a diameter of 57–90 mm (angle of expansion 9°). The conch cross section is circular. The chamber height varies between 27 mm (at 77 mm corresponding conch cross section) and 34 mm (at 60 mm corresponding conch cross section) (RCL 0.35–0.57). The decreasing septal spacing indicates a near adult size of the specimen. The conch is ornamented with c. 1 mm wide imbricated transverse lirae, with a maximum height of lirae towards the aperture. At the pro-siphuncular side, a shallow conchal furrow is preserved. The siphuncle is subcentrally positioned.

The second specimen, PMU#7(16), is a 69 mm long fragment of a phragmocone with a diameter of 59–67 mm (angle of expansion 7°), circular conch cross section and a chamber height of 36 mm at a conch cross section diameter of 65 mm (RCL 0.55). The siphuncle is c. 26 mm from the conch margin at a diameter of 65 mm. It has a diameter of 7 mm at the same position. Septal necks are subortochoanitic. The connecting ring is slightly expanded, forming slightly fusiform siphuncular segments (Figs 9I, 16D). No endosiphuncular and cameral deposits are present.

Remarks. The two specimens are assigned to *Ordogeisonoceras* with a question mark, although general conch features such as shape and position of the siphuncle and septal necks and the ornamentation are identical to that of other species of *Ordogeisonoceras*. But no endosiphuncular or cameral deposits have been observed. The new species differs from other *Ordogeisonoceras* species such as *O. foerstei* (Strand, 1934) and *O. amplicameratum* Frey, 1995 mainly in having a more centrally positioned siphuncle. *O. tartuensis* Kröger & Aubrechtová, 2017 differs in having a lower angle of expansion (< 6°) and a more narrow and not imbricated ornamentation. However, only two specimens of *O.*? *uppsalaensis* are known, both are fragments of relatively large phragmocones (conch diameter > 55 mm). Because all fragments known from *O. tartuensis* are less than 33 mm in diameter, and do not represent adult specimens, the chances are high that *O.? uppsalensis* represents the late growth stages of *O. tartuensis*. More material is needed to test this hypothesis.

Ordogeisonoceras tartuensis Kröger & Aubrechtová, 2017

(Figs 9C, 16F, H, I, 18A, 20A)

2017 *Ordogeisonoceras tartuensis* Kröger & Aubrechtová: p. 27, Figs 20H, 21B, 22A

2017 *Ordogeisonoceras*? sp. Kröger & Aubrechtová: p. 28, Figs 20I, 21A.

Diagnosis (after Kröger & Aubrechtová 2017). Siphuncle central to slightly subcentral in position, 0.14 to 0.17 in diameter (relative to shell diameter), septal necks suborthochoanitic, shell sculptured with fine straight and transverse lirae (8–12 per one mm).

Material. A total of 29 specimens from Amtjärn (1), Furudal (1), Kullsberg (26) and Skålberget (1), all Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages (see Data Supplement 1).

Occurence. Kullsberg Limestone Formation, Sweden, and Vasalemma Formation, Estonia, late Sandbian–early Katian stages.

Type locality and horizon. Vasalemma, northern Estonia, Vasalemma, Formation, Keila Regional Stage, late Sandbian Stage.

Description. Specimen RMo 125642 is a complete body chamber with a length of 102 mm and a diameter of 21–27 mm (angle of expansion c. 3°). The peristome is not directly transverse but forms a slightly oblique angle on the flanks and a shallow hyponomic sinus on one side of the conch (Fig. 18A). This slightly oblique shape of the peristome is reflected in the pattern of the transverse ornamentation, which also forms a shallow hyponomic sinus (see also Fig. 20A, specimen PMU #D1443). A number of 27 measurements reveal an angle of expansion that increases with growth until a diameter of c. 30 mm and varies between c. 2–7° (median 4.4°) (Fig. 21A). The septal spacing varies between RCL 0.2–0.38 (median 0.28, n =

8; Fig. 21B).

The largest specimen, PMU #D1448, is a portion of a body chamber with one adapical septum and a diameter of 33 mm. It is not known, if this reflects the adult size. In this specimen, the position of the septum is slightly shifted from the center, revealing the position of the hyponomic sinus, which is on the pro-siphuncular side. Additionally, a faint, shallow periphract (muscle impression) is preserved at the base of the body chamber. The periphract forms a simple dorsomyarian (= on anti-siphuncular side) sinus. The siphuncle is slightly subcentral, with a relative diameter of the septal perforation of 0.1–0.15 mm. Siphuncular segments in specimen PMU 29042 are very slightly barrel-shaped (Figs 9C, 16F, see also Fig. 16H–I). Septal necks are at the tenuous border between suborthochoanitic to orthochoanitic (Figs 9C, 16F, see also Fig. 16H–I). In the five sectioned specimens (RMo 181903, 181912, 181915, 181920), neither endosiphuncular, nor endocameral deposits have been observed.

Remarks. The species was described in detail by Kröger & Aubrechtová (2017). The additional material from the Kullsberg Limestone Formation provides further information on the variability of the angle of expansion (Fig. 21A), ornamentation (Figs 18A, 20A), chamber spacing (Fig. 21B) and shape of the siphuncle, and septal necks (Figs 9C, 16F, H–I). With these new data, it can be demonstrated that the specimens assigned to *Ordogeisonoceras*? sp. in Kröger & Aubrechtová (2017) are within the variability of *O. tartuensis* and should be assigned to this species (Fig. 21).

Family **Proteoceratidae** Flower, 1962

Genus ***Isorthoceras*** Flower, 1962

Type species. *Orthoceras sociale* Hall in Miller, 1877, from the Elgin Member, Maquoketa Formation, latest Katian Stage, Graf, Iowa, USA; by original designation.

Diagnosis (adapted from Flower 1962; Frey 1995 and Kröger 2013)**.** Orthoconic longicones with subcircular cross-section and subdued ornamentation, smooth or with fine transverse and/or longitudinal lirae, siphuncle subcentral, with barrel-shaped early segments and subcylindrical later segments, septal necks suborthochoanitic–cyrtochoanitic, endosiphuncular annuli growing forward and backward, joining those of adjacent segments to form continuous parietal lining of uniform thickness throughout segments. Mural to episeptal cameral deposits exist.

Isorthoceras cf. ***cavi*** Kröger & Aubrechtová, 2017

(Figs 18F, 20B)

2017 *Isorthoceras cavi* Kröger & Aubrechtová: p. 22, Figs 20B, D, 21D, F, 22D.

Material. Two specimens, RMo 125621 and PMU #D1399, from Kullsberg, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.
Occurence. Northern Estonia, Vasalemma Formation, and Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.
Type locality and horizon. Rummu, northern Estonia, Vasalemma Formation, Keila Regional Stage, late Sandbian Stage.
Diagnosis. *Isorthoceras* with a straight shell, low to medium angle of expansion (2.5–6°). Conch ornamented with transverse striae (2–4 per one mm) that form a broad, shallow lobe and sinus and are slightly oblique on lateral sides, and with longitudinal lirae (8–10 per one mm).
Description. The specimen PMU #D1399 is a 73 mm long fragment of a phragmocone and part of the body chamber, with a diameter of 12.3–18.2 mm (angle of expansion 4.6°), with c. 3–4 chambers per corresponding conch diameter and a nearly central, narrow siphuncular perforation (diameter c. 0.1 of corresponding conch cross section) (Fig. 18F). The conch is ornamented with irregularly spaced transverse lirae (c. 2–3 per one mm) that form a shallow lobe and sinus across the conch circumference, and with faint longitudinal lirae (c. 8 per one mm) (Fig. 20B).
Remarks. The specimen described above differs from the type material in having slightly less pronounced and more irregularly spaced transverse lirae, but otherwise meets the diagnostic features of *I. cavi*. The siphuncular characters of the specimen are not investigated because all other external characters are identical to known species of *Isorthoceras*. The other small fragment from Kullsberg, RMo 125621, can be unquestionably identified as *I. cavi* based on ornamentation and general shell features.

Isorthoceras maris Kröger & Aubrechtová, 2017
(Figs 18B–C)

2017 *Isorthoceras maris* Kröger & Aubrechtová: p. 24, Figs 20B, 21E, 22E.

Material. One specimen (two fragments of a single individual), RMo 125648–125649, from

Kullsberg, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.

Occurence. Kullsberg Limestone Formation, central Sweden, Vasalemma Formation, Estonia, late Sandbian–early Katian(?).

Type locality and horizon. Vasalemma, northern Estonia, Vasalemma Formation, Keila Regional Stage, late Sandbian Stage.

Diagnosis. *Isorthoceras* ornamented with sharp transverse lirae (3–4 per one mm), with two lobes and two saddles across the conch circumference. Angle of expansion of c 3°. Episeptal cameral deposits.

Description. The specimen (two fragments of a single individual) is a phragmocone and a body chamber, with a length of 53 mm, and a cross section diameter of 2–7 mm (angle of expansion 5°). The specimen is ornamented with 4–6 transverse lirae per one mm, which form two lobes and two saddles across the conch circumference. The preserved part of the body chamber is 14 mm long.

Remarks. The Kullsberg specimen is smaller than the two previously known fragments of this species from the Vasalemma Formation (diameters of 7−10 mm). The specimen adds some information on the earlier ontogenetic stages and growth variability, of angle of expansion and ornamentation changes during growth. As expected, the ornamentation is more narrow (absolutely) and the angle of expansion is slightly higher earlier in ontogeny.

Isorthoceras nikwis sp. nov.

(Figs 9B, 16B, 18H)

Holotype. Specimen RMo 125641, herein figured at Fig. 18H.

Diagnosis. *Isorthoceras* ornamented with fine longitudinal lirae (8–9 per one mm) and subdued, irregularly spaced growth lines; angle of expansion up to 10°; conch cross section circular or weakly compressed, conch weakly curved; sutures slightly oblique, shifted towards aperture at convex side of conch curvature; siphuncle central or slightly shifted towards concave side of conch curvature; adult conch diameter c. 22 mm. Longitudinal color bands (c. 35 around circumference).

Derivation of name. Referring to the Germanic nikwis, a shape shifting water spirit in the Scandinavian folklore.

Material. Holotype and an additional number of 9 specimens from Furudal (1), and Kullsberg (8), all Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages (see Data Supplement 1).

Type locality and horizon. Kullsberg, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages

Description. The holotype is a fragment of a phragmocone with a nearly circular cross section, with a diameter of 6.9–16.4 mm and a length of 76 mm (angle of expansion c. 8°). The conch surface is ornamented with fine longitudinal lirae, c. 8 per one mm, and with subdued irregularly spaced growth lines. The siphuncle is central or slightly subcentral, with a diameter of the siphuncular perforation of 0.8 mm at a conch diameter of 11 mm. The septa are slightly oblique towards the aperture at the concave side of conch curvature and have a distance of c. 1.8 mm at a diameter of 11 mm.

The largest specimen is RMo 125610, which is a fragment of a body chamber with a maximum diameter of 22 mm and a relatively low angle of expansion of 3.4°. Traces of longitudinal color bands are preserved in specimen RMo 125610 and in the holotype; they are c. 2 mm wide in the former, and c. 1 mm wide in the latter.

Specimen RMo 125620 (Figs 9B, 16B) has a conch diameter of 8–11 mm and its siphuncle is central, with slightly expanded and barrel-shaped siphuncular segments and very short suborthochoanitic septal necks. The apical chambers of this specimen contain episeptal deposits.

Remarks. The group of cancellate *Isorthoceras* with dominant longitudinal elements and relatively weak transverse elements comprises *Isorthoceras suave* (Angelin in Angelin & Lindström, 1880) with an angle of expansion of up to 9°, *I.albersi* (Miller & Faber, 1894) with an angle of expansion of c. 7–8°, *I. tenuitextum* (Hall, 1847) (= *Geisonoceras strigatum* Hall, 1847, sensu Ruedemann, 1926) with an angle of expansion of only 6°, and the small *I. angelini* Kröger, 2013, which reaches an adult conch diameter of only 15 mm. *I. suave*, which is similar to *I. nikwis* sp. nov. in general conch shape and apical angle, differs from the latter in having less pronounced and more widely spaced longitudinal lirae. *I. albersi* (Miller & Faber, 1894) and *I. tenuitextum* differ from *I. nikwis* sp. nov. in having a smaller angle of expansion and an eccentric siphuncle during juvenile growth stages (with diameter of more than 5 mm). *I. padisense* Kröger & Aubrechtová, 2017 differs in having an eccentric siphuncle and a slightly wider spacing of the longitudinal lirae.

Isorthoceras sylphide sp. nov.

(Figs 9A, 16A, 18G, 20D)

Holotype. Specimen PMU #91, herein figured at Figs 18G, 20D.

Diagnosis. *Isorthoceras* ornamented with very fine, subdued reticulate ornamentation of longitudinal and transverse lirae (10 per one mm, respectively); angle of expansion up to 10°; conch cross section circular or weakly compressed, conch weakly curved; sutures slightly oblique, inclined towards aperture at convex side of conch curvature; siphuncle central or slightly shifted towards concave side of conch curvature; adult conch diameter c. 30 mm. Longitudinal color bands (c. 40 around circumference) occur.

Derivation of name. Referring to the Sylphs, tender, nymph-like water ghosts in European mythology.

Material. Holotype and an additional number of 6 specimens from Amtjärn (1), and Kullsberg (6), all Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages (see Data Supplement 1).

Type locality and horizon. Amtjärn, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.

Description. The holotype is a fragment of a phragmocone and body chamber, with a diameter of 11–28 mm and a length of c. 100 mm (Fig. 18G). The conch cross section is nearly circular. The conch is ornamented (Fig. 20D) with minute, subdued, narrowly spaced transverse and longitudinal lirae (c. 10 per one mm) and with irregularly spaced, directly transverse fine growth lines. The chambers are c. 6 mm long at a conch cross section of c. 23 mm (RCL = 0.26). The siphuncle is subcentral with a septal perforation of c. 1 mm in diameter at a conch diameter of 12 mm. Siphuncular segments are expanded, barrel-shaped, with a maximum diameter of c. 1.9 mm at a conch diameter of 12 mm. The septal necks are short cyrtochoantic or suborthochoantic (see also Figs 9A, 16A, specimen PMU 29028). Episeptal cameral deposits occur. The holotype is also the largest of the specimens of this species. A comparison of the angle of expansion of three other specimens assigned to *I. sylphide* sp. nov. indicates an increasing angle of expansion up to a conch diameter of c. 20 mm.

Remarks. *Isorthoceras sylphide* sp. nov. is most similar to *I. suave* (Angelin in Angelin & Lindström, 1880) with respect to its fine reticulate ornamentation and longitudinal color bands. The former, however, differs from the latter in having more narrowly spaced, more subdued lirae. In *I. suave*, only five longitudinal lirae occur per one mm.

Isorthoceras urdr sp. nov.

(Figs 5B, D, 18E, 20C)

Holotype. Specimen RMo 125617–19, herein figured at Figs 5B, D, 18E, 20C.

Diagnosis. *Isorthoceras* ornamented with narrowly spaced transverse lirae (6–10 per one mm) that form a distinct hyponomic sinus at the convex side of conch curvature; angle of expansion up to 5°; conch cross section circular or weakly depressed, conch weakly curved; siphuncle nearly central; adult conch diameter c. 18 mm; conch surface colored with c. 1–2 mm wide, irregularly spaced longitudinal bands.

Derivation of name. Referring to the Urdr, a being in the Scandinavian mythology, comparable with one of the fates in the classical mythology.

Material. Holotype and an additional number of four specimens from Kullsberg, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages (see Data Supplement 1).

Type locality and horizon. Kullsberg, Kullsberg Limestone Formation, central Sweden, late Sandbian–early Katian(?) stages.

Description. The holotype is a 34 mm long fragment of a phragmocone with a 8.4 mm–10 mm in diameter and septal distance of 3.5 mm at its apicalmost chamber. A color pattern of c. 1 mm wide longitudinal bands is visible on the surface of the specimen (Fig. 5B, D, 18E). Additionally, the conch surface is ornamented with narrowly spaced transverse lirae (c. 10 per one mm; Fig. 18E, 20C), which form a distinct hyponomic sinus at the convex side of the weakly curved conch.

The most complete specimen, RMo 125612, is a portion of a 68 mm long phragmocone with a diameter of 6.5–10.5 mm (angle of expansion 4°). The conch cross section is nearly circular. The siphuncle is central.

The largest specimen is RMo 125625, which is a c. 50 mm long portion of a complete adult body chamber and two chambers of the phragmocone (diameter 16.5–18 mm). The body chamber is nearly tubular and has an internal shell thickening at a distance of c. 5 mm from the peristome. The conch surface is ornamented with narrowly spaced transverse lirae (c. 6–10 per one mm), which form a characteristic hyponomic sinus. The hyponomic sinus is preserved at the adult peristome. A number of c. 1 mm wide longitudinal color bands occur on parts of the surface. The distance between the preserved sutures is c. 2.5 mm. The septal perforation is centrally positioned.

Remarks. *Isorthoceras urdr* sp. nov. differs from other *Isorthoceras* species in having a narrow transverse ornamentation, such as *I. junceum* (Hall, 1847) and *I. romingeri* (Foerste, 1932); and in having a distinct hyponomic sinus. *I. urdr* sp. nov. differs from the latter two species in having a low angle of expansion.

Isorthoceras sp.

(Fig. 20F)

Material. Specimen RMo 125609 from Kullsberg, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.

Description. The specimen is a nearly straight fragment of a body chamber with no septa preserved, with a diameter of 19–22 mm and a length of 45 mm (angle of expansion 4°). The conch surface is ornamented with fine transverse lirae (c. 10 per one mm) and on the concave side of conch curvature with subdued, similarly spaced longitudinal lirae. These lirae form a faint reticulate pattern. Additionally, c. 1.5 mm wide longitudinal color bands are preserved around the complete circumference.

Remarks. The fragmentary character of the specimen does not allow for a determination at the species level. General conch shape, ornamentation and color bands identify the specimen as an *Isorthoceras*, which is very similar to *I. rogersensis* and *I. sylphide*. But, in *I. rogersensis* the intensity of the longitudinal ornamentation is not described as irregular across the circumference (see Frey 1995). The ornamentation of *I. sylphide* is more subdued.

Genus ***Clothoceras*** gen. nov.

Type species. *Clothoceras thornquisti* gen. *et* sp. nov., from Kullsberg, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.

Diagnosis. Slender orthoconic or slightly cyrtoconic conch, ornamented with directly transverse lirae, c. 2 per one mm, which are imbricated with the sharp ridge or the lirae directed towards the peristome; chambers narrowly spaced with RCL of c. 0.13–0.19; siphuncle tubular or slightly expanded within chambers with rsd 0.8 and with suborthochoanitic or orthochoanitic septal necks; siphuncular position eccentric with SPR 0.46.

Derivation of name. Referring to Clotho, the youngest of the three fates (Moirai) in Greek mythology.

Occurrence. As for the type species, by monotypy.

Remarks. *Clothoceras* gen. nov. is erected for transversally ornamented proteoceratids with exceptionally narrowly spaced chambers. The only two known specimens do not show endosiphuncular or cameral deposits, leaving some uncertainty regarding the family assignment of this new genus.

Clothoceras thornquisti sp. nov.

(Figs 9E, 16G, 18D, 20E)

Holotype. Specimen RMo 125651, herein figured at Figs 9E, 16G, 18D.

Diagnosis. As for genus, by monotypy.

Derivation of name. In honor of the Austro-German Geologist Alexander Thornquist (1868–1944).

Material. Holotype and one additional specimen, RMo 125650, from Kullsberg, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.

Type locality and horizon. Kullsberg, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages.

Description. The holotype is a fragment of a phragmocone and body chamber, with a diameter of 11.5–12 mm and a length of 18 mm. The portion of the phragmocone is 3 mm in length only, comprising two closely spaced chambers (RCL 0.13; Fig. 18D). The septal perforation is at a distance of c. 3 mm from the conch margin and has a diameter of c. 0.8 mm. The conch is ornamented with directly transverse lirae, c. 2 per one mm, which are imbricated with the sharp ridge directed towards the peristome.

The second specimen, RMo 125650, is a fragment of a portion of a phragmocone and part of a body chamber, with a diameter of 12–14 mm and a length of 23 mm. The chamber distance is 2.5 mm at a diameter of 13 mm (RCL 0.19). The conch is similarly ornamented (Fig. 20E) as in the holotype; both specimens have ring-like, irregularly spaced internal shell thickenings, which form conspicuous constrictions on the inner mold. The position of the siphuncle is eccentric, 5.3 mm from the conch margin (SPR 0.46) in specimen RMo 125651. The septal necks are orthochoanitic and the siphuncular segments are tubular, with a diameter of 0.8 of the corresponding conch diameter.

Remarks. The two available specimens have relatively poorly preserved, recrystallized internal structures, with short portions of the siphuncle visible in longitudinal median sections. The visible parts of the siphuncle are relatively thin (0.08 of the corresponding conch diameter) and sub-tubular, slightly expanded and with suborthochoanitic or orthochoanitic septal necks, which is characteristic of the adult parts of proteoceratids. However, the new species differs from other proteoceratid genera in having very short sutural distances. A species with a proteoceratid-like siphuncle and with a RCL of 0.17–0.2 is described as *Michelinoceras dnestrovense* Balashov, 1975 from the Late Ordovician of Podolia, but too little is known about this latter species in order to compare it with *Clothoceras thornquisti* sp. nov.

The lamellose, imbricated transverse ornamentation of the new species is generally similar to *Isorthoceras lineolatum* (Hall, 1847), *Isorthoceras elongatocinctum* Portlock (1843), and

Geisonoceras heintzi Strand, 1934, but its septal spacing is much narrower than the *Isorthoceras*-like RCL of 0.25–0.3 of these latter species. *Geisonocerina podolica* Balashov 1975, which is otherwise very similar, has a central siphuncle, is larger in proportions, and the septa are more asymmetrically shaped.

Family **Tripteroceratidae** Flower, 1941

Genus ***Allumettoceras*** Foerste, 1926

Type species. *Tripteroceras pauquettense* Foerste, 1924, from Leray-Rockland Beds, early Sandbian Stage, Pauquette Rapids, Ottawa River, Quebec, Canada, by original designation.
Diagnosis (after Evans 1994). Orthocones with depressed conch cross section, with flattened pro-siphuncular side and rounded antisphuncular side; with moderately deep chambers; sutures with broad lobe on pro-siphuncular side; septal necks cyrtochoanitic; siphuncular segments expanded; parietal endosiphuncular deposits; episeptal and hyposeptal deposits; siphonal and cameral deposits suppressed in many forms.

Allumettoceras mjoesense Sweet, 1958

(Figs 12A–B, 13A–C)

1958 *Allumettoceras mjoesense* Sweet: 84–86, pl. 3, fig. 7., pl. 4., fig. 5, pl. 21, fig. 9
1994 *Allumettoceras mjoesense* Sweet, Evans: 327, fig.4.

Material. Five specimens; PMU #1396, #1397, RMo 149721a, 149721b, and 149722 from Kullsberg, Dalarna, central Sweden, Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages (see Data Supplement 1).
Type locality and horizon. Hovindsholm, Helgøya, Lake Mjøsa, in the Nes-Hamar district of the Oslo Region, Norway, Cephalopod Shale, upper Elnes Formation, late Darriwilian–early Sandbian stages.
Diagnosis (compiled after Sweet 1958). Relatively large, rapidly expanding *Allumettoceras* with depressed, subelliptical conch cross section with broadly rounded anti-siphuncular and pro-siphuncular sides and with a siphuncle position considerably shifted from the conch margin.
Description. Four of the specimens are similar to the type material in size range, with conch heights and widths between 17–25 mm, and 24–30 mm, respectively. The specimens are fragments of phragmocones and body chambers with sub-elliptical cross sections, with

slightly flattened rounded pro-siphuncular sides and broadly arched anti-siphuncular sides and with a relative conch width of 1.1–1.2.

Specimen PMU #1396 is a fragment of a complete adult body chamber and parts of a phragmocone (Figs 12B, 13B). At the position of its last septum, the conch height/width is 24/28 mm (relative conch width 1.2). Close to the adult aperture, the specimen has its maximum conch height/width 29/37 mm (relative conch width 1.3). The body chamber has a length of 88 mm and the adoral 5 mm are slightly constricted. The conch cross section of the adoral part of the adult body chamber is considerably more elliptically depressed, with similarly shaped anti-siphuncular and pro-siphuncular sides. The conch surface of all known fragments is smooth. The siphuncle is positioned between the center and the conch margin, with a SPR of 0.17–0.2 in all specimens. In specimen RMo 149721b, the siphuncular perforation has a diameter of 2 mm and the siphuncular segments are barrel-shaped and expand towards a diameter of 3 mm at a conch height of 26 mm (relative to conch heights 0.08, 0.11, respectively). The septal necks are cyrtochoanitic. Five to six phragmocone chambers occur on a distance equal to the corresponding conch height. No endosiphuncular and cameral deposits have been observed.

Remarks. The species diagnosis of *A. mjoesense* is from Sweet (1958). Additionally, Sweet (1958) provided a detailed description of the holotype and a second specimen, which can be directly compared with the specimens from the Kullsberg Limestone Formation. The specimens from the Kullsberg Limestone Formation, which are similar in size with the type material of Sweet (1958), fall within the variability of the latter with regard to the angle of expansion, relative distance of sutures, position and shape of the siphuncle, but differ in having a less depressed conch cross section (Fig. 15). Sweet (1958) mentioned that the angle of expansion of this species varies relatively strongly. The same high variability can be observed within the Kullsberg Limestone material. Specimen PMU #1396 from the Kullsberg Limestone is a fragment of an adult conch, which adds some information on the formerly unknown adult conch cross section and body chamber morphology. The adult body chamber is more symmetrical and more depressed than in younger growth stages (Figs 13A–C).

Results

Taphonomy and preservation

Because all specimens described and analysed herein are from museum collections and are in most cases isolated from the matrix limestone, details on taphonomy are limited. All specimens are recrystallized to calcite and in almost all cases the ornament of the shell and microscopic details of the connecting ring are well preserved. Color marks are preserved on conch surfaces of several specimens. Nearly all of the specimens are fractured and preserved as fragments. The general type of preservation is very similar to that of the cephalopods of the Boda Limestone Formation (Kröger 2013). This similarity of preservation and the general similarity in the geological setting of the Kullsberg and Boda Limestone formations suggests a similar taphonomic history. It can be assumed that the cephalopods of the Kullsberg Limestone, like those of the Boda Limestone, were predominantly collected from shelly concentrations in synsedimentary fissure fillings of the mounds, from so-called "pockets" (see discussion in Kröger *et al.* 2016).

The shells are almost free of epibionts and no shell boring have been observed. The only shell with epibionts is a tarphycerid (*Discoceras nilssoni* sp. nov., holotype, RMo 141723–24) with a bryozoan overgrowth (Fig. 4C). The growth pattern of the bryozoan colony in this specimen is not consistent with the cephalopod shell growth and life position and hence can be interpreted as post-mortem. This near lack of syn-vivo and/or post-mortem overgrowth on Kullsberg cephalopods is similar to that of the Boda Limestone, but in strong contrast with the abundant epibionts on cephalopods of the time equivalent reef cephalopods of the Vasalemma Formation (Kröger & Aubrechtová 2017).

Diversity

The 181 cephalopod specimens from the Kullsberg Limestone contain 26 identifiable species, which belong to 16 genera, 12 families, and six orders. Among these cephalopods, the Orthocerida are most diverse (7 genera) and most abundant (106 of 160 identifiable specimens) (Table 1). The most abundant species are the orthocerids *Ordogeisonoceras tartuensis* Kröger & Aubrechtová, 2017 (29 specimens, 18% of total), and *Striatocycloceras undulostriatum* Hall, 1847 (23 specimens, 14% of total). This predominance of orthocerids is also known from the Boda Limestone Formation (Kröger 2013; Kröger & Ebbestad 2014), which differs mainly in the high abundance of barrandeocerids. Discosorids are the second most abundant group in the Kullsberg Limestone. The composition of the Kullsberg and Boda limestone cephalopod assemblages in turn strongly contrasts with that of the Vasalemma Formation, in which actinocerids are the most common and endocerids are absent (Fig. 22).

In a cluster analysis and principle component analysis (PCA) based on the relative generic diversity of the occurring orders, the Kullsberg Formation forms a nested pattern with late Sandbian / early Katian assemblages that were formerly combined within the Baltica-Appalachian cluster (BAPP, Kröger & Aubrechtová 2017) and assemblages of South China (Fig. 23). This nested pattern, in turn, is in strong contrast to the assemblages of Norway and the US-Appalachians (BELB-cluster of Sohrabi & Jin 2013; for individual composition of these clusters see Kröger & Aubrechtová 2017, Data Supplement 3). The main feature of BAPP- Kullsberg cluster is the combined relative orthocerid–actinocerid diversity.

The genus-level diversity and evenness of the Kullsberg Limestone is slightly higher than that of the contemporaneous Vasalemma Formation but the taxonomic distinctness is higher in the latter (Table 2). In the Vasalemma Formation, seven orders are present, including the exotic Cyrtocerinida. The high taxonomic distinctness of the Vasalemma assemblage is combined with a high endemicity (17 of 22 species; 77%). In contrast, the more diverse Kullsberg Limestone has an endemicity of 62 % (16 of 26 species). This comparatively low endemicity of the Kullsberg Limestone is closely similar to that of the orthocerid dominated Boda Limestone, which has a species level endemicity of 59 % (Kröger & Ebbestad 2014).

Palaeogeography

The composition of the cephalopod assemblage of the Kullsberg Limestone Formation fits well with the previously published palaeogeographic pattern of late Sandbian / early Katian assemblages (Harper *et al.* 2013; Sohrabi & Jin 2013; Candela 2015; Kröger & Aubrechtová 2017). This match is evident in a cluster analysis and PCA of the generic composition of selected cephalopod assemblages (Fig. 24). Therein, the Kullsberg Limestone clusters with the Vasalemma Formation next to a cluster that combines assemblages of the North China Block and Australia (for individual composition and discussion of these clusters see Kröger & Aubrechtová 2017).

The reefal assemblages of the nearly time equivalent and geographically relatively nearby (550 km linear distance) Vasalemma and Kullsberg Limestone formations share relatively few common cephalopod species. Only seven species co-occur in the Vasalemma and Kullsberg Limestone formations, which is approximately one third of the total species diversity (27 % of the Kullsberg species, 32 % of the Vasalemma species).

Interpretation

The cephalopod assemblage of the Kullsberg Limestone takes a central position when comparing other Late Ordovician assemblages from reef habitats of the Baltoscandian region;

it is nearly time equivalent to the late Sandbian reefs of the Vasalemma Formation of Estonia, and the Mjøsa and Steinvika formations in Norway, and it represents the stratigraphically older generation of mud mounds of the Siljan area, central Sweden. Hence, the Kullsberg assemblage can be analysed in evolutionary and spatial context across the Baltic Basin. The depositional and palaeogeographic setting of the Ordovician reefs (including mud-mounds) of the Baltic Basin was discussed in detail in Kröger *et al.* (2016), and therein, it was concluded that by the late Sandbian Stage, a basin-wide reef belt established across Baltoscandia, with shallow water metazoan-built reefs and deeper water mud-mounds. The Vasalemma, Mjøsa, and Steinvika formations contain shallow water metazoan-built reefs and the Kullsberg Limestone contains deeper water mud mounds. Hence, the Estonian, Norwegian, and Swedish reef sites differed in depositional depth and position on the Baltica palaeocontinent (Kröger *et al.* 2016).

Habitat dependencies of the cephalopod assemblage are most evident in the two generations of the Siljan mud-mounds. The assemblages of both the stratigraphically older Kullsberg and the stratigraphically younger Boda limestones mounds are strongly dominated by orthocerids and contain very few or no actinocerids. By contrast, actinocerids are dominant or very common in the shallower Estonian and Norwegian reefal depositional environments. The differences in depositional depth are probably also the main cause for the strong contrast in the presence of (mainly post-mortem) epizoans on the cephalopod shells; about 15 % of the Vasalemma cephalopods are encrusted, whilst epizoans are almost absent on the cephalopods of the Kullsberg mounds.

Generally, the faunal composition of the analysed assemblages is highly differentiated with little species overlap (c. one third of the species) between Kullsberg and Vasalemma formations, and almost no overlap between the Norwegian and Swedish–Estonian assemblages (two Norwegian species also occur in the Kullsberg Limestone, one Norwegian species also occurs in the Vasalemma Formation). In total a number of c. 48 species are known from these reef habitats and only nine of them occur in multiple reef settings across the basin. This situation is fundamentally different compared with that of the early Darriwilian Stage, as described in Kröger & Rasmussen (2014), where the assemblages were generally less diverse and strongly dominated by one or two ubiquitous endocerid species. This is an important finding, because it indicates that the establishment of reefs in the region involved a higher on-site (α) and in-between site (β) diversity. This general pattern suggests that depth gradients alone are poor predictors of faunal differences between sites within a common habitat, but that instead, the differences are dependent on the (common) habitat type (reefal, hardground, soft ground, etc). Our results encourage for further analyses of a wider spectrum of organisms across Baltoscandia and beyond, with the aim to gain a better insight into the dynamics of diversification during the Middle–Late Ordovician and its drivers.

Conclusions

Cephalopods are an abundant and extraordinarily rich component of the fossil assemblages of the Late Ordovician reef settings of Baltoscandia. Generally, these cephalopod assemblages are highly endemic, and show very little taxonomic faunal overlap.

The cephalopod assemblage from the late Sandbian–early Katian mud mounds of the Kullsberg Limestone, described herein, yields 26 species, which belong to 16 genera, 12 families and six orders. A comparison of the Kullsberg Limestone assemblage with that from the nearly time equivalent, shallower reef settings of the region (Vasalemma Formation, Estonia) reveals that the former is 1) distinctively dominated by orthocerids and endocerids, 2) slightly less endemic, and 3) almost entirely lacks shell-epibionts. With these three features the Kullsberg Limestone assemblage is more similar in its taxonomic composition to the stratigraphically younger, late Katian–early Hirnantian assemblage of the Boda Limestone, which is interpreted to represent a similar relatively deep and distal depositional environment. Hence, a highly differentiated depth zonation and habitat structuring of the cephalopod fauna occurred during the early Late Ordovician in the region. This contrasts with far smaller Middle Ordovician regional diversities (in its α and β components) and can also be seen as an effect of the widespread development of reefs during the early Late Ordovician time.

On the global scale, the Kullsberg Limestone cephalopod assemblage clusters with time equivalent warm water assemblages of North America and South China. This clustering supports earlier comparisons based on brachiopod faunas.

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Figure captions

Fig. 1. Geological setting of Siljan ring graben, central Sweden. Circles indicate selected individual mud mounds of the Kullsberg Limestone Formation with outcrops described herein (modified from Ebbestad & Högström 2007).

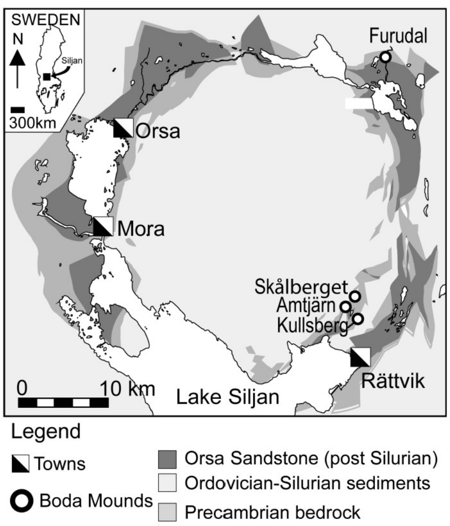

Fig. 2. Schematic overview on the stratigraphy of cephalopod assemblages compared in this report.

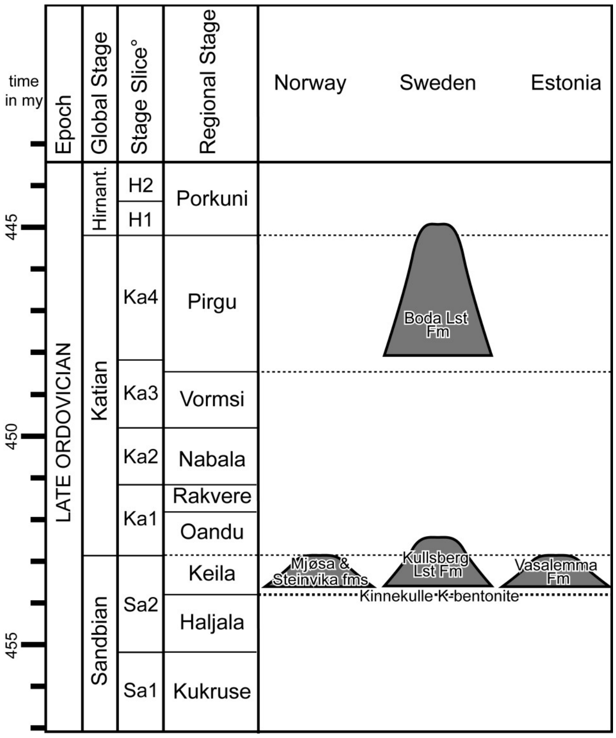

Fig. 3. Schematic cross sections of tarphycerids from the Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages, Dalarna, central Sweden. **A**, *Discoceras amtjaernense* sp. nov., RMo 125686, from Kullsberg; **B**, *Discoceras amtjaernense* sp. nov., RMo 125685, from Kullsberg; **C**, *Discoceras nilssoni* sp. nov., holotype, RMo 141723–24, from Furudal.

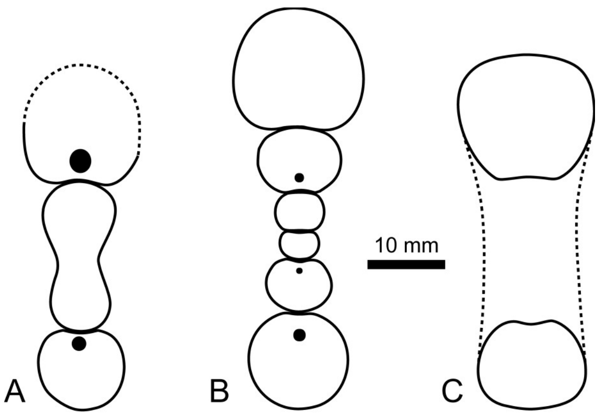

Fig. 4. Tarphycerida from the Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages, Dalarna, central Sweden. **A**–**B**, *Discoceras amtjaernense* sp. nov., holotype, PMU #D736, from Amtjärn; **C**, *Discoceras nilssoni* sp. nov., holotype, RMo 141723–24, from Furudal; scale bar 10 mm.

Fig. 5. Cephalopods with preserved color pattern from the Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages, Dalarna, central Sweden. **A**, **C**, *Discoceras amtjaernense* sp. nov., RMo 125682, from Amtjärn; **B**, **D**, *Isorthoceras urdr* sp. nov., holotype, RMo 125617–19, from Kullsberg; scale bar 10 mm.

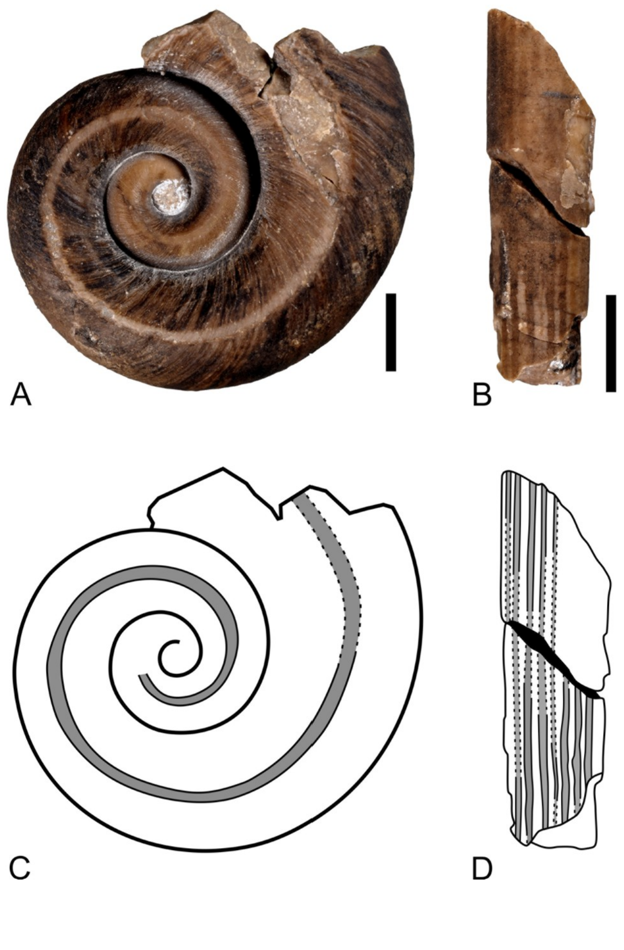

Fig. 6. Comparison of selected whorl parameters of species of *Discoceras* Barrande, 1867. **A**, Whorl expansion rate (WER), **B**, Whorl width index (WWI). Black circles, *D. amtjaernense* sp. nov.; gray circle, holotype of *D. amtjaernense* sp. nov.; white circles, *D. vasalemmense* Kröger & Aubrechtová, 2017; triangles with tip down, *D. fleischeri* Sweet, 1958; triangles with tip up, *D. roemeri* Strand, 1934.

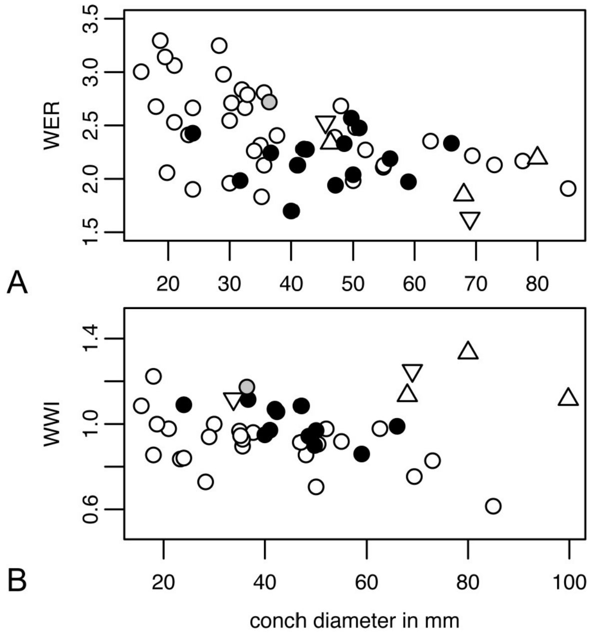

Fig. 7. Discosorida from the Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages, Dalarna, central Sweden. **A**, *Furudaloceras tomtei* gen. *et* sp. nov., holotype, PMU D#1392, from Furudal; **B**–**C**, *Kullsbergoceras nissei* gen. *et* sp. nov., PMU #3, from Kullsberg, (B), lateral view, (C) view of pro-siphuncular side; **D**–**E**, *Kullsbergoceras nissei* gen. *et* sp. nov., holotype, RMo 141708, from Kullsberg, (D) lateral view, (E) view of pro-sipuncular side; scale bar 10 mm.

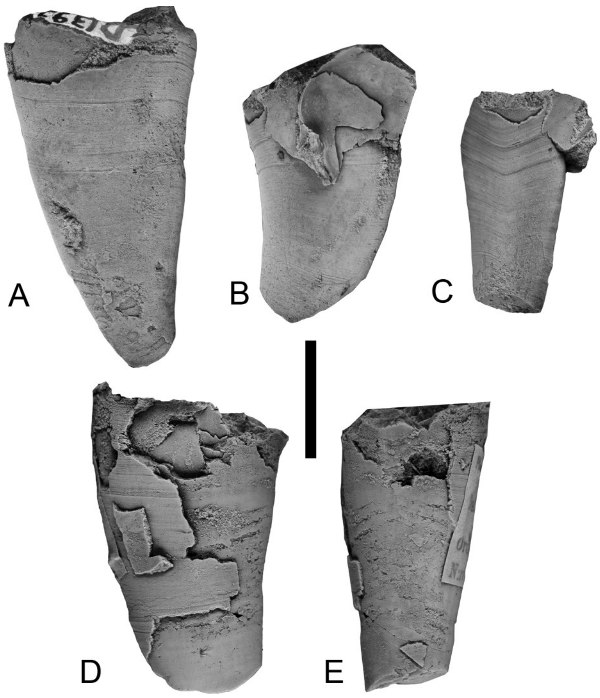

Fig. 8. Details of the siphuncle and the septal neck of cephalopods from the Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages, from Kullsberg (except [B]: from Skålberget), Dalarna, central Sweden; scale bar 5 mm (except [E] and [F]: 1 mm); all are polished median sections directed with apex down. **A**, *Kullsbergoceras nissei* gen. *et* sp. nov., PMU #D1450, specimen is heavily recrystallized and expanded siphuncle is visible only as light colored area (arrow); **B**, *Danoceras skalbergensis* sp. nov., holotype, PMU 28980; **C**, *Valkyrioceras dalecarlia* gen. *et* sp. nov., RMo 125624; **D**, *Hoeloceras muroni* Kröger & Aubrechtová, 2017, PMU #5; **E**, *Isbergoceras niger* gen. *et* sp. nov., holotype, RMo 125652, specimen is heavily recrystallized, septal necks are not preserved, septal neck shape can only be interpreted from the form of siphuncular constriction at position of septal perforation (arrows); **F**, *Furudaloceras tomtei* gen. *et* sp. nov., RMo 141712, specimen is heavily recrystallized, septal neck and siphuncular segments shape poorly visible (arrows).

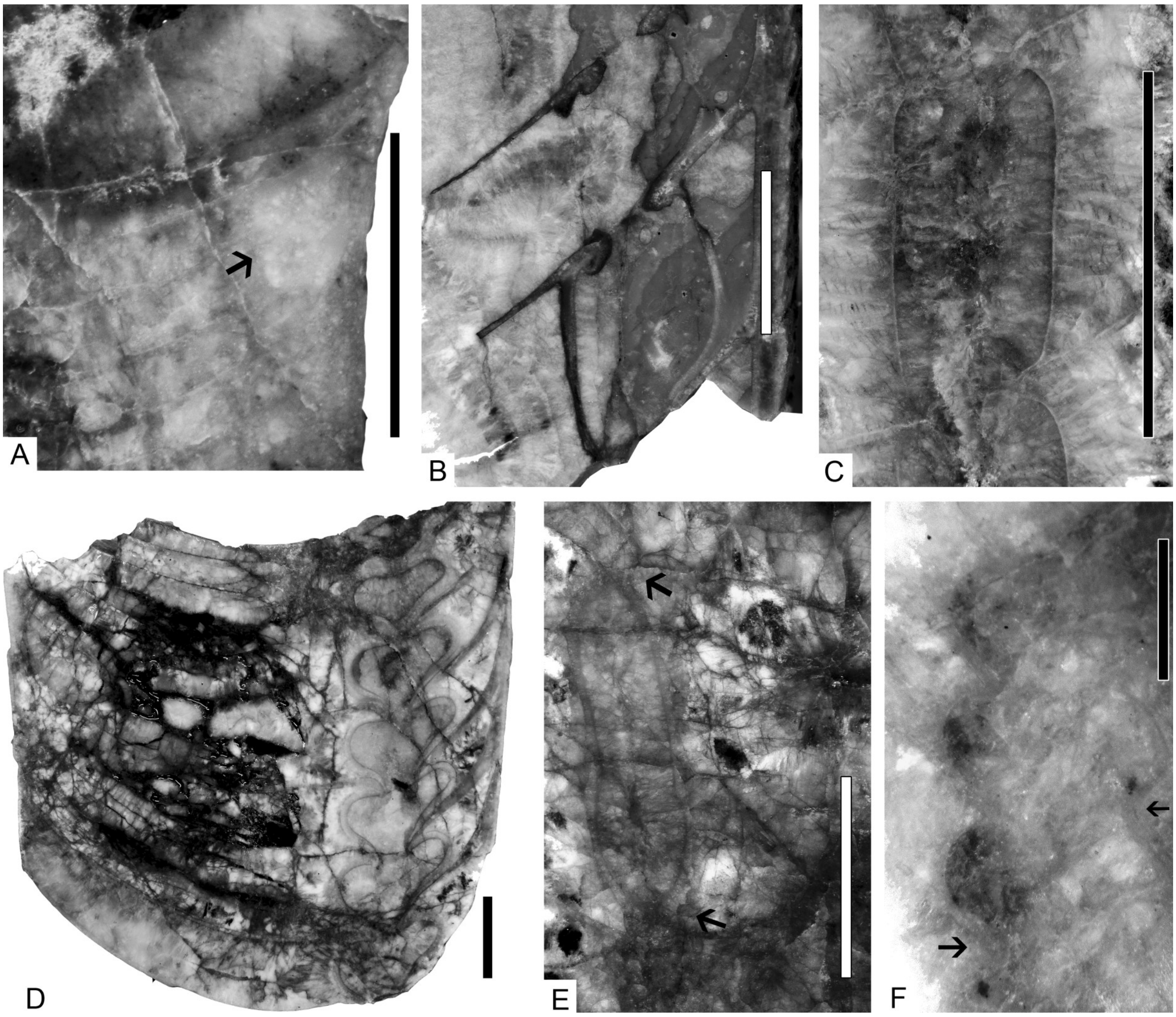

Fig. 9. Camera lucida drawings of longitudinal sections of siphuncle and septal necks of cephalopods of the Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages, Dalarna, central Sweden; solid lines, septa; dotted lines, connecting rings; grey areas, siphuncular deposits; not to scale. **A**, *Isorthoceras sylphide* sp. nov., PMU 29028; **B**, *Isorthoceras nikwis* sp. nov., RMo 125620; **C**, *Ordogeisonoceras tartuensis* Kröger & Aubrechtová, 2017, PMU 29042; **D,** *Furudaloceras tomtei* gen. *et* sp. nov., RMo 141712; **E**, *Clothoceras thornquisti* gen. *et* sp. nov., holotype, RMo 125651; **F**, *Valkyrioceras dalecarlia* gen. *et* sp. nov., RMo 125624; **G**, *Danoceras skalbergensis* sp. nov., holotype, PMU 28980; **H**, *Pleurorthoceras clarkvillense* (Foerste, 1927), PMU #107; **I**, *Ordogeisonoceras*? *uppsalaensis* sp. nov., PMU #7(16).

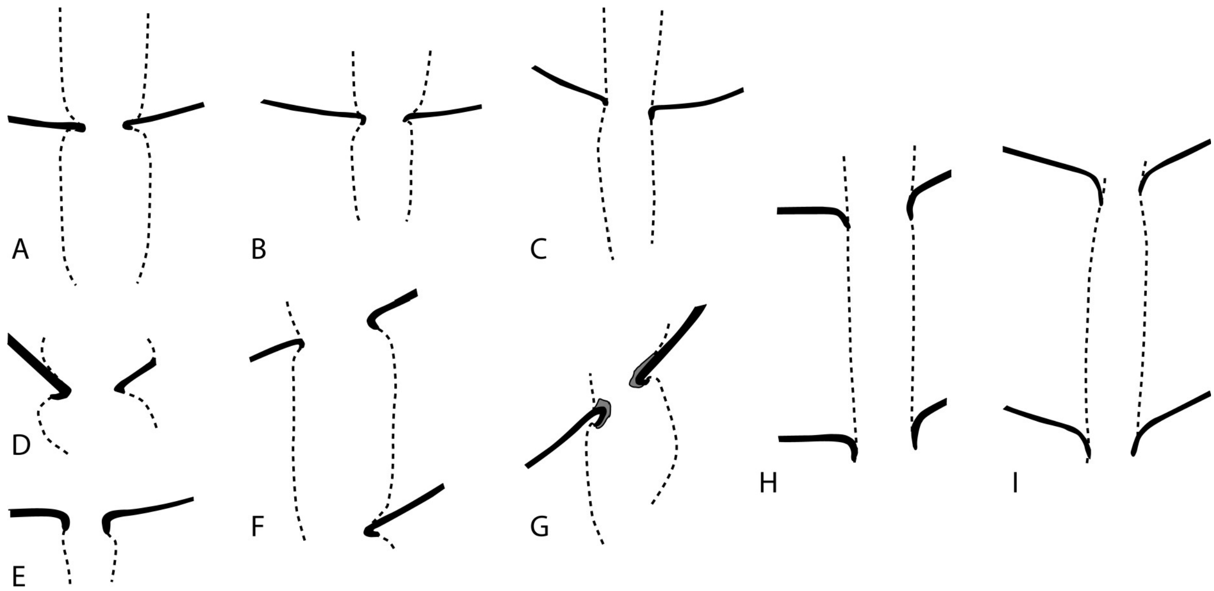

Fig. 10. Schematic cross sections of discosorids and oncocerids from the Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages, Dalarna, central Sweden. **A**, *Kullsbergoceras nissei* gen. *et* sp. nov., PMU #D1450, from Kullsberg; **B**, *Kullsbergoceras nissei* gen. *et* sp. nov., PMU # 1393, from Kullsberg; **C**, *Isbergoceras consobrinum* gen. *et* sp. nov., RMo 125654, from Kullsberg; **D**, *Beloitoceras thorslundi* sp. nov., holotype, PMU 28981, from Skålberget.

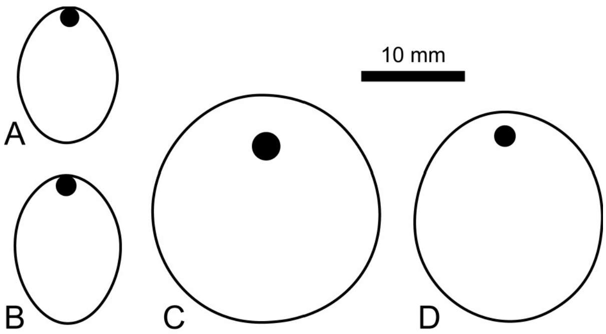

Fig. 11. Oncocerida from the Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages, Dalarna, central Sweden. **A**–**B**, *Beloitoceras stoermeri* Sweet, 1958, holotype, RMo 125653, from Kullsberg, (A) view of pro-siphuncular side, (B) lateral view, scale-bar 10 mm; **C**, *Isbergoceras consobrinum* gen. *et* sp. nov., holotype, RMo 125654, from Kullsberg, lateral view, scale as in (A); **D**–**E**, *Isbergoceras niger* gen. *et* sp. nov., holotype, RMo 125652, from Kullsberg, (D) lateral view, (E) view of pro-siphuncular side, scale as in (A); **F**–**G**, *Danoceras skalbergensis* sp. nov., holotype, PMU 28980, from Skålberget, (F) view of pro-siphuncular side, (G) lateral view, scale-bar 10 mm; **H**–**I**, *Beloitoceras thorslundi* sp. nov., holotype, PMU 28981, from Skålberget, (H) lateral view, (I) view of pro-siphuncular side, scale as in (A).

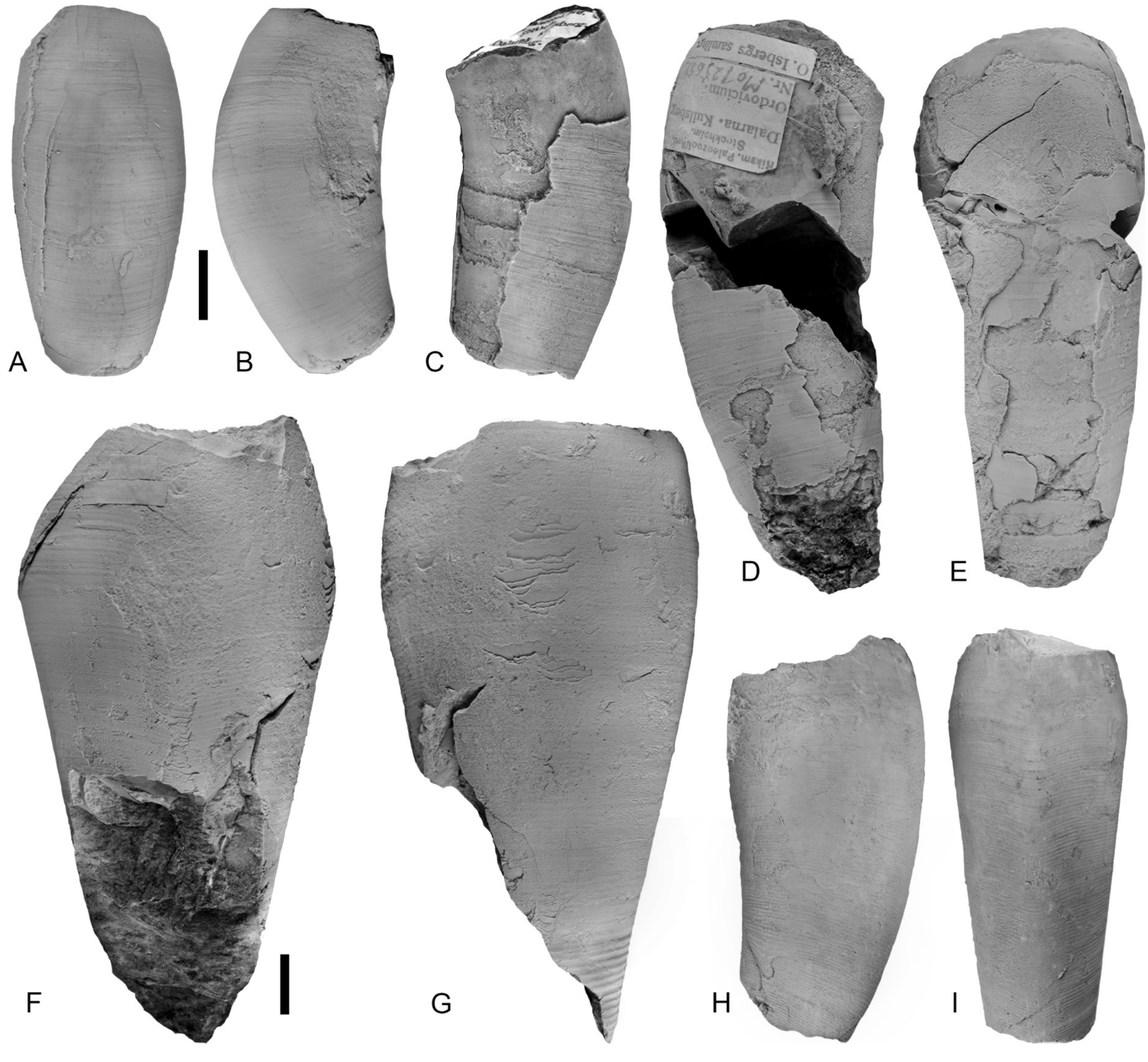

Fig. 12. Cephalopods from the Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages, Dalarna, central Sweden. **A**–**B**, *Allumettoceras mjoesense* Sweet, 1958, (A) specimen PMU D#1397, from Kullsberg, nearly adult body chamber, view of anti-siphuncular side, (B) specimen PMU D#1396, from Kullsberg, nearly adult body chamber, view of pro-siphuncular side, scale bar 10 mm; **C**, *Valkyrioceras dalecarlia* gen. *et* sp. nov., holotype, RMo 125640, from Kullsberg, lateral view, scale as in (B); **D**, *Hoeloceras muroni* Kröger & Aubrechtová, 2017, PMU #5(16), from Kullsberg, lateral view, scale bar 10 mm.

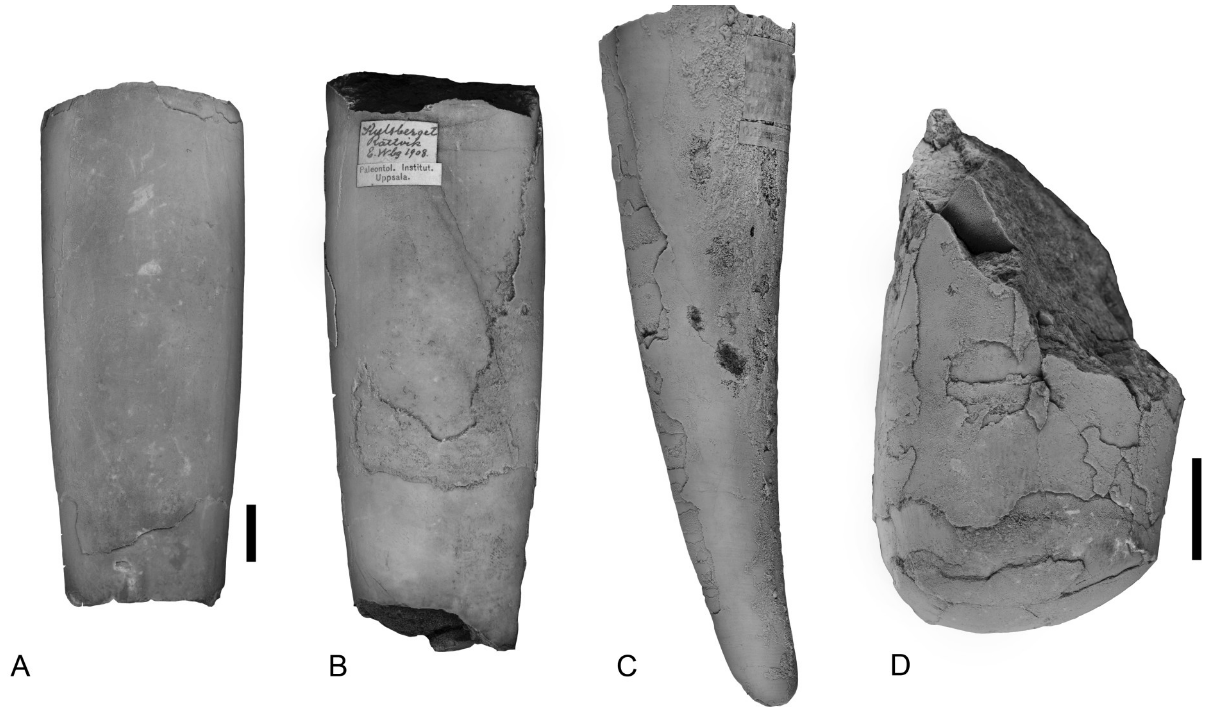

Fig. 13. Schematic cross sections of depressed orthocones and cyrtocones from the Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages, Kullsberg, Dalarna, central Sweden. **A**–**C**, *Allumettoceras mjoesense* Sweet, 1958, (A) RMo 149721, (B) PMU # 1396, (C) PMU # 1397; **D**–**E**, *Hoeloceras muroni* Kröger & Aubrechtová, 2017, (D) PMU #103, (E) PMU #5(16); **F**, *Valkyrioceras dalecarlia* gen. *et* sp. nov., RMo 9067.

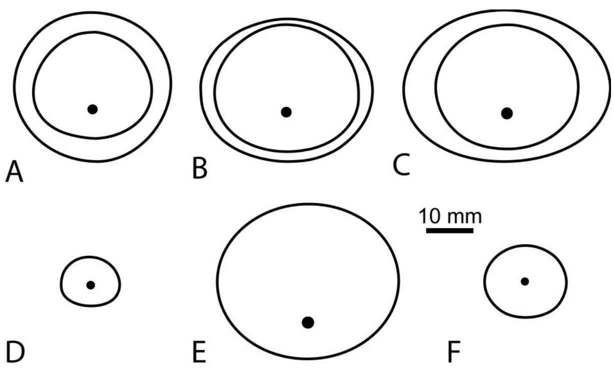

Fig. 14. Endocerids from the Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages, Dalarna, central Sweden. **A**, *Cameroceras motsognir* sp. nov., holotype, RMo 9281C–D, from Furudal, scale-bar 10 mm; **B**–**C**, *Cameroceras motsognir* sp. nov., PMU D#1401, from Kullsberg, scale as in (E); **D**–**E**, *Cameroceras motsognir* sp. nov., PMU D#1400, from Kullsberg, scale-bar 10 mm; **F**, *Endoceras naekki* sp. nov., holotype, PMU D#1389, from Skålberget, scale as in (A); **G**, *Endoceras naekki* sp. nov., PMU D#1394, from Kullsberg, lateral view, scale as in (A); **H**, detail of ornamentation of (G), scale-bar 10 mm.

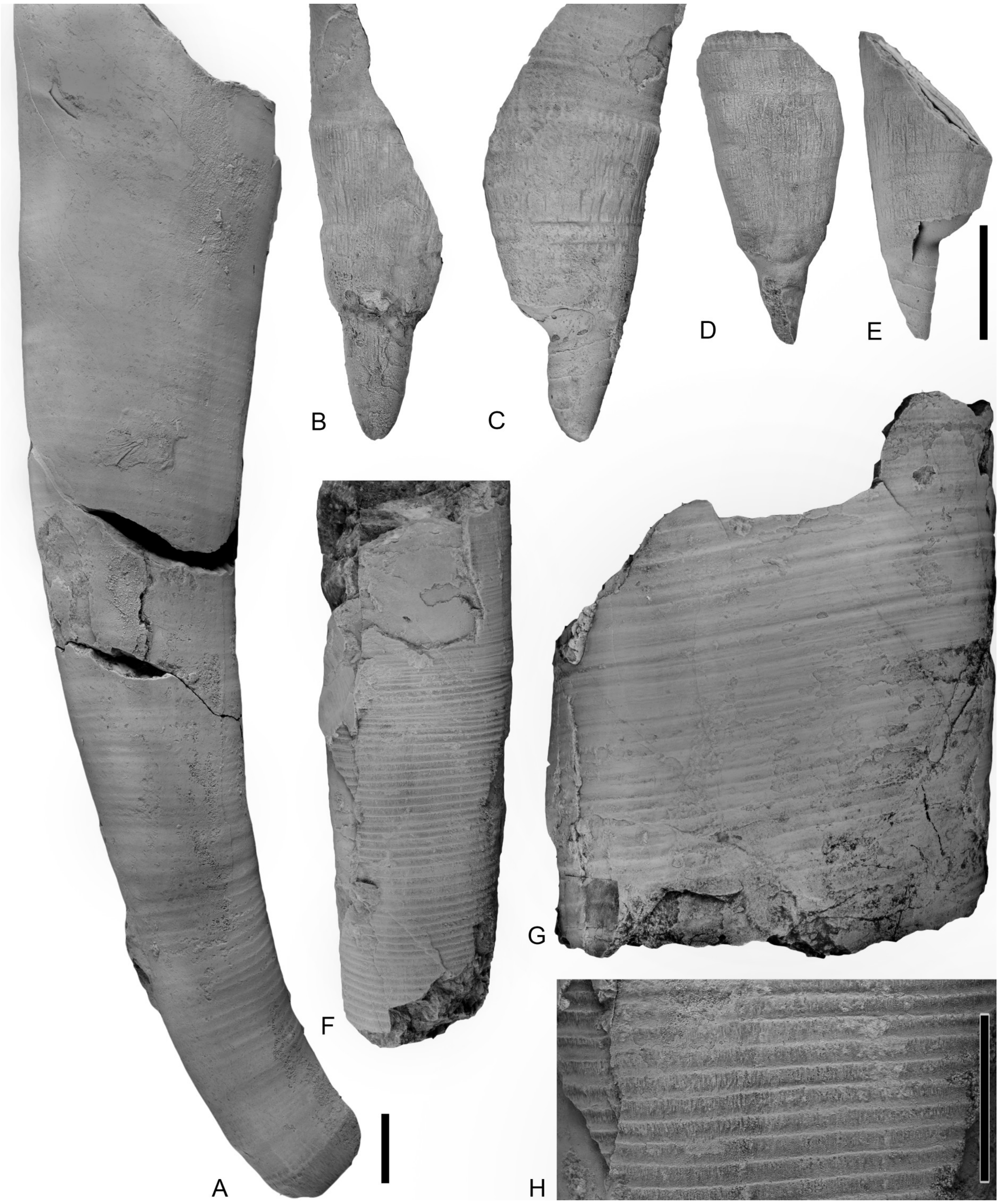

Fig. 15. Comparison of selected conch parameters of depressed ortho/cyrtoconic cephalopods. **A**, angle of expansion, **B**, relative conch width (conch height/conch width), **C,** relative position of the siphuncle (SPR). Circles, *Valkyrioceras dalecarlia* gen. *et* sp. nov.; triangles, *Hoeloceras muroni* Kröger & Aubrechtová, 2017; white diamonds, *Allumettoceras mjoesense* Sweet, 1958; black diamonds, type material of *Allumettoceras mjoesense* Sweet, 1958 figured in Sweet (1958).

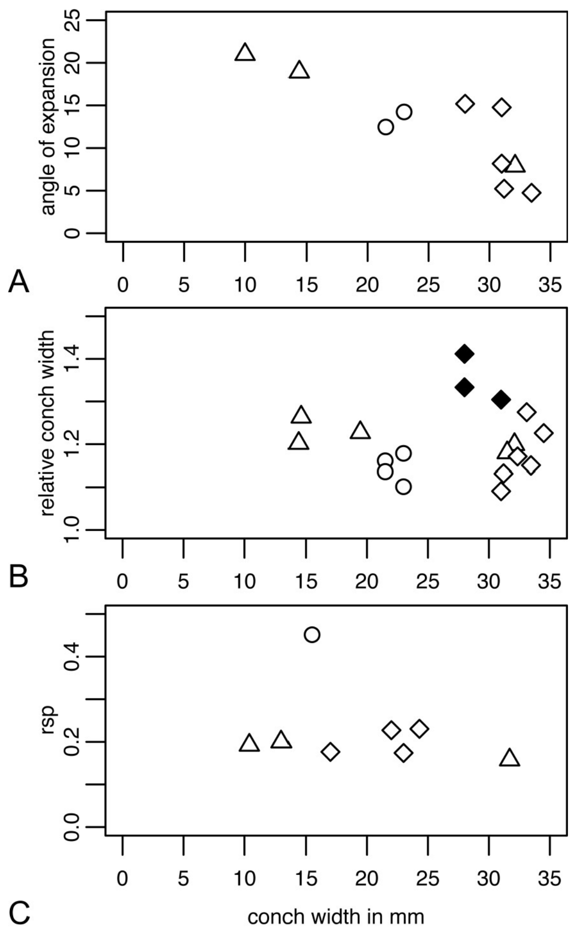

Fig. 16. Details of siphuncle and septal neck of cephalopods from the Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages, from Kullsberg (except [A] and [D]: from Amtjärn), Dalarna, central Sweden; scale bar 5 mm (except [G]: 1 mm); all are polished median sections directed with apex down. Most of the specimens are heavily recrystallized. **A**, *Isorthoceras sylphide* sp. nov., PMU 29028, from Amtjärn; **B**, *Isorthoceras nikwis* sp. nov., RMo 125620, note mural (m) and hyposeptal deposits (h); **C**, *Pleurorthoceras clarksvillense* (Foerste, 1927), PMU #107; **D**, *Ordogeisonoceras*? *uppsalaensis* sp. nov., PMU #7(16), from Amtjärn; **E**, *Valkyrioceras dalecarlia* gen. *et* sp. nov., RMo 9066; **F**, *Ordogeisonoceras tartuensis* Kröger & Aubrechtová, 2017, PMU 29042; **G**, *Clothoceras thornquisti* gen. *et* sp. nov., holotype, RMo 125651, septal neck marked with arrow, scale bar 1 mm; **H**–**I**, *Ordogeisonoceras tartuensis* Kröger & Aubrechtová, 2017, (H) RMo 181920, (I) RMo 181912

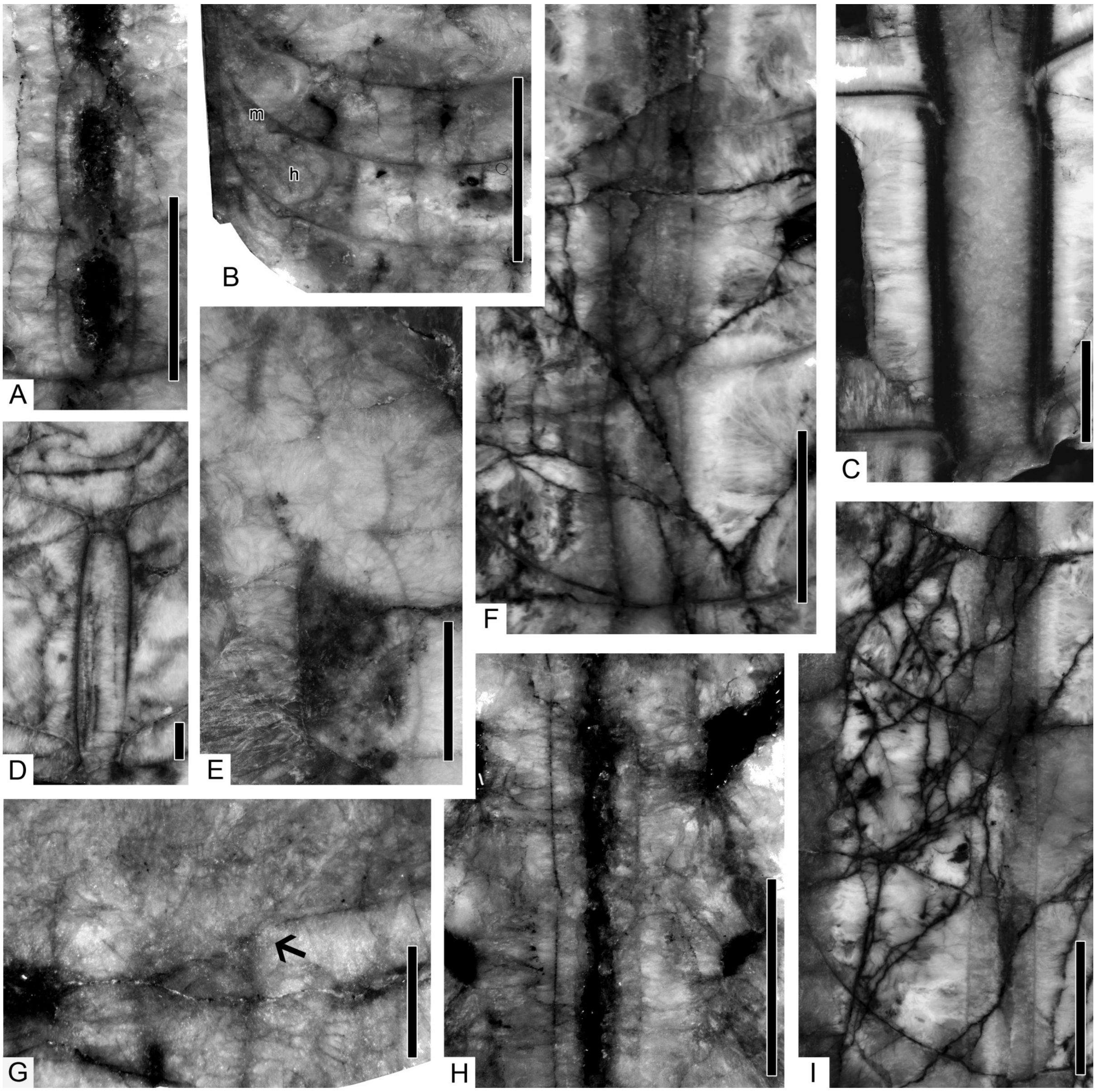

Fig. 17. Comparison of selected conch parameters of cephalopods assigned to *Pleurorthoceras clarksvillense* (Foerste, 1927). **A**, angle of expansion; **B**, relative chamber height (RCL); **C,** relative position of the siphuncle (SPR). Circles, specimens from the Kullsberg Limestone Formation; diamonds, specimens from the Cincinnati Arch Region (from Frey 1995); triangles, specimens from the Vasalemma Formation (Kröger & Aubrechtová 2017).

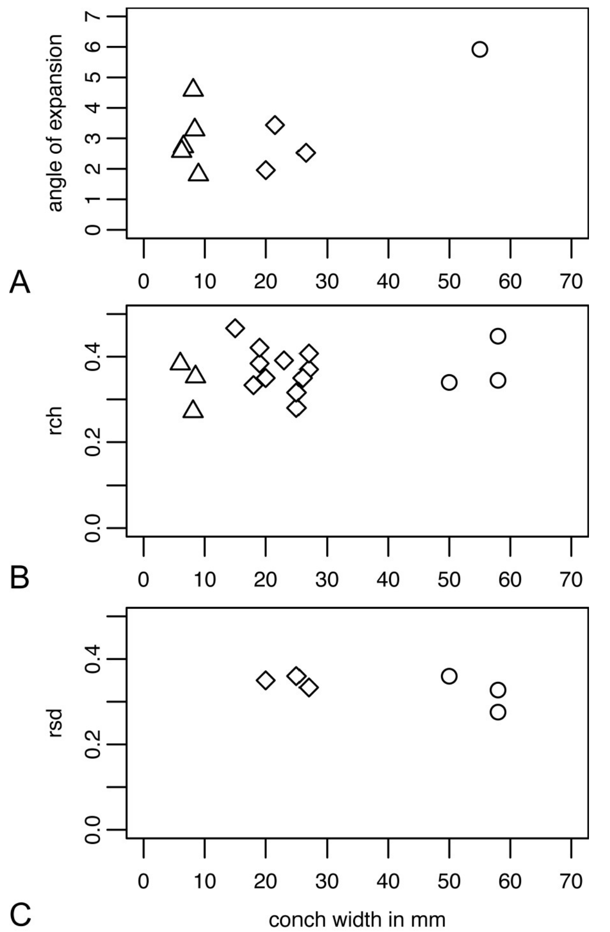

Fig. 18. Orthocerida from the Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages, from Kullsberg (except [G], from Amtjärn), Dalarna, central Sweden. **A**, *Ordogeisonoceras tartuensis* Kröger & Aubrechtová, 2017, RMo 125642, complete body chamber, lateral view, scale bar 10 mm; **B**–**C**, *Isorthoceras maris* Kröger & Aubrechtová, 2017, (B) RMo 125648, scale bar 10 mm, (C) RMo 125649, scale as in (B); **D**, *Clothoceras thornquisti* gen. *et* sp. nov., holotype, RMo 125651, note the two short chambers at apical end, scale as in (B); **E**, *Isorthoceras urdr* sp. nov., RMo 125617-19, scale as in (B); **F**, *Isorthoceras cavi* Kröger & Aubrechtová, 2017, PMU #D1399, scale as in (B); **G**, *Isorthoceras sylphide* sp. nov., holotype, PMU #91, scale as in (B); **H**, *Isorthoceras nikwis* sp. nov., holotype, RMo 125641, scale as in (B); **I**, *Striatocycloceras undulostriatum* (Hall, 1847), PMU #28, scale as in (A).

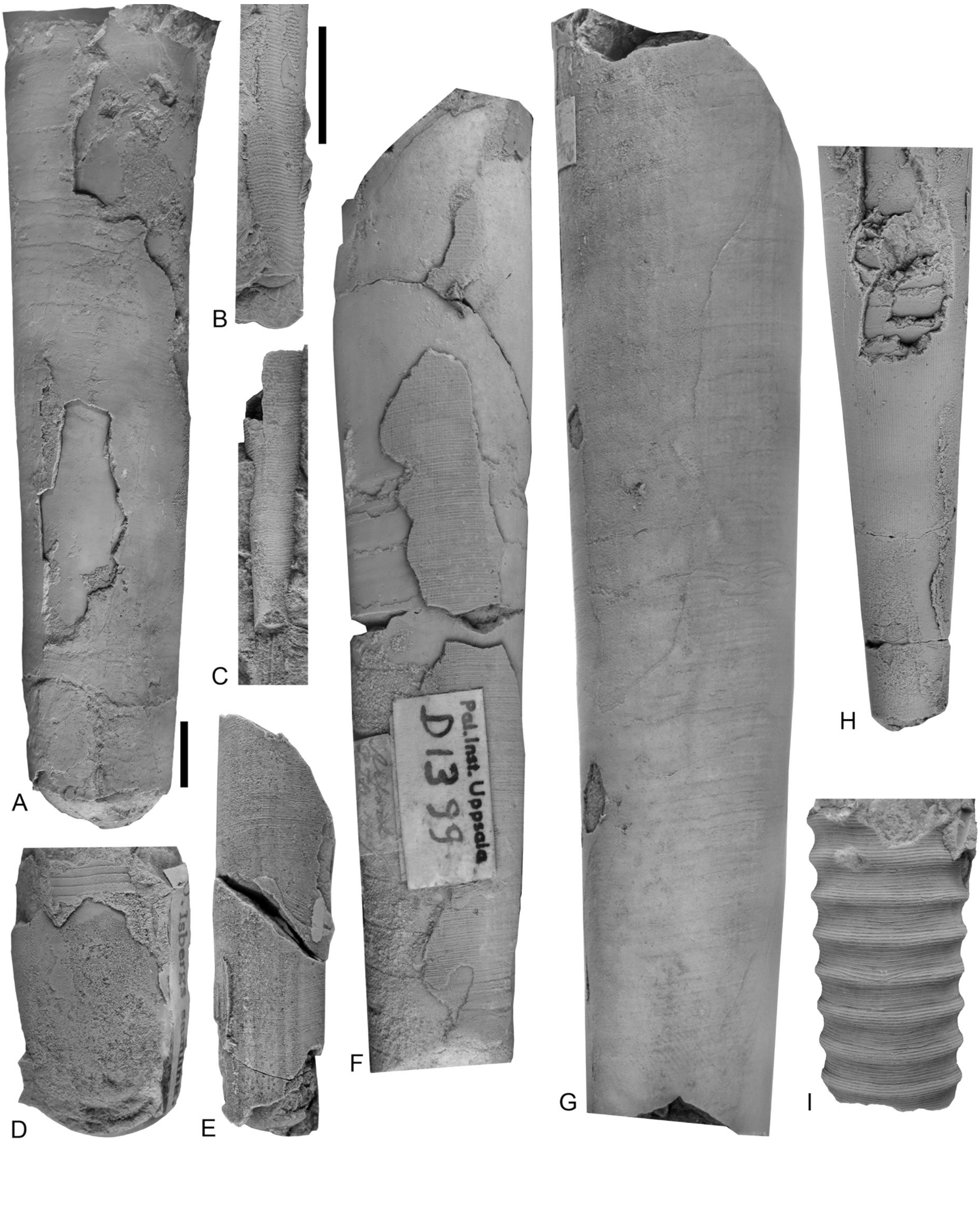

Fig. 19. *Ordogeisonoceras*? *uppsalaensis* sp. nov., holotype, PMU #8(16), from the Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages, Ordovician, from Kullsberg, Dalarna, central Sweden, not whitened, scale bar 50 mm.

Fig. 20. Details of ornamentation of transversally lirate Orthocerida from the Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages, from Kullsberg (except [D], from Amtjärn), Dalarna, central Sweden; scale bar 10 mm, all figures in the same scale. **A**, *Ordogeisonoceras tartuensis* Kröger & Aubrechtová, 2017,

PMU #D1443; **B**, *Isorthoceras cavi* Kröger & Aubrechtová, 2017, PMU #D1399; **C**, *Isorthoceras urdr* sp. nov., holotype, RMo 125617–19; **D**, *Isorthoceras sylphide* sp. nov., holotype, PMU #91; **E**, *Clothoceras thornquisti* gen. *et* sp. nov., RMo 125650; **F**, *Isorthoceras* sp., RMo 125609.

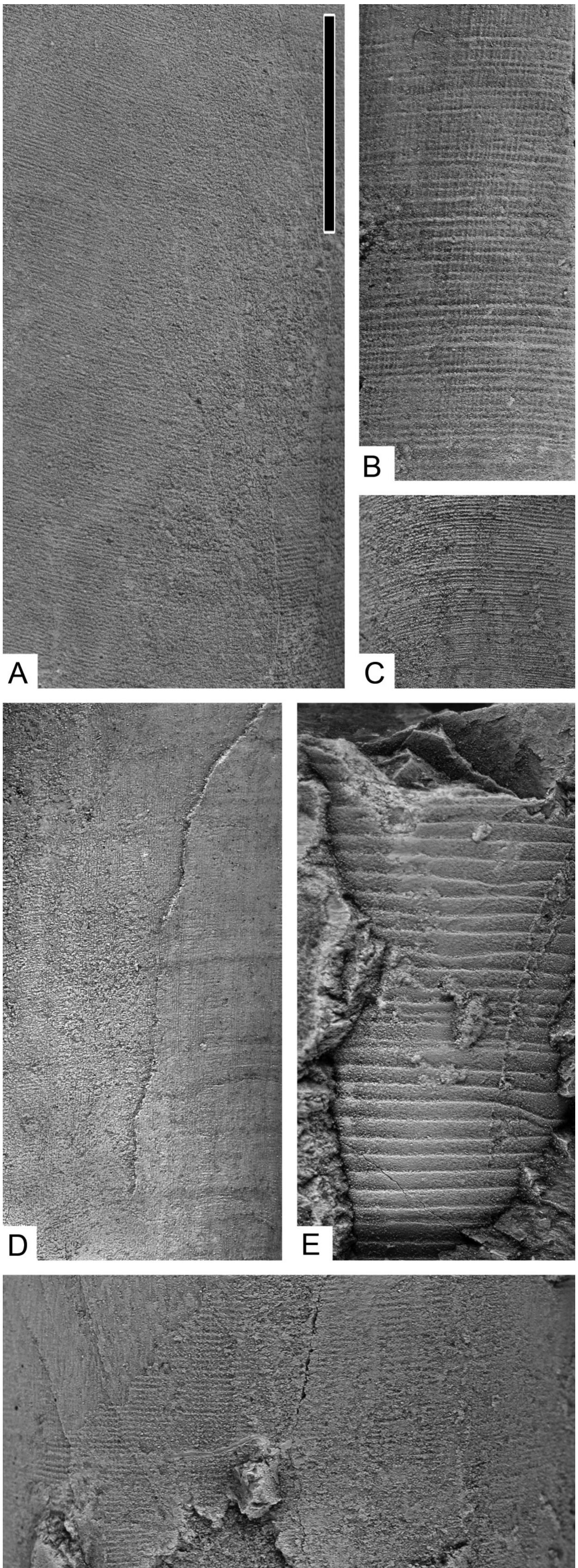
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Fig. 21. Comparison of selected conch parameters of specimens assigned to *Ordogeisonoceras tartuensis* Kröger & Aubrechtová, 2017. **A**, angle of expansion; **B**, relative chamber height (RCL). Circles, specimens from the Kullsberg Limestone Formation; diamonds, specimens from Vasalemma Formation assigned to Ordogeisonoceras sp. in Kröger & Aubrechtová (2017); triangles, specimens from the Vasalemma Formation (Kröger & Aubrechtová 2017).

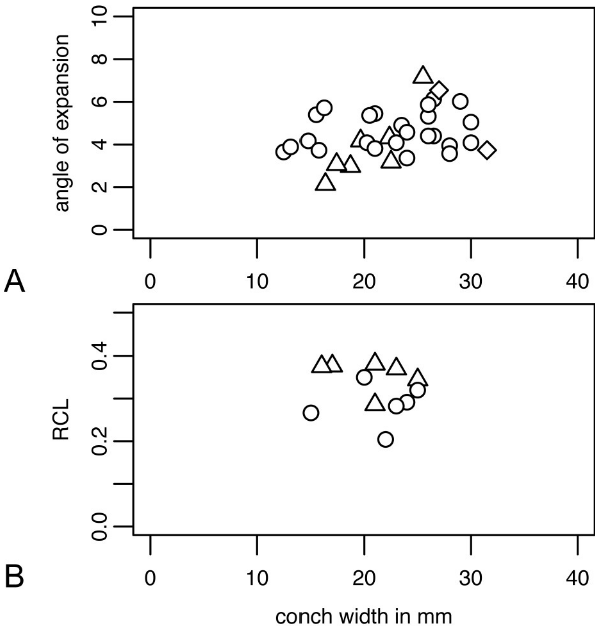

Fig. 22. Comparison of selected late Sandbian–early Katian cephalopod assemblages by relative abundance of cephalopod orders (n = number of specimens). **A**, Vasalemma Formation, Estonia, latest Sandbian Stage; **B**, Kullsberg Limestone Formation, latest Sandbian–earliest Katian(?) stages, central Sweden; **B**, Boda Limestone Formation, late Katian–Hirnantian stages, central Sweden.

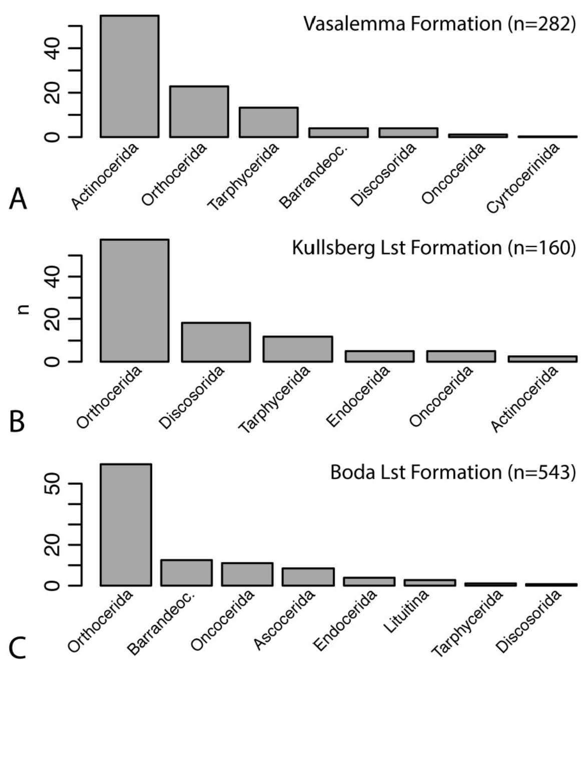

Fig. 23. Comparison of selected late Sandbian–early Katian cephalopod assemblages by relative diversity of cephalopod orders (number of genera per cephalopod order). **A**, Cluster dendrogram based on Bray-Curtis distance matrix and average clustering method; **B**, Principal Component Analysis (PCA) – plot with proportions explained by PC1=65.50%, PC2=16.19%. BAPP, Baltica-Appalachian cluster; BELB, Baltica–epicontinental Laurentia cluster; Kullsberg, Kullsberg Limestone Formation; Vasalemma, Vasalemma Formation (Kröger & Aubrechtová 2017); NOR, Frognerkilen, Mjøsa, and Steinvika formations, Norway (Strand 1934; Sweet 1958); NCH, North China, mainly Sheshan Formation; SCH, South China, mainly Pagoda Formation; USEast, Trentonian of New York, USA, and Ontario, Canada; USMid, Illinois, Indiana, Iowa, Kentucky, Minnesota, Wisconsin, USA; USApp, Pennsylvania, Tennessee, Virginia, USA (see Kröger & Aubrechtová 2017, Data Supplement 3 for details).

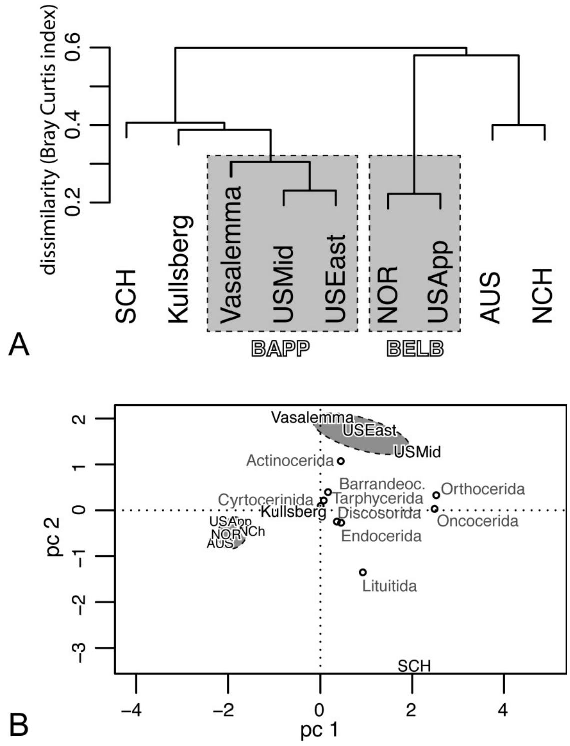

Fig. 24. Comparison of selected late Sandbian–early Katian cephalopod assemblages by genera occurrences. **A**, Cluster dendrogram based on Raup-Crick distance matrix and average clustering method; **B**, Principal Component Analysis (PCA) – plot with proportions explained by PC1=33.02%, PC2=23.86%; Vasalemma, Vasalemma Formation; NOR, Frognerkilen, Mjøsa, and Steinvika formations, Norway (Strand 1934; Sweet 1958); NCH, North China, mainly Sheshan Formation; SCH, South China, mainly Pagoda Formation; USEast, Trentonian of New York, USA, and Ontario, Canada; USMid, Illinois, Indiana, Iowa, Kentucky, Minnesota, Wisconsin, USA; USApp, Pennsylvania, Tennessee, Virginia, USA (see Kröger & Aubrechtová 2017, Data Supplement 3 for details).

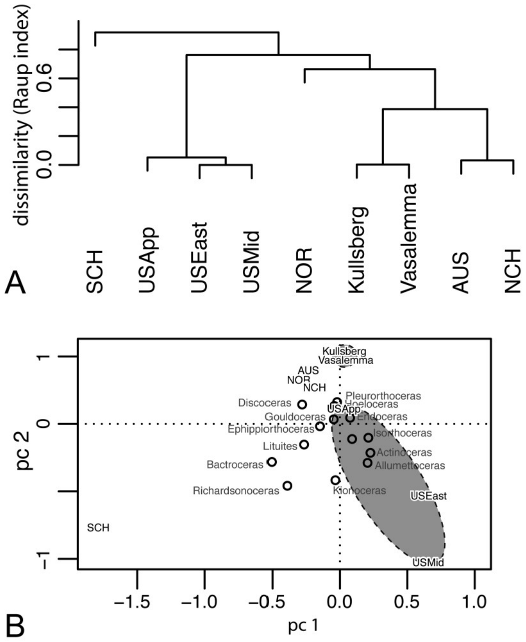

Table 1. Summary of cephalopod occurrences in the Kullsberg Limestone Formation, late Sandbian–early Katian(?) stages, central Sweden. For details see Data Supplement 1.

Species	Amtjärn	Furudal	Kullsberg	Skålberget
Alumettoceras mjoesense Sweet, 1958			5	
Beloitoceras stoermeri Sweet, 1924			1	
Beloitoceras thorslundi sp. nov.				1
Cameroceras motsognir sp. nov.			4	
Cameroceras sp.	2		2	1
Clothoceras thornquisti sp. nov.			2	
Danoceras skalbergensis sp. nov.				1
Discoceras amtjaernense sp. nov.	9		9	
Discoceras nilssoni sp. nov.		1		
Endoceras naekki sp. nov.			3	
Endocerida indet.			1	
Furudaloceras tomtei sp. nov.	1	15	1	
Hoeloceras muroni Kröger & Aubrechtová, 2017	1		3	
Isbergoceras consobrinum sp. nov.			1	
Isbergoceras niger sp. nov.			1	
Isorthoceras cavi Kröger & Aubrechtová, 2017			2	
Isorthoceras maris Kröger & Aubrechtová, 2017			1	
Isorthoceras nikwis sp. nov.		1	9	
Isorthoceras sp.	3		5	
Isorthoceras sylphide sp. nov.	2		5	
Isorthoceras urdr sp. nov.			5	
Isorthoceras verdandi sp. nov.			2	
Kullsbergoceras nissei sp. nov.		4	8	
Oncocerida indet.			1	
Ordogeisonoceras tartuensis Kröger & Aubrechtová, 2017	1	1	26	1
Ordogeisonoceras uppsalaensis sp. nov.	1		1	
Orthocerida indet.			5	
Pleurorthoceras clarkvillense (Foerste, 1927)	1		2	
Striatocycloceras undulatostriatum (Hall, 1847)	1		22	
Valkyrioceras dalecarlia sp. nov.			4	

Table 2. Species level diversity of Late Ordovician reefal cephalopod assemblages of Baltoscandia. $S_{rarified}$, rarified diversity; S_{SQS}, diversity after the shareholder quorum subsampling method of Alroy (2010); S_{asy}, diversity based on extrapolated Hill numbers using the method of Chao et al. (2014); ° data from Kröger (2013); * data from Kröger & Aubrechtová (2017).

	Boda Limestone Formation (Katian–early Hirnantian stages)°	Kullsberg Limestone Formation (late Sandbian–early Katian(?) stages)	Vasalemma Formation (late Sandbian)*
Raw richness (S)	63	26	19
Sample size (N)	543	160	282
$S_{rarified}$	42	-/-	16
S_{SQS}	56	-/-	13
S_{asy} (+/- 95% confidence)	93 (73-157)	31 (27-51)	21 (19-33)
Pielou's evenness (J)	7.4 (7.16-7.30)	4.8 (4.5 – 4.88)	2.38 (2.33-2.35)
Taxonomic distinctness (Δ)	3.66	3.36	3.75