Concentrations of juvenile and small adult cephalopods in the Hirnantian cherts (Late Ordovician) of Porkuni, Estonia

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The quarry in the north Estonian village of Porkuni provides a succession of shallow-water limestones and cherts spanning the Ashgillian *Normalograptus*? *extraordinarius* graptolite Biozone. This interval comprises the initial pulse of the end-Ordovician extinction. The succession of Porkuni contains abundant and extraordinarily well-preserved fossils. 71 cephalopod specimens were extracted from these strata at Porkuni. Many of these specimens are fragments of juvenile shells or small adults. The embryonic shells of the cephalopods are usually preserved and provide insight into their early ontogeny. The faunal composition is considered as autochthonous and reflects a "palaeo-nursery" in a Hirnantian reef environment. The collected specimens represent twelve genera and four orders. Small oncoceridans and orthoceridans dominate the association. The rate of endemism is very high, since only two genera found in Porkuni, are known from outside Baltoscandia. The new genera *Parvihebetoceras*, *Pomerantsoceras*, *Porkunioceras*, and the new species *Parvihebetoceras wahli*, *Pomerantsoceras tibia*, *Porkunioceras tuba*, and *Strandoceras orvikui* are erected.

Key words: Cephalopoda, Nautiloidea, mode of life, end-Ordovician extinction, Ashgillian.

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Introduction

The name Porkuni was given to the youngest regional stage of the Ordovician of Baltoscandia. The Porkuni Regional Stage is equivalent to the Hirnantian of Great Britain or the Gamachian of North America. Thus, it represents a time interval just at the beginning of the end-Ordovician extinction event. Brenchley (2004) emphasised the existence of two main extinction events, one at the start of the Hirnantian at the *Normalograptus*? *extraordinarius* graptolite Biozone and a second at the late Hirnantian. The Hirnantian *N. extraordinarius* Biozone of the Porkuni Regional Stage is exposed at the stratotype (Hints et al. 2000) within a quarry in the scenic nineteenth century estate park of the village of Porkuni in northern Estonia (Fig. 1).

The significance of the quarry is the palaeogeographical and palaeoecological setting of its strata and its well-preserved fossils. The beds of the quarry of Porkuni represent a succession of shallow water skeletal limestones with intercalated coral-stromatoporoid-bryozoan bioherms (Hints et al. 2000) within a sub-tropical palaeogeographic position (Cocks and Torsvik 2004). Webby et al. (2004) highlighted the Hirnantian rugose coral fauna of Baltoscandia, which is exceptional with regards to its diversity and high survival rates; 75% of the total of the genera survived into the Silurian. Moreover, Webby et al. (2004) emphasised that the Hirnantian coral morphotypes became influential in shaping the Silurian evolutionary development of rugose corals. Anstey et al. (2003) described a similar pattern for bryozoans at the Ordovician–Silurian boundary interval. The Porkuni quarry, which yields this fauna is therefore a unique archive of a potential survival and recovery fauna of the end-Ordovician extinction event.

Besides reef building organisms, the strata of the Porkuni quarry yield a very rich and diverse autochthon fauna of molluscs and echinoderms. Cephalopods are commonly preserved in some horizons. I hypothesise that these cephalopods, similar to the rugose corals and bryozoans, became influential in shaping the post-Ordovician evolutionary development of its group. In the present study this hypothesis will be evaluated.

Institutional abbreviations.—GIT, Tallinna Tehnikaülikooli Geoloogia Instituut, Tallinn, Estonia; KIG PGI, Kafedra Instituta Paleontologii, Universitet St. Petersburg, St. Petersburg, Russia; NMB, Museum für Naturkunde, Berlin, Germany; TUG, Tartu Ülikool Geoloogiamuuseum, Tartu, Estonia.

Material

A total of 71 nautiloid specimens were available for this study. The material comprises specimens of the collections of the NMB, TUG, and GIT. These have been collected since the nineteenth century by Wilhelm Dames, Walther Rosenberg (at reposition of NMB), Arwed von Wahl (in collection of GIT), Karl Orviku, and Ülle Sirk. However, the bulk of the

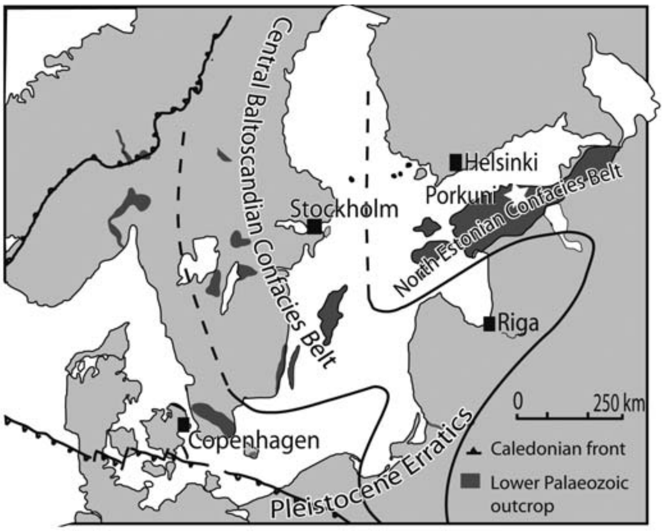

Fig. 1. Distribution of Early Palaeozoic strata in Baltoscandia and position of Porkuni, Estonia within Baltoscandia. After Jaanusson (1976).

material was collected by Mare Isakar (Tartu) and Björn Kröger (stored in the collection of TUG) during two field trips in 2002 and 2004.

The originals of five species described by Kiselev et al. (1990), allegedly collected from the site (*Leurorthoceras* sp., *Strandoceras sphinx*, *Monomuchites* cf. *bacotense*, *Ephippiorthoceras* cf. *dowlingi*, *Gorbyoceras* cf. *duncanae*), are deposited in the Palaeontological collection of the University of St. Petersburg. None of these specimens appear to be from the Porkuni Regional Stage or the Porkuni outcrop. These specimens came from different localities of Silurian age (*Leurorthoceras* sp., steinkern of glauconitic-arenitic limestone, Early Silurian, without locality; *Strandoceras sphinx,* steinkern of bright mudstone from Dolgaonitse/Bratilov near Kingisepp; *Monomuchites* cf. *bacotense*, steinkern of yellowish dolomitic mudstone, Early Silurian, labelled with "Pribaltiki" (= Baltic States: Lithuania, Latvia, Estonia); *Ephippiorthoceras* cf. d*owlingi*, steinkerns of glauconitic-arenitic limestone, Early Silurian, Saeve near Sandla).

Geological setting

Friedrich Schmidt (1858) described the Porkuni quarry for the first time in detail, using the German name for the village, Borkholm, and its conspicuous beds were termed "Borkholmer Schicht". Schmidt (1858) recognised four different limestone beds in the approximately 6 m thick, highly fossiliferous succession. These beds served to subdivide the lower part of the Porkuni Regional Stage (the Ärina Formation) into four members: the Röa Member, the Vohilaid Member, the Siuge Member and the Tõrevere Member (Fig. 2; see also Oraspõld 1975; Hints et al. 2000). Without exception, all cephalopods collected in Porkuni during the past centuries come from the Siuge Member.

The Siuge Member consists of a succession of roughly 1.5 m slightly dolomitised biomicritic wackestones to micritic-bioclastic packstones. The skeletal grains include fragments of crinoids, ostracods, and brachiopods. Grains of quartz only account for less than 10% of the total sediment (Oraspõld 1975). A relatively high content of bitumen is characteristic of the sediments of the Siuge Member. The limestones consist of cross-bedded channel-fillings with thin argillaceous interlayers (Fig. 3). Locally, layers or nodules of chert occur at the bottom of the channel structures. The layers with chert nodules have a thickness of less than five centimetres and contain numerous small but macroscopic remains of predominantly bryozoan zooaria, ostracod-tests, and echinoderm ossicles. Gastropods, bivalves, graptolites, and cephalopods are less common, but occur in considerable numbers. The exceptional well-preserved fossils are evidence of a very early diagenetic formation of the cherts.

Two modes of preservation are characteristic for the cephalopods of the Siuge Member. Shell fragments more than one centimetre in diameter are preserved in the bioclastic limestone. These shells are strongly re-crystallised. Details of the external shell are moderately well preserved, but internal characters such as structures of the siphuncle and septal necks are poorly preserved. Contrarily, the cherts contain predominantly cephalopod fragments of a few millimetres in size. These fragments are completely silicified and display minute details of internal and surface characters, but the original shell ultrastructure and the structure of the connecting ring is not preserved.

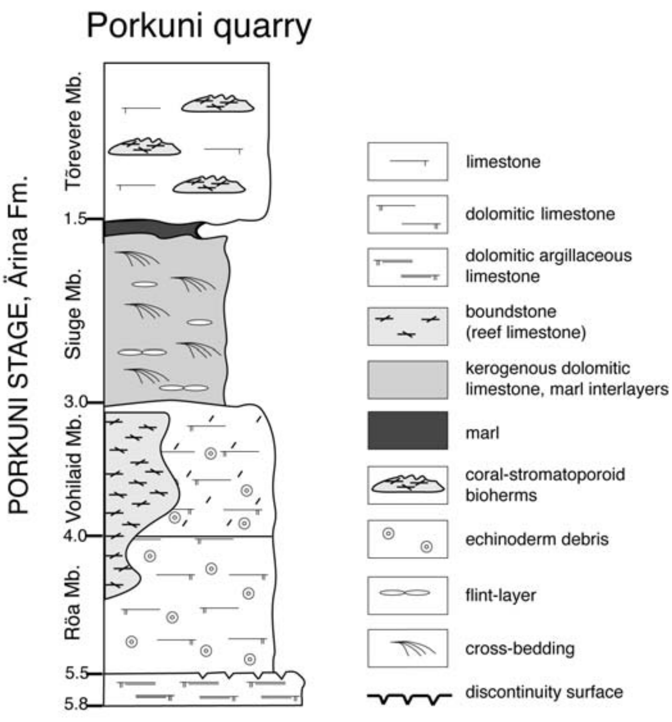

Fig. 2. Sedimentology and stratigraphic division of the Porkuni section, Estonia.

Fig. 3. Detail of the Siuge Member of Porkuni, Estonia. Line drawing outlines the bedding surfaces in the bioclastic limestone. Shaded areas emphasize the fossiliferous chert nodule beds. The chert nodules occur occasionally at the bottom of small scaled channels and other topographic depressions.

Systematic palaeontology

Order Orthocerida Kuhn, 1940

Family Orthoceratidae M'Coy, 1844

Gen. et sp. indet. A

Figs. 4B, 5A.

Material.—Four specimens displaying apex characters and juvenile growth stages from Chert of the Siuge Member; Porkuni Regional Stage, Late Ordovician, Estonia.

Description.—Specimen TUG 1227/9 is fragment with three chambers. Minimum cross section diameter is 1.2 mm, length 2.4 mm, chamber length 0.8 mm. Cross section is slightly compressed. Shell is smooth, no growth lines are visible. Septa have shallow curvature. Siphuncle is subcentral.

Specimen TUG 1227/1 is a fragment of most apical nine millimetres of the conch (Fig. 4B). Diameter of conch is at adoral end 1.4 mm, at position of first chamber 1.3 mm. Maximum diameter of fragment is 1.45 mm at distance 1.4 mm from tip, forming slightly inflated interval of first six chambers. Extreme tip of apex is not known. Distance between first and second chamber is 0.4 mm, significantly shorter than subsequent chambers (see Table 1). Between sixth and seventh septum (at distance of 3.8 mm from apex) abrupt increase of thickness of outer shell of conch (0.03–0.05 mm) occurs. Siphuncle is slightly subcentral, diameter approximately 0.1 of conch cross section. Septal necks are suborthochoanitic, with length of 0.08 mm at sixth septum.

Remarks.—The species under consideration resembles *Michelinoceras* sp. A of Ristedt (1968) but differs in having an apex diameter that is more then two times larger, a more centrally positioned siphuncle, and more narrowly spaced septa. The species under consideration differs from *Michelinoceras elongatum* (Yü, 1930) in having an eccentric siphuncle, a shallower septal curvature and short septal necks. The diagnostic characters of *Michelinoceras* are a tubular siphuncle with long orthoconic septal necks and an apex with inconspicuous spherical initial chamber, which differs considerably from the species under consideration. Because characters of more mature specimens are not available a generic or species determination is impossible.

Gen. et sp. indet. B

Figs. 4H, 5C.

Material.—Three fragments of apical parts of the phragmocone (TUG 1227/2, 3, 4) from Chert of the Siuge Member, Porkuni Regional Stage, Late Ordovician, Estonia.

Description.—Specimen TUG 1227/2, is a fragment of most apical part of shell with length of 12 mm, maximum cross section diameter 1.6 mm, and 18 chambers (Fig. 4H). Conch is slightly bent. Subspherical initial chamber has length of 0.66 mm and cross section diameter of one millimetre. Slight constriction occurs at 0.5 mm from apex. Caecum elongate, starting at 0.14 mm from apex, with siphuncular diameter 0.16 mm. Length of second chamber is significantly shorter (0.5 mm) than initial and subsequent chambers (for length of subsequent chambers see Table 1). Septal spacing in younger chambers is narrower than in older chambers. Septal necks are suborthochoanitic.

Specimen TUG 1227/4 is a complete embryonic specimen, representing single-chambered phragmocone and body chamber. Length of entire shell is 2.4 mm, maximum diameter 1.2 mm, length of single chamber of phragmocone is 0.45 mm, diameter at septum is 1 mm. Surface of shell is smooth.

Specimen TUG 1227/3 is a fragment that is broken off close to apex with minimum diameter 1.35 mm, maximum diameter 1.6 mm, length 5.2 mm, and angle of expansion is less than three degrees. Thickness of siphuncle is 0.2 mm at diameter 1.52 mm. Siphuncle is very slightly expanded within chambers. Septal necks are suborthochoanitic. Septal curvature shallow. Shell surface is smooth.

Remarks.—These fragments resemble *Pleurorthoceras* Flower, 1962 because they display suborthochoanitic septal necks and their very slightly expanded siphuncle is con-

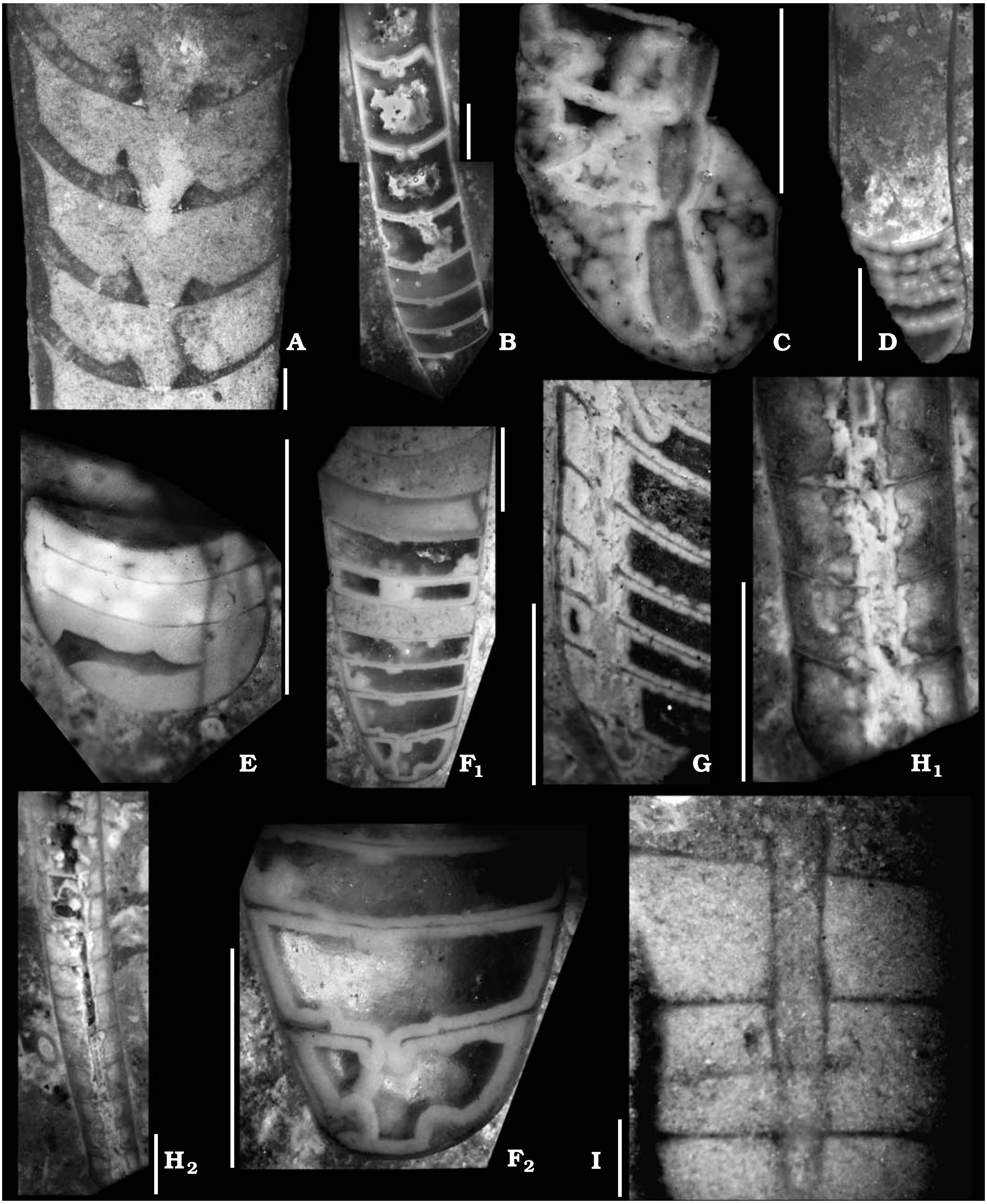

Fig. 4. Polished median sections of cephalopods of the Siuge Member of Porkuni, Estonia. **A**. Ereditidae gen. et spec. indet, TUG 101/66a, detail of a siphuncular segment showing the annular endosiphuncular deposits. **B**. Orthoceratidae gen. et spec. indet. A, TUG 1227/1. **C**. *Parvihebetoceras wahli* sp. nov., TUG 1227/10, note the asymmetrical development of the siphuncular necks. **D**. *Pomerantsoceras tibia* spec. nov. 1227/45, fragment of apical part. →

Table 1. Septal distances of apical chambers of the Porkuni cephalopods. Number one accounts for initial chamber, subsequent chambers in ascending sequence. See text for details.

Species	# TUG	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	17	18
Graciloceratidae gen. et sp. indet. A	1227/34	0.8	0.5	0.4	0.4	0.5	0.6	0.5										
Graciloceratidae gen. et sp. indet. B	1227/25	0.5	0.6	0.4	0.4	0.5	0.4	0.8	0.9									
Orthoceratidae gen. et spec. indet. A	1227/1	0.8	0.4	0.5	0.6	0.8	1.1	1.4	1.4									
Orthoceratidae gen. et sp. indet. B	1227/2	0.7	0.5	0.6	0.6	0.7	0.7	0.7	0.6	0.6	0.6	0.5	0.5	0.5	0.5	0.6	0.5	0.4
Orthoceratidae gen. et sp. indet. B	1227/3	0.5	0.6	0.7	0.5	0.6	0.6	0.8	0.7	0.8								
Porkunioceras tuba sp. nov.	1227/24	0.8	0.4	0.2	0.2	0.3	0.4	0.4	0.5	0.5	0.6	0.6	0.6	0.6				
Strandoceras orvikui sp. nov.	1227/27	0.4	0.3	0.3	0.4	0.4	0.3	0.4	0.4	0.5	0.5	0.3	0.4	0.4	0.4			
Strandoceras orvikui sp. nov.	1227/30	0.4	0.3	0.3	0.3	0.4	0.4	0.4	0.4									

stricted at the septal foramina. However, the fragments differ from known species of *Pleurorthoceras* in having a slightly cyrtoconic growth axis, a higher angle of expansion and a shallow septal concavity. These differences may represent specifics of the early growth stages that are not known in the type of the genus. Because all Porkuni fragments are from minute juvenile shells a specific taxonomic attribution is impossible.

The specimens may be conspecific with one of the species of a group of poorly known smooth longicone orthochoanites of the Middle and Late Ordovician of Baltoscandia that have been mentioned and listed in Balashov (1953) as *nomina nuda* such as *Michelinoceras balticum* nom. nud., *M. kukersiense* nom. nud., and a species falsely referred to as *Orthoceras dimitatum* Münster, 1840 (= *Hemicosmorthoceras dimidiatum* Sowerby in Murchinson, 1839, a characteristic Devonian species) by Eichwald (1860) and Balashov (1953). Smooth orthochoanitic longicones represent also a common element of the cephalopod fauna of the Haljala Regional Stage, Middle Ordovician of north Estonia. The entire group of these species needs a revision.

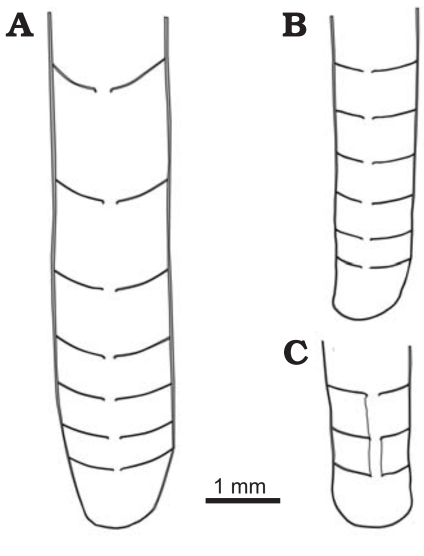

Fig. 5. Camera lucida drawings of median sections of **A**. Orthoceratidae gen. et sp. indet. A, TUG 1227/1. **B**. Ulrichitidae gen. et sp. indet., TUG 1227/44. **C**. Orthoceratidae gen. et sp. indet. B, TUG 1227/2.

Family Ulrichitidae Chen in Chen et al., 1981

Gen. et sp. indet.

Figs. 4A, 5C, 6D, 7E, 8.

Material.—Two specimens displaying internal characters of nearly adult growth stages (TUG 101/66a, TUG 1227/13), one fragment displaying adolescent growth stages, two specimens with preserved apex (TUG 1227/44, 47) from Chert of the Siuge Member, Porkuni Regional Stage, Late Ordovician from Porkuni, north Estonia.

Description.—Specimen TUG 101/66a has shell length of 49 mm, minimum cross section diameter seven millimetres, maximum diameter of 13 mm, and angle of expansion of seven degrees. Outer shell is poorly preserved, but apparently smooth (Fig. 7E). Cross section is circular. Chamber height is approximately one-third of shell diameter. Conch margin is slightly concave in lateral view. Twelve septa occur over total length of fragment. Septal distance is approximately one-fourth of cross section diameter. Septa are shallowly concave and slightly oblique, sloping in adoral direction at pro-siphuncular side. Siphuncle is slightly subcentral. Septal perforation is approximately 0.1 of conch cross section. Septal necks are achoanitic to very short loxochoanitic (Fig. 4A). Siphuncular segments are expanded within chambers, oval in longitudinal section with maximum diameter approximately 0.26 of conch cross section. Siphuncular segments are more expanded within chambers at side that is closer to conch margin. Episeptal and mural deposits occur in all chambers.

E. *Pomerantsoceras tibia* sp. nov., TUG 1227/20, the apparent spherical shape of the apex is an artefact that resulted from the oblique section of a part of the specimen, the partially preserved thin siphuncular tube, fakes a prochoanitic septal neck at the second septum, but the septal necks are always achoanitic. **F**. Graciloceratidae gen. et sp. indet. B., TUG 1227/25, apical part (F_1), enlarged part of same specimen (F_2), note the suborthochoanitic septal necks. **G**. Graciloceratidae gen. et sp. indet. A, TUG 1227/34. **H**. Orthoceratidae gen. et sp. indet. B, TUG 1227/2 detail of most apical part of fragment (H_1), overview of apical part of the fragment (H_2). **I**. *Piersaloceras gageli* Teichert, 1930. TUG 1227/32, section represents not a median section, but a section along the growth axis, sectioned roughly from flank to flank of the shell. Scale bars 1 mm.

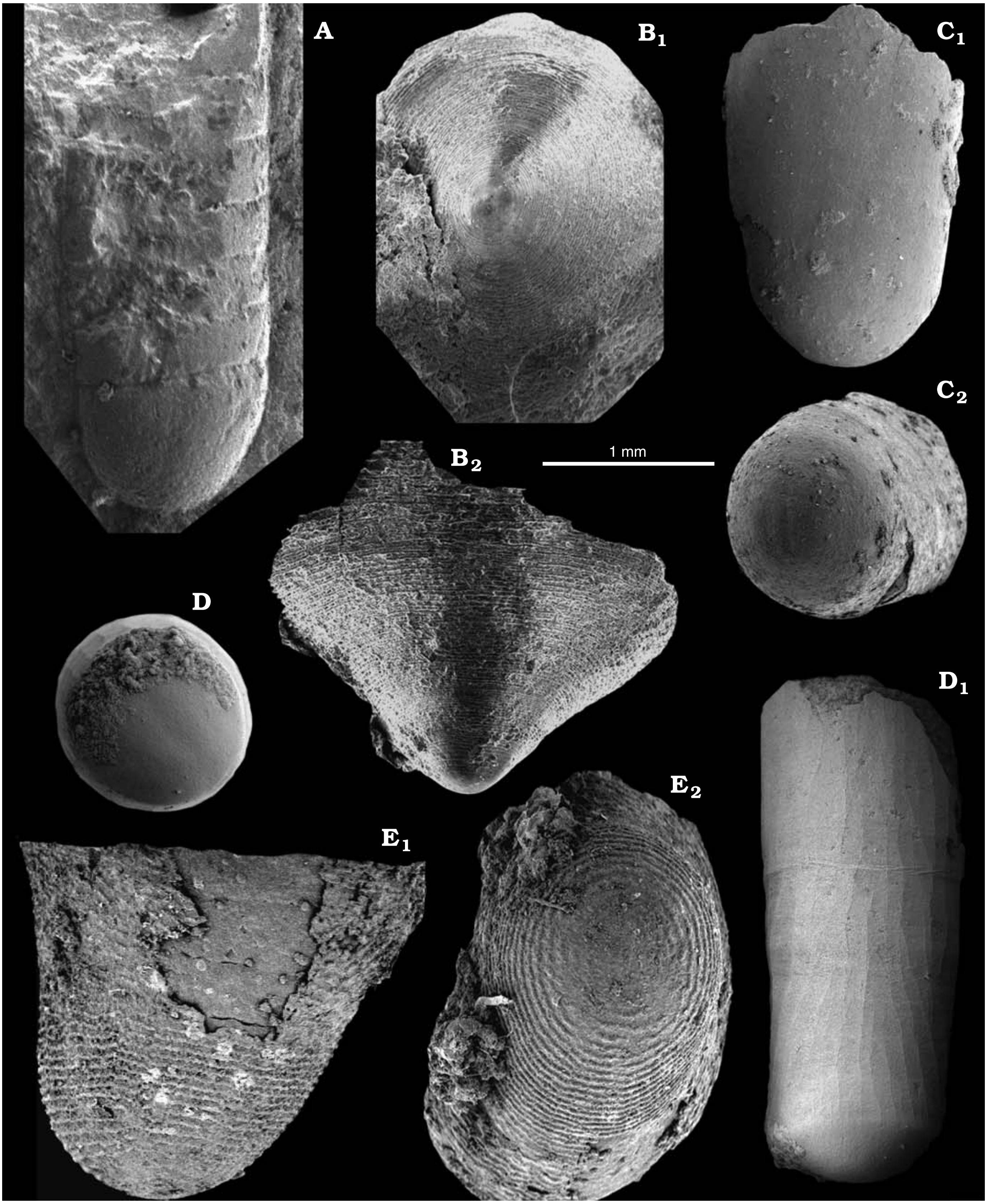

Fig. 6. Apices of cephalopods of the Siuge Member of Porkuni, Estonia. **A**. ?*Pomerantsoceras tibia* sp. nov., TUG 1227/40, internal mould of the apex. **B**. *Porkunioceras tuba* sp. nov., TUG 1227/26, apical view (B_1), lateral view (B_2). **C**. *Pomerantsoceras tibia* sp. nov., TUG 1227/43, lateral view (C_1), and apical view C_2), note the cicatrix. **D**. Ereditidae gen. et sp. indet., TUG 1227/44, apical view (D_1), note the lack of the cicatrix, lateral view (D_2). **E**. Oncoceratidae gen. et sp. indet., TUG 1227/37, lateral view (E_1), apical view (E_2).

Apex TUG 1227/147 (Fig. 6D) has oblique, flat, saucer-shaped tip with 0.9 mm diameter. Surface of apex is smooth with only very fine growth lines that form faint sinus parallel to apex tip. Sinus occurs at anti-siphuncular side, thus growth lines aperture of embryonic shell slightly bend-forward at opposite side of siphuncle. Faint shell constriction occurs at distance of about one millimetre from tip. Surface of shell is ornamented with faint, angular, kinked longitudinal ridges but otherwise smooth.

Apex TUG 1227/44 (Fig. 8) has first septum 0.7 mm from tip, second at one millimetre from tip. Less than two septa occur at distance similar to cross section. Septal curvature is very shallow. Septal necks are very short loxochoanitic-achoanitic. Siphuncle position is eccentric. Septal perforation is 0.1 of conch cross section. Thin episeptal deposits occur at prosiphuncular side.

Remarks.—The specimens described above are assigned to the same species because of the similarity of internal characters. In all the specimens, the septal necks are achoanitic or nearly so, the siphuncle is subcentral, and the septa have a very shallow concavity. In fragments displaying later growth stages, remnants of the connecting rings are preserved. The siphuncular segment of these specimens is very conspicuous, having a more expanded side in direction toward the prosiphuncular conch margin. The septal spacing and the expansion rate of apical fragments are larger than that of specimens representing later growth stages. However, in many known orthoceridans the apicalmost conch is slender with wider septal distance in later growth stages.

The surface of the fragment representing later growth stages is smooth. In the contrary, the apical fragments have shallow longitudinal structures starting a few millimetres from the tip. Supposedly, these faint structures do not occur in more adolescent growth stages or are not visible because of the comparatively poor preservation of larger specimens.

Very similar apices from the earliest Silurian of Siberia have been described by Miagkova (1967: table 3, fig. 1) as *Kionoceras muyagkirum* Miagkova, 1967. These apices also show a blunt cap-shaped tip and kinked longitudinal lirae appear at some distance from the tip. Miagkova (1967: 11) described in the diagnosis of *K. muyagkirum* the septal necks as very short orthochoanitic but provides a figure (Miagkova 1967: fig 2.) that shows suborthochoanitic septal necks in later growth stages, leaving an ambiguous impression for the reader. Her assignment of the species to *Kionoceras* Hyatt, 1884 emphasizes the aspect of her figure 2, because *Orthoceras doricum* Barrande, 1868, the type species of *Kionoceras*, displays septal necks that are at the tenuous border between orthocoanitic and suborthochoanitic. However, species with very short to achoanitic septal necks occur in the same horizon that are very similar to *K. muyagkirum* with respect to the general conch shape and ornamention, such as *Malgaoceras* Miagkova, 1967, and *Mongoceras* Miagkova, 1967. The latter two display very short septal necks and expanded siphuncular segments and represent Ereditidae in the sense of Chen et al. (1981). *Malgaoceras*, *Mongoceras*, and *K. muyagkirum* represent a group of Early Silurian orthocones that are very similar to each other. They are ornamented with faint longitudinal and transverse elements or smooth; the siphuncle of these orthocones is sometimes slightly expanded, sometimes nearly tubular and the septal necks are generally very short. They are grouped in *Eridites* Zhuravleva, 1961 or *Kionoceras* Hyatt, 1884, respectively (e.g., *Kionoceras styliforme* Chen and Liu in Chen et al., 1981, and *Eriditus crassus* Chen in Chen et al., 1981). This entire group is in need of a revision. The assignation of the specimens described above within the Ereditidae emphasizes the close relationship with the kionoceratidans of Miagkova (1967) and the Chinese ereditidans.

Family Dawsonoceratidae Flower, 1962

Genus *Dawsonoceras* Hyatt, 1884

Type species: *Orthoceras annulatum* Sowerby, 1818, Wenlockian, Coalbrookdale, Shropshire, England.

Diagnosis.—Slender, circular or slightly compressed orthocones with symmetrically curved septa and straight transverse sutures. Sutures are parallel to annulation, positioned in groove of each annulation. Annulations are regularly spaced with fine transverse ornament or growth lines. Growth lines are in some species festooned. In some species, longitudinal ridges occur that may form nodes at ridges of annulations. Siphuncle is subcentral in early growth stages, central in late growth stages, narrow, but expanded within chambers. Septal necks are short suborthochoanitic to achoanitic, in advanced forms short reticulate. Incipient annulosiphuncular deposits and mural cameral deposits are known (after Kröger and Isakar 2006).

Dawsonoceras fenestratum Eichwald, 1860

1860 *Cycloceras fenestratum* sp. nov.; Eichwald 1860: 1231, 1232, pl. 48: 14a, b.

2006 *Dawsonoceras fenestratum* (Eichwald); Kröger and Isakar 2006: 156, figs. 8B, 10B, 12C, F, G (cum syn).

Material.—Eight specimens of different growth stages from the Siuge Member (Porkuni Regional Stage) of north Estonia at TUG and NMB.

Diagnosis.—*Dawsonoceras* with angle of expansion of less than ten degrees in juvenile stages. Tubular adult body chamber has diameter of approximately 25 mm. Five-six annulations occur at distance similar to shell diameter. Approximately 20 longitudinal striae occur around shell circumference, approximately fifteen growth lines or transverse striae occur per cycle of annulations. Septal necks are achoanitic. Siphuncle is subcentral, expanded within the chambers (after Kröger and Isakar 2006).

Remarks.—The species was described by Kröger and Isakar (2006) in detail. It is listed herein in order to document the entire cephalopod fauna of Porkuni.

Stratigraphic and geographic range.—Dolomitic limestones of the Siuge Member, Porkuni Regional Stage , Estonia; erratics of the same lithology, northern Germany; type specimen

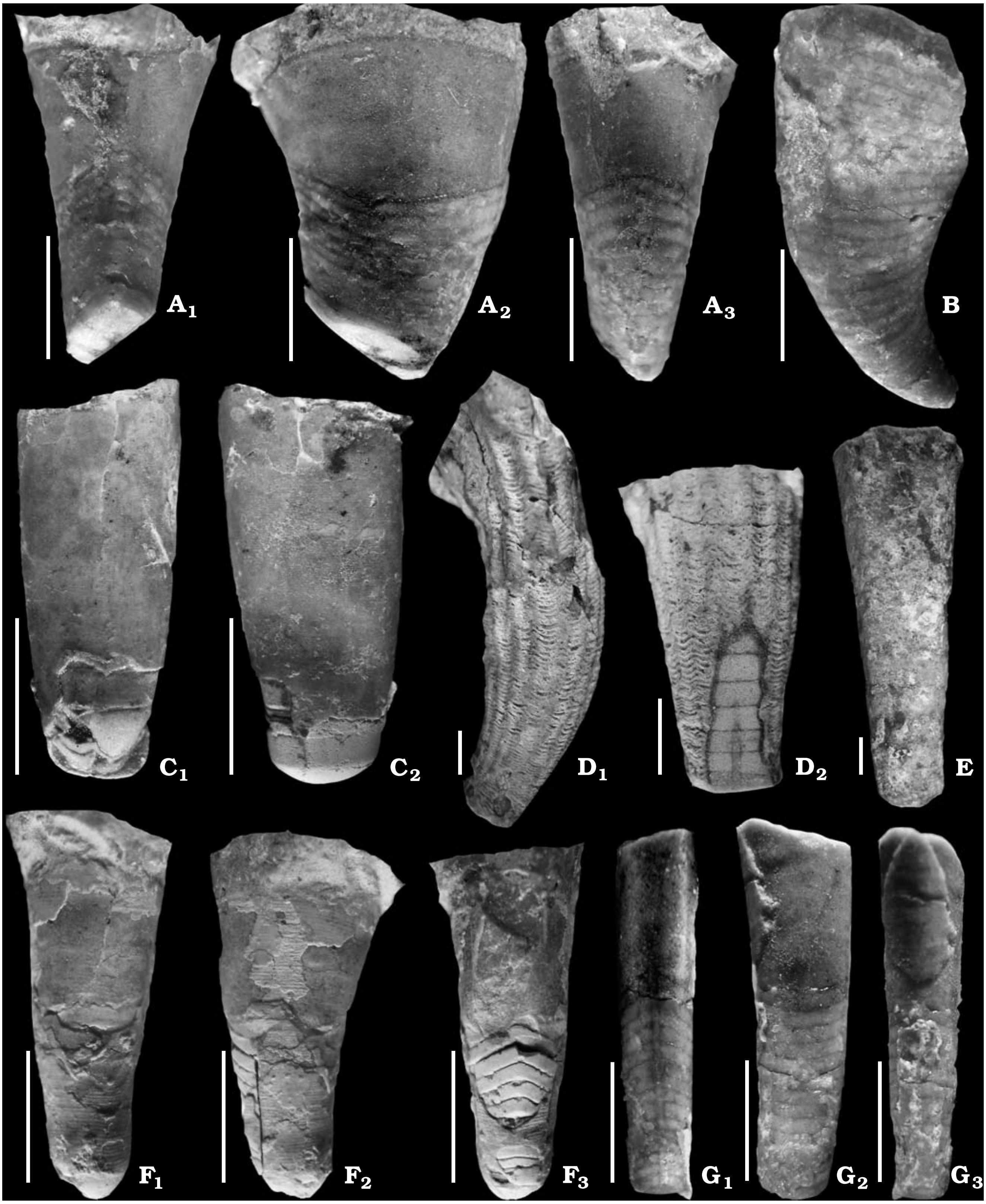

Fig. 7. Cephalopods of the Siuge Member of Porkuni, Estonia. **A**. *Strandoceras orvikui* sp. nov., TUG 1227/ 27, holotype, dorsal view (A_1), lateral view (A_2), ventral view (A_3). **B**. *Strandoceras orvikui* sp. nov., TUG 1227/28. **C**. *Parvihebetoceras wahli* sp. nov., TUG 1227/13, holotype, in lateral view, left (C_1) and right (C_2), note the convex outline of the body chamber. **D**. *Piersaloceras gageli* Teichert, 1930, TUG 1227/32, in lateral (D_1) and ventral (D_2) views. **E**. Eriditidae gen. et sp. indet., TUG 101/66a, in lateral view, see also Fig. 4A. **F**. *Porkunioceras tuba* sp. nov., TUG 1227/24, holotype, complete specimen, in dorsal (F_1), lateral (F_2), and ventral (F_3) views. **G**. *Pomerantsoceras tibia* sp. nov., TUG 1227/14, holotype, in ventral (G_1), lateral (G_2), and dorsal (G_3) views. Scale bars 5 mm.

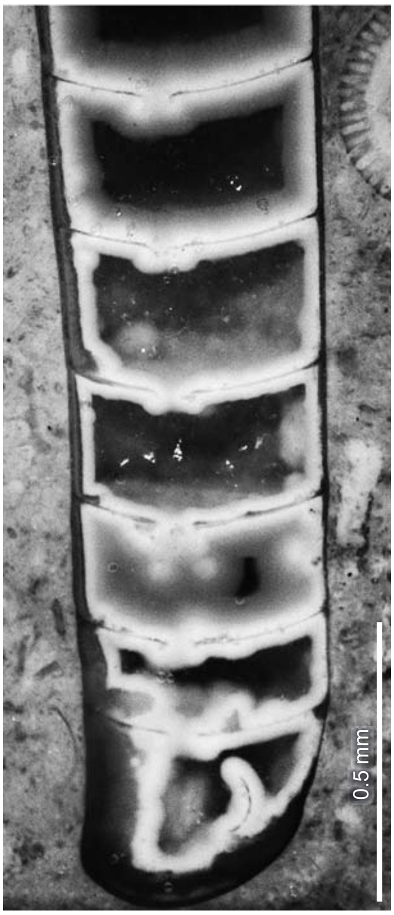

Fig. 8. Polished median section of the apex of Ériditidae gen. et sp. indet., TUG 1227/44 from the Siuge Member, Porkuni, Estonia. Note the blunt apex, the eccentric septal perforations and the achoanitic septal necks.

from Saunja Formation, Nabala Regional Stage-Kõrgessaare Formation, Vormsi Regional Stage (questionable), Late Ordovician, Mõnuste (Kirna), Estonia.

Order Ascocerida Kuhn, 1949

Family Hebetoceratidae Flower, 1941

Genus *Parvihebetoceras* nov.

Derivation of the name: From Latin *parvus*, small, referring to the small adult size of the genus.

Type species: *Parvihebetoceras wahli* sp. nov., by monotypy.

Diagnosis.—Ascocerida with orthoconic adult shell with slightly depressed or circular cross section. Apical angle of conch is low. Truncated adult shell is nearly tubular. *Parvihebetoceras* differs from all other ascoceridans in having small, truncated adult shell, displaying few closely spaced, shallow concave septa with straight, directly transverse sutures. Conch surface is smooth or ornamented with faint growth lines. Sutures adapical of septum of truncation are straight, shallowly concave, and closely spaced. Chamber height is less than one-third of cross section diameter. Septum of truncation occurs at cross section diameter of about four millimetres. Adult cross section diameter is approximately seven millimetres. Siphuncular diameter is approximately one-tenth of conch diameter. Siphuncle is positioned between centre of conch and conch margin. Siphuncular diaphragm occurs slightly adorally of the septum of truncation. Septal necks are asymmetric, more elongated at ventral side, achoanitic and suborthochoanitic in juvenile growth stages, suborthochoanitic in adult growth stages. Apex is bullet-shaped, slightly cyrtoconic, cicatrix present, with diameter at first septum approximately 1.4 mm. No endosiphuncular deposits are known.

Remarks.—The genus in consideration differs from the enigmatic *Hebetoceras* Flower, 1941, with which it is comparable because of its orthoconic truncated conch, in having a smaller adult size and a smooth shell. *Hebetoceras mirandum* Flower, 1941, the type species of *Hebetoceras* is poorly known making a more precise comparison difficult. The genus of consideration represents without doubt an ascoceratid. Evidence for this comes from the shape of the septal necks and the type of truncation. The Middle–Late Silurian *Sphooceras* Flower, 1962 differs in having a septum of truncation that is covered by a conspicuous callus and does not show the typical septal diaphragm. It is assumed that the truncated specimens represent adult individuals because the nearly completely preserved body chamber reveals a terminal constriction, which is visible as convex outline of the lateral view (Fig. 7B).

Stratigraphic and geographic range.—Siuge Member, Porkuni Regional Stage, Late Ordovician from Porkuni, north Estonia.

Parvihebetoceras wahli sp. nov.

Figs. 4C, 7C, 9.

Derivation of the name: In honour to the Estonian geologist Arwed von Wahl who collected some of the specimens mentioned here during his work in Porkuni in the 1920s (Wahl 1923).

Holotype: TUG 1227/13.

Type locality: Porkuni, north Estonia.

Type horizon: Siuge Member, Porkuni Regional Stage, Late Ordovician.

Material.—Nine specimens, displaying juvenile, adolescent and mature growth stages in collection of TUG.

Diagnosis.—Same as for genus, by monotypy.

Description.—Holotype TUG 1227/13 (Fig. 7C) is most complete fragment of collection representing complete body chamber and three chambers of phragmocone, including septum of truncation. Holotype preserves fine surface ornamentation with simple transverse growth lines with distance of 0.1 mm. Body chamber length is 12 mm, slightly bulged at most adoral one-third of fragment.

Specimen TUG 1227/41 (Fig. 9) is 5.55 mm long fragment of conch with three chambers. Apical septum, which is septum of truncation, is strongly concave, 0.19 mm thick, with anvil-shaped septal necks and septal perforation that is 0.18 mm in diameter. Siphuncular tube is thin, tubular. Diaphragm occurs at 0.6 mm adoral of septum of truncation, there, siphuncle diameter is 0.28 mm. Siphuncular tube api-

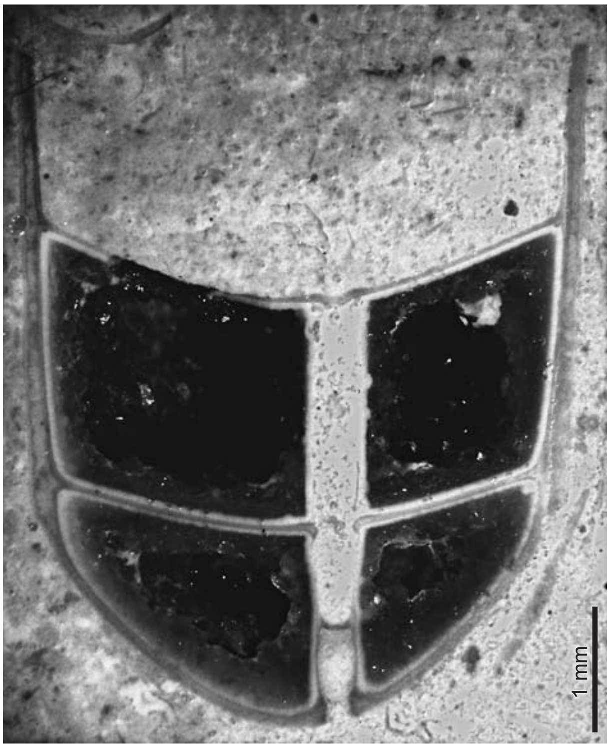

Fig. 9. Polished median section of *Parvihebetoceras wahli* sp. nov., TUG 1227/41, from the Siuge Member, Porkuni, Estonia showing the truncated part of the shell with septum of truncation and fractured outer shell. Note also the siphuncular diaphragm, 0.6 mm adoral of the septum of truncation.

cal of diaphragm is inflated. Adoral two septa are 0.03 mm thick, respectively and each septal perforation has diameter of 0.26 mm. Septal necks are thickened, suborthochoanitic. Outer shell is fractured at position of septum of truncation.

Specimen TUG 1227/12 is fragment of conch with four chambers, displaying position of septum of truncation, one adapical and one adoral septum. Length of fragment is approximately six millimetres. Cross section is circular with diameter 3.5 mm. Distance between succeeding adoral septum and septum of truncation is 1.4 mm. Distance between septum of truncation and preceding adapical septum is 1.36 mm, adoral and adapical septum have shallow curvature, septum of truncation with deep curvature. Thickness of septum of truncation is 0.12 mm, of adoral and adapical septum is 0.08 mm, shell thickness is 0.3 mm. Septal necks and remains of siphuncular tube are preserved at adoral septum. Position of siphuncle is subcentral. At cross section diameter 3.4 mm septal perforation is one millimetre from conch margin. Diameter of septal perforation is 0.3 mm (about 0.1 of cross section diameter). Remains of siphuncular tube are slightly expanded. Dorsal side of septal necks are suborthochoanitic-cyrtochoanitic with length of 0.1 mm. Sepal necks at ventral side are strongly recursive, cyrtochoanitic with length of 0.12 mm.

Specimen TUG 1227/11 is fragment of truncated conch displaying three adoral chambers. Length of fragment is 5.4 mm. Cross section is circular with four millimetres in diameter. Distance of truncated septum from succeeding adoral septum is 1.5 mm and from proceeding adoral septum is two millimetres. Truncated septum is 0.08 mm thick, cap-shaped with deep curvature (1.4 mm deep). Adoral septa are 0.04 mm thick with shallow curvature (0.3 mm deep). Shell thickness is 0.14 mm mural part of septa inclusive. Septum of truncation occurs at cross section diameter of five millimetres. Distance to succeeding youngest septum is 1.7 mm from the preceding oldest septum of fragment is one millimetre.

Additional five specimens display only two or a single septum with cross section diameter of 2–3 mm. Conch smooth with circular cross section. Specimen TUG 1227/10 (Fig. 4C) is fragment of apex with two millimetres length, 1.7 mm maximum diameter. Fragment is slightly cyrtocone. Shell of conch is smooth and very thin (>0.01 mm). Three chambers are preserved with distance between septa from apical to adoral chamber: 0.88 mm (initial chamber), 0.54 mm (second chamber), 0.42 mm (third chamber). Cross section diameter at first septum is 1.4 mm, at second septum 1.5 mm. Septa have very shallow curvature. Siphuncle is empty, subcentral with ventral side toward concave side of curvature of shell. Siphuncle is slightly expanded. Septal necks are asymmetrical with ventral side suborthochoanitic and dorsal side achoanitic. Caecum is 0.7 mm long, 0.4 mm thick, with distance of 0.12 mm from outer shell of tip. Apex is bullet shaped, slightly bent, with oblique surface of 0.7 mm and approximately 45° toward growth axis near ventral side of tip.

Remarks.—It is not known if the truncation of the shell in *Parvihebetoceras* is a single event in the ontogeny or if there are multiple truncations. However, the presence of three fragments with a septum of truncation that shows nearly identical cross section diameters at around four millimetres indicates a single event when reaching maturity.

The attribution of the apex fragment TUG 1227/10 (Fig. 4C) to the species under consideration is somewhat questionable. However, it is justified by the characteristic asymmetric shape of the septal necks and the characteristic very shallow curvature of the septa that occur in the apical fragment as well as in later growth stages. Moreover, the only known apex of Ascocerida described by Lindström (1890) in *Parascoceras* Miller, 1932, resembles the fragment of TUG 1227/10 with respect to general and siphuncular shape. The apex of *Parascoceras* is slightly cyrtocone and bullet-shaped, the siphuncle is subcentral, and septal necks are suborthochoanitic. This is similar to specimen TUG 1227/10. Furthermore, specimen TUG 1227/10 could not be attributed to any other cephalopod fragment of Porkuni. It is therefore concluded that it represents an apex of *Parvihebetorthoceras wahli* sp. nov.

The presence of a cicatrix is assumed by a very characteristic oblique surface at the tip of the apex. Such a surface is also present in *Pseudorthoceras* Girty, 1911 (Kröger and Mapes 2004) and the living *Nautilus*. This surface displays the same dimension of the lentoid structure of the cicatrix (initial shell of the conch) in *Nautilus* (compare Tanabe and Uchiyama 1997). The presence of the cicatrix in Ascocerida gives evidence for a close relationship between Ascocerida and Pseudorthocerida

Stratigraphic and geographic range.—Chert of the Siuge Member, Porkuni Regional Stage, Late Ordovician, Estonia.

Order Oncocerida Flower in Flower and Kummel, 1950

Family Oncoceratidae Hyatt, 1884

Gen. et sp. indet

Fig. 6E.

Material.—One specimen preserving the apex (TUG 1227/37).

Description.—Specimen TUG 1227/37 (Fig. 6E) is fragment of apex with total length of 0.14 mm, maximum dorso-ventral diameter of 0.16 mm, and maximum lateral diameter of 0.09 mm. Conch is strongly compressed, cyrtoconic, ornamented with transverse lirae, starting with initial diameter of 0.03 mm. Initial lira surrounds oval area that contains cicatrix with length of less than 0.03 mm. Up to 0.08 mm conch length simple lirae, spaced at distance of 5 μm and approximately 20 in number. Subsequent lirae more widely spaced, shallower, crenulated and more irregularly spaced. Only surface characters known.

Occurrence.—Cherts of the Siuge Member of the Porkuni Regional Stage, Late Ordovician of Estonia.

Remarks.—The genus and species assignation of the single fragment is impossible solely on surface characters. A similar ornamentation occurs in several other oncoceridans (see below). It may be noted that all known oncoceridans with a crenulated shell display a circular or slightly depressed cross section. Contrarily, the fragment described above is strongly compressed in cross section.

Family Graciloceratidae Flower in Flower and Kummel, 1950

Genus *Piersaloceras* Teichert, 1930

Type species: *Piersaloceras gageli* Teichert, 1930, by monotypy. Lyckholm Stage, (= Nabala, Vormsi, and Pirgu Regional Stage), Late Ordovician, Piirsalu, Estonia.

Diagnosis.—Slightly cyrtocone gracilоceratid with angle of expansion of 13°. *Piersaloceras* differs from all other Graciloceratidae in having crenulated frills and longitudinal ribs. Cross section of conch is nearly circular or slightly depressed. Adult body chamber is tubular, less curved than juvenile growth stages. Similar to other Graciloceratidea *Piersaloceras* displays thin tubular siphuncle, positioned between centre and conch margin at convex side of curvature of growth axis. Sutures are straight or with very low lobe at flanks. Septal spacing is narrow, septal curvature shallow. Septal necks are achoanitic or very short suborthochoanitic. Siphuncle is slightly expanded within chambers. No endosiphuncular deposits are known (after Teichert 1930).

Remarks.—This monotypic genus was regarded by Dzik (1984) as a junior subjective synonym of *Zitteloceras* Hyatt, 1884. However, the siphuncle of *Piersaloceras* is much further from the shell margin than that of *Zitteloceras*, and there are differences in siphuncular shape and length of septal necks that justify the generic distinction between *Piersaloceras* and *Zitteloceras*. The classification of *Piersaloceras* within the Oncocerida is disputed. The genus was originally classified within the Kionoceratidae by Teichert (1930) with regard to its characteristic ornamentation. Dzik (1984) also emphasised the ornamentation when he classified the genus within *Zitteloceras* and the Rutoceratidae. However, in the Rutoceratidae, a characteristic Devonian family, the siphuncle is invariably ventral and the septal necks are clearly longer (orthochoanitic-cyrtochoanitic, Sweet 1964). Following Balashov (1962) and Sweet (1964), *Piersaloceras* is classified within the Graciloceratidae. The characteristic features of the Graciloceratidae are an eccentric or marginal, thin, tubular siphuncle at the convex side of the conch, and a sculpture that consists of longitudinal and transverse elements. This is similar to *Piersaloceras.* The classification of the genus in consideration within the Graciloceratidae of the Oncocerida is thus fully justified.

A crenulated frilled shell similar to that found in *Piersaloceras* is developed in the Middle and Late Silurian oncoceridans *Hercocyrtoceras* Foerste 1928, *Corbuloceras* Horný, 1965, and *Torquatoceras*, Stridsberg, 1988. Additionally, a scalloped or festooned sculpture that may represent an incipient stadium of crenulated frilled shells is present in *Dawsonoceras* Hyatt, 1884 and *Cedarvilleoceras* Shimizu and Obata, 1935, *Cyrtorizoceras* Hyatt, 1900, and *Zitteloceras* Hyatt, 1884. These cephalopods, although similarly ornamented, belong to very different higher taxa of the Middle Ordovician–Middle Silurian time interval. Because of the obvious homeomorphy of this sculpture pattern, an adaptive merit of this pattern is discussed by Stridsberg (1988). However, fabricational noise or non-adaptional constraints are alternative explanations. A further discussion needs a thorough investigation of the specific sculpture pattern.

Occurrences.—Pirgu Regional Stage–Siuge Member, Porkuni Regional Stage, Late Ordovician of north Estonia.

Piersaloceras gageli Teichert, 1930

Figs. 4I, 7D.

1930 *Piersaloceras gageli* sp. nov.; Teichert 1930: 282, pl. 6: 9–10.

Type locality: Piirsalu, north Estonia.

Type horizon: Pirgu Regional Stage, Late Ordovician.

Material.—Two specimens displaying juvenile–adult growth stages (TUG 1227/32, 38).

Diagnosis.—Same as for genus, by monotypy.

Description.—Specimen TUG 1227/32 (Figs. 4I, 7D) is a fragment of juvenile—adult growth stages with maximum lateral diameter of 15.2 mm, minimum diameter 6.5 mm, and length 38 mm. Deformed conch is dorso-ventrally crushed. Shell thickness is 0.3 mm at maximum diameter. Youngest septum is 10 mm adapical of adoral margin of fragmented adult body chamber, there lateral diameter is 13.8 mm. Distance to preceding septum is 1.8 mm. Septal spacing is 0.13 of cross section diameter. Septal crowding at youngest three septa. Septal distance is 1.4 mm at cross section diameter of 6.5 mm (0.2 of cross section diameter), where siphuncular diameter is 0.5 mm (0.08 mm of cross section diameter). Tubular, thin walled siphuncle that is clearly removed from shell wall. Septal necks are achoanitic. Surface is sculptured with 20 prominent longitudinal ribs around circumference and with numerous crenulated lirae. Lirae form forward bending saddles at position of ribs, approximately four lirae per one millimetre at lateral diameter of 15.2 mm. Lirae are thin adorally imbricated shell lamellae.

Specimen TUG 1227/38 is adult body chamber with cross section diameter of 18 mm. Adult peristome is slightly bulged outward. Growth axis is nearly straight.

Remarks.—The species represents the youngest record of the genus. However, Teichert (1930: 303) already mentioned that the stratigraphic range of *Piersaloceras* probably reaches toward the "Borkholm'sche Schicht". Shell shape and ornamentation of *Piersaloceras* are very similar to *Corbuloceras* of the Bohemian Late Silurian. However, the spacing of the septa of the latter is wider, the siphuncular tube is thicker and slightly expanded within the chambers, and the siphuncle is closer to the venter in the latter.

Stratigraphic and geographic range.—Pirgu Regional Stage —Dolomitic limestones of the Siuge Member, Porkuni Regional Stage, Late Ordovician of north Estonia.

Genus *Pomerantsoceras* nov.

Derivation of the name: In honour of Marko Pomerants who is an activist in protection and restoration of natural and historical monuments of the scenic Porkuni, Estonia.

Type species: *Pomerantsoceras tibia* sp. nov., monotypic.

Diagnosis.—*Pomerantsoceras* differs from other Graciloceratidae mainly in having slowly enlarging, only sightly cyrtoconic conch which resembles orthoceratidans. Cross section is compressed with ratio conch width/height 0.8. Septal spacing is narrow with approximately 0.2–0.25 of conch height. Septal curvature is very shallow. Sutures have shallow lateral lobe. Septal necks are achoanitic. Siphuncle is marginal, positioned at convex side of conch curvature, and very thin tubular with cross section less than 0.10 of conch. Apex is spherical and cap-shaped, without constriction, with cicatrix. No endosiphuncular deposits are known. Adult conch length is approximately 20 mm.

Remarks.—The enigmatic *Michelinoceras*? *ivorense* Flower, 1946 from the Late Ordovician of Indiana, USA resembles *Pomerantsoceras* with respect to the shape of the conch and septal spacing, but its internal characters are not known.

Stratigraphic and geographic range.—Siuge Member, Porkuni Regional Stage, Late Ordovician from Porkuni, north Estonia.

Pomerantsoceras tibia sp. nov.

Figs. 4D, E, 6A, C, 7G.

Derivation of the name: From Latin *tibia*, flute, referring to the longiconic shell.

Holotype: TUG 1227/14.

Type locality: Porkuni, north Estonia.

Type horizon: Siuge Member, Porkuni Regional Stage, Late Ordovician.

Material.—Eighteen specimens displaying embryonic, juvenile, adolescent and mature growth stages in collection of TUG.

Diagnosis.—Same as for genus, by monotypy.

Description.—Holotype TUG 1227/14 (Fig. 7G) is fragment of juvenile growth stages with nearly complete body chamber and total length of 16 mm. Maximum dorso-ventral diameter is 4.7 mm, maximum lateral diameter 3.8 mm, minimum dorso-ventral diameter 2.9 mm, minimum lateral diameter 2.6 mm. Shell surface is smooth. Conch is slightly cyrtocone. Body chamber length is 7.8 mm. Last septum is at dorso-ventral diameter 3.8 mm, lateral diameter 3.2 mm. Distance between last septum and preceding septum is 0.8 mm. Siphuncle is marginal at convex side of growth axis with septal perforation of approximately 0.3 mm at last septum. Sutures form saddle at ventral side and lobe at flanks. Curvature of last chamber is 0.4 mm deep.

Specimen TUG 1227/17 is largest specimen of this species in collection. Maximum diameter of fragment is 15 mm in dorso-ventral diameter, 11 mm in lateral diameter, last chamber is at 13 mm dorso-ventral diameter.

Six fragments of apices are preserved. Apex is smooth, cap shaped and with faint cicatrix (Fig. 6C). Size of apex shows considerable variation. At second septum, dorso-ventral diameters of specimens are 0.96–1.24 mm.

Specimen TUG 1227/20 (Fig. 4E) is apex with four most apical chambers. Distances of apical septa beginning with initial septa are: 0.36, 0.2, 0.14. Dorso-ventral diameter at first septum is 1.04 mm, at second septum 1.2 mm, at fourth septum 1.24 mm. Siphuncle is tubular, marginal at convex side of growth axis curvature. Diameter of siphuncle at second septum is 0.1 mm with achoanitic septal neck. Connecting ring is thin.

Remarks.—The species is one of the most common cephalopods of the Siuge Member of Porkuni. It differs from *Porkunioceras tuba* sp. nov. in having a lower expansion rate, smooth surface and a small rounded apex.

Stratigraphic and geographic range.—Chert and dolomitised limestone of the Siuge Member, Porkuni Regional Stage, Late Ordovician from Porkuni, north Estonia.

Genus *Porkunioceras* nov.

Derivation of the name: From Porkuni, referring to the type locality.

Type species: *Porkunioceras tuba* sp. nov., monotypic.

Diagnosis.—*Porkunioceras* differs from other Graciloceratidae in having nearly straight breviconic conch with angle of expansion of approximately 10°–30° that is ornamented with transverse raised lirae. Seven transverse lirae occur at one millimetre. Genus in consideration differs from *Pomerantsoceras* in having stumpy, ornamented shell. Cross section is compressed with ratio conch width/height 0.7. Septal spacing is narrow with approximately 0.2–0.25 of shell diameter. Septal curvature is very shallow. Sutures have shallow lateral lobe. Septal necks are achoanitic. Siphuncle is marginal, positioned at convex side of conch curvature and very thin, tubular with cross section 0.10 of conch. Apex is acute. Second septum of apex occurs at cross section diameter of approximately two millimetres. No endosiphuncular deposits known. Adult length of the conch amounts to approximately 15 mm.

Occurrences.—Siuge Member, Porkuni Regional Stage, Late Ordovician from Porkuni, north Estonia.

Porkunioceras tuba sp. nov.

Figs. 6B, 7F.

Derivation of the name: From Latin *tuba*, tube, referring to the brevi-conic shell.

Holotype: TUG 1227/24.

Type locality: Porkuni, north Estonia.

Type horizon: Siuge Member, Porkuni Regional Stage, Late Ordovician.

Material.—One complete specimen displaying juvenile, adolescent and mature growth stages, TUG 1227/24, one apex with two chambers, TUG 1227/26 in collection of TUG.

Diagnosis.—Same as for the genus, by monotypy.

Description.—Holotype TUG 1227/24 (Fig. 7F), is nearly complete conch of adult specimen. Mature growth stage is indicated by shape of body chamber that is slightly bulged at position somewhat adoral of peristome. Peristome is straight. Total length of specimen is 13 mm, maximum dorso-ventral diameter 7.2 mm, maximum lateral diameter 4.8 mm, body chamber length 4.5 mm. Shell surface is ornamented with straight transverse, raised lirae, eight occur per one millimetre. Last septum has dorso-ventral diameter of 4.3 mm, lateral diameter 3.9 mm. Second septum is 0.8 mm from tip at cross section diameter 2.1 mm. Distance between initial and second septum is 0.4 mm. For measurements of all thirteen chambers of specimen, see Table 1. Apex is acute, shell at apex is not preserved. Siphuncle is marginal at convex side of slightly cyrtoconic growth axis, with diameter 0.2 mm at cross section diameter 2.1 mm.

Specimen TUG 1227/26 (Fig. 6B) is fragment of two apical-most chambers of shell and apex. Tip of apex is acute, like "jelly bag cap", smooth, with elevation of approximately 0.3 mm. Transverse striation starts at base of acute tip. Second septum occurs at cross section diameter of 2.2 mm measured in dorsoventral direction and 1.6 mm measured in lateral direction.

Remarks.—The fragment of the apex can easily be assigned to *Porkunioceras tuba* because the holotype is a nearly complete specimen that only lacks a part of the most apical chambers. In the holotype, a part of the apex is preserved. The apex fragment TUG 1227/26 exactly fits to the fragmented apex of the holotype.

Stratigraphic and geographic range.—Chert of the Siuge Member, Porkuni Regional Stage, Late Ordovician from Porkuni, north Estonia.

Gen. et sp. indet A.

Fig. 4G.

Material.—Three fragments of apices (TUG 1227/34, 35, 36) in the collection of TUG from Chert in the Siuge Member, Porkuni Regional Stage, Late Ordovician, Porkuni, north Estonia.

Description.—Fragment TUG 1227/34 (Fig. 4G) preserves seven apical chambers and complete body chamber of juvenile specimen. Shell is smooth. Total length is 10 mm, maximum dorsoventral diameter 6.5 mm, length of phragmocone 4.5 mm with maximum dorsoventral diameter of four millimetres. Distance between two youngest septa is 0.48 mm. Depth of curvature of septa is one millimetre. Siphuncle is at convex side of shell, close to margin (0.26 mm from margin at youngest septum), tubular with septal perforation at youngest septum with diameter 0.24 mm. Septal necks are achoanitic. Initial septum occurs at distance of 0.16 mm from tip. Initial septal perforation is 0.3 mm wide with achoanitic septal neck. Caecum with diameter 0.34 mm touches shell wall 0.36 mm adapically from initial septum. Septal distance of entire chambers of fragment see Table 1.

Remarks.—The fragments of consideration provide not enough information for a proper species assignation. However, the shape and position of the siphuncle, and the shape of the siphuncular necks allow an assignment to the Graciloceratidae.

Gen. et sp. indet. B.

Fig. 4F.

Material.—One complete specimen, TUG 1227/25, displaying embryonic and juvenile growth stages, in the collection of TUG from Chert in the Siuge Member, Porkuni Regional Stage, Late Ordovician, Porkuni, north Estonia.

Description.—Fragment represents apical part of nearly complete juvenile specimen with length of six millimetres. Shell is slightly cyrtocone, smooth, with compressed cross section, maximum lateral diameter is 1.8 mm, maximum dorsal-ventral diameter 2.5 mm. Post-apical angle of expansion (measured from 3–9 septum) is 8.41. Diameter is 0.7 mm at position 4.75 mm from apex and 0.15 mm at position one millimetre from apex. Shell thickness at apex is 20 μm, at position 4.75 mm from apex 40 μm. Thickness of ninth septum approximately six micrometres. Apex is blunt, cap-shaped. Septal curvature is very shallow. For information on septal spacing, see Table 1. Diameter of septal perforation at first septum is 0.12 mm, at ninth septum is 0.18 mm (0.07 of cross section diameter). Septal necks are very short suborthochoanitic with length of 60 μm at second septum. Position of siphuncle is between centre and conch margin at convex side of conch curvature. Siphuncular tube is not preserved.

Remarks.—The specimen in consideration can be assigned to the Graciloceratidae because it displays a narrow, eccentric siphuncle and very short septal necks and a breviconic shell. However a specific and generic determination is not possible at the basis of the single juvenile specimen.

Order Discosorida Flower in Flower and Kummel, 1950

Family Cyrtogomphoceratidae Flower, 1940

Genus *Strandoceras* Flower, 1946

Type species: *Protophragmoceras tyriense* Strand, 1934, Gastropod Limestone, Ashgillian, Late Ordovician, Stavnestangen, Ringerike, Norway.

Diagnosis.—*Strandoceras* is unique within Cyrtogomphoceratidae with regard to its general shell shape. *Strandoceras* is strongly compressed cyrtocone with narrowly rounded venter that is circumvented by shallow longitudinal furrow at left and right flank in direct vicinity of siphuncle. In commonality with other Cyrtogomphoceratidae, *Strandoceras* has siphuncle at concave margin of conch, sutures with shallow lateral lobe and acute ventral saddle, septal necks are short cyrtochoanitic. Siphuncular tube is thick, strongly expanded within chambers. Aperture is open with shallow peristomal saddle at flank. *Protophragmoceras* Hyatt in Zittel, 1900 differs in more symmetric siphuncular shape and non-marginal siphuncular position. Moreover, *Protophragmoceras* is less compressed and displays peristome with sharp hyponome at venter (after Flower, 1946).

Remarks.—The genus was assigned to the Cyrtogomphoceratidae by Teichert (1964). However, Dzik (1984) regarded the genus as a subjective junior synonym of *Protophragmoceras* Hyatt in Zittel, 1900 of the Phragmoceratidae. The idea of Dzik (1984) can not be followed here because *Strandoceras* clearly differs in several aspects from *Protophragmoceras* (see genus diagnosis).

Occurrences.—Middle to Late Ordovician, Baltoscandia and Wales.

Included species.—*Codoceras schmidti* Teichert, 1930, *Cyrtoceras sonax* Salter, 1866, *Phragmoceras sphynx* Schmidt, 1858, *Strandoceras strandi* Sweet, 1958, *Protophragmoceras tyriense* Strand, 1934.

Strandoceras orvikui sp. nov.

Figs. 7A, B, 10.

Derivation of the name: In honour of the Estonian geologist Karl Orviku (1903–1981).

Holotype: TUG 1227/27.

Type locality: Porkuni, north Estonia.

Type horizon: Porkuni Regional Stage, Late Ordovician.

Material.—Five specimens displaying embryonic, juvenile and adolescent growth stages in the collection of TUG.

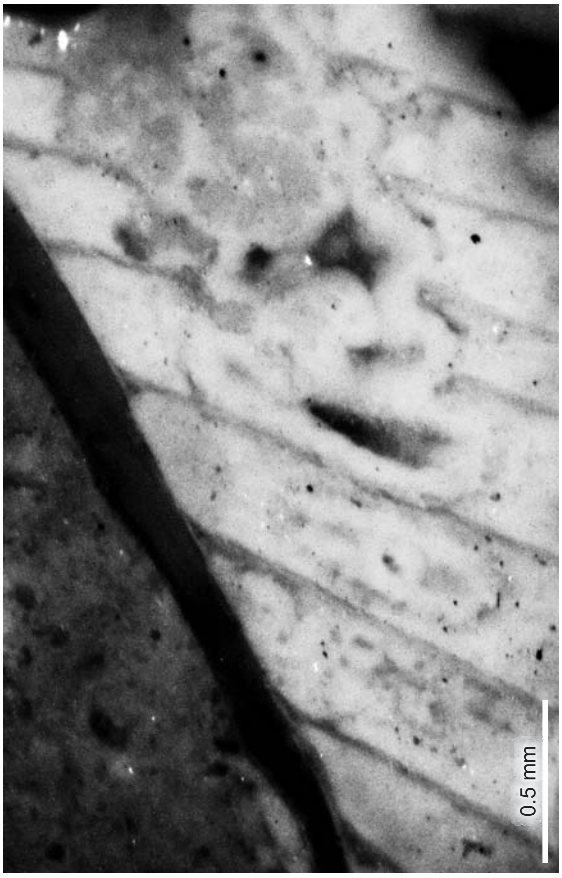

Fig. 10. Polished median section of *Strandoceras orvikui* sp. nov., TUG 1227/30 from the Siuge Member, Porkuni, Estonia showing siphuncular tube near apex. In contrast to members of the Graciloceratidae, the siphuncular tube is thick and strongly expanded between the septa.

Diagnosis.—Smooth *Strandoceras* with very high dorsoventral angle of expansion of 20–30°. Conch is strongly compressed; lateral diameter is approximately 0.7 of dorsoventral diameter. Similar as in other species of *Strandoceras* narrow longitudinal ridge occurs at concave side of conch growth axis. Septal spacing is very narrow, 0.12 of dorsoventral diameter. Siphuncular tube is approximately 0.2 of dorsoventral diameter. Apex is smooth, blunt, not constricted from juvenile conch. Second septum occurs at cross section diameter of approximately 0.24 mm.

Description.—Holotype TUG 1227/27 (Fig. 7A) is fragment of juvenile specimen with nearly complete body chamber. Entire length of specimen is 14 mm, maximum dorsoventral diameter 12 mm, maximum lateral diameter 9 mm, minimum dorsoventral diameter 6 mm, minimum lateral diameter 4 mm. Shell is smooth with faint irregular growth lines. Conch is cyrtocone. Approximately 15 longitudinal furrows occur at surface of steinkern representing internal longitudinal ridges at shell. Peristome has shallow hyponomic sinus and shallow saddle at flanks (with 1.4 mm elevation). Complete body chamber length is 6 mm. Last septum occurs at dorsoventral diameter 9.6 mm, and lateral diameter 6.5 mm. Distance between last septum and preceding septum is 0.5

mm. Siphuncle is marginal at concave side of conch with diameter of approximately 1 mm at 6 mm dorso-lateral diameter. Sutures form sharp saddle at ventral side and lobe at flanks. Curvature of last chamber is 1.2 mm deep.

Specimen TUG 1227/28 (Fig. 7B) is fragment of most apical 18 mm of juvenile conch with maximum dorso-ventral diameter 11.3 mm, maximum lateral diameter 7 mm. Septal distance at maximum diameter is 1.3 mm. Shell at apex has faint irregularly spaced growth lines. Internal mould of shell has several longitudinal ridges representing impressions of longitudinal furrows at inner shell surface.

Specimen TUG 1227/30 (Fig. 10) is a fragment of most apical 14 chambers of phragmocone. Fragment has length of 4.6 mm, maximum dorso-ventral diameter 5.5 mm, distance from initial septum to apex is 0.04 mm, distance from initial septum to second septum is 0.03 mm, there, dorsoventral diameter measures 0.24 mm. For information about septal distances of entire specimen see Table 1. Septal perforation at position of maximum dorsoventral diameter of fragment is 0.6 mm. Diameter of siphuncular tube between youngest preserved chambers is 0.9 mm.

Specimen TUG 1227/29 is fragment of juvenile specimen with eight chambers and incomplete body chamber. Length of fragment is 6 mm, maximum dorsoventral diameter 5.3 mm, thickness of shell wall is 0.08 mm, thickness of septa 0.02 mm. Septal spacing is 0.28–0.44 mm, see Table 1. Dorsoventral diameter at youngest septum is 3.1 mm, there septal perforation measures 0.4 mm and maximum diameter of siphuncular tube is 0.6 mm. Septal necks are achoanitic. Siphuncle is inflated between chambers. Connecting ring is thick.

Occurrences.—Chert and dolomitised limestone of the Siuge Member, Porkuni Regional Stage, Late Ordovician from Porkuni, north Estonia.

Palaeoecological setting

The cephalopod association of the dolomitised limestone differs from that of the cherts. *Dawsonoceras fenestratum* (Eichwald, 1860), and *Piersaloceras gageli* (Teichert, 1930), are invariably known from the dolomitised limestone, whereas all other species, except *Strandoceras orvikui* sp. nov. and *Pomerantsoceras tibia* gen. et sp. nov. are only known from the chert nodules. Taphonomic processes, effects of preservation and differences in the original microhabitat may have caused these differences. In the dolomitised limestones, fragments of larger organisms such as large brachiopods, fragments of nearly adult *Dawsonoceras fenestratum* or fragments of larger gastropods commonly occur. These usually small fragments of larger organisms are interpreted as evidence for high transport energy or strong bio-erosion in the dolomitised limestones. Fragments of larger shells are absent in the chert nodules. Alternately, the chert nodules contain masses of skeletal remains of small organisms (<10 mm) lacking any traces of abrasion and even the most fragile skeletons of bryozoans are perfectly preserved. The absence of fragments of larger organisms and of traces of abrasion on fragile skeletons of bryozoans or at cephalopod apices excludes high-energy transportation over long distances of the chert fossils. Therefore, the cherts are interpreted as local, autochthonous accumulations of skeletons of small organisms within protected areas of the palaeo-surface of the Siuge Member. The chert is concentrated in the niches of morphological depressions such as channel structures. It is assumed that the channel structures of the Siuge Member represent local high energetic events (such as storms or tidal currents). The topographic depressions of deactivated channels subsequently functioned as traps for the remains of the local organisms and organic matter. The concentration of small organisms and siliceous material was by high probability the source of the chert nodules. Quick fossilisation within the cherts provided the excellent preservation. Consequently, the cherts are interpreted as local microhabitats of low current energy in a shallow water (above storm wave base) depositional setting with generally high current energy (compare also Oraspõld 1975; Nestor and Einasto 1997). The Siuge Member in general represents an inter-reef, or back-reef environment (Hints et al. 2000) within a sub-tropical palaeogeographic position (Cocks and Torsvik 2004).

This sedimentological interpretation has consequences for the interpretation of the cephalopod association found in the Siuge Member. The large cephalopods have been reworked and do not necessarily represent autochthonous elements. In contrast, the small conchs found in the cherts are regarded as remnants of the original inhabitants of the water column above the sediments deposited in topographic traps with a low energy microhabitat. The lack of fragments of larger specimens is interpreted as reflecting patterns of the original local faunal composition. The majority of the specimens found in the cherts are juvenile or embryonic conchs. Other specimens, however, such as *Parvihebetoceras wahli* sp. nov., *Porkunioceras tuba* gen. et sp. nov., and *Strandoceras orvikui* are cephalopods with a very small adult size. Therefore, the cephalopod fauna of the cherts of the Siuge Member can be regarded as a palaeo-habitat of juvenile and minute cephalopods probably reflecting a protected environment that is occasionally affected by strong currents or water turbulences by storms, in a back-reef or inter-reef setting.

Palaeogeographical implications

Only two genera (*Dawsonoceras* Hyatt, 1884, *Strandoceras* Flower, 1946) and none of the species of Porkuni are reported from elsewhere outside of Baltoscandia; this makes the cephalopod association of Siuge Member very distinctive.

The majority of Porkuni cephalopods are oncoceridans. Oncoceridans are a major component also in Late Ordovician associations of northwestern Europe (Evans 1993), eastern North America (Flower 1946; Frey 1995) and in Kazakhstan (Barskov 1972). In northwestern Europe and in eastern North America, however, proteoceridans and endoceridans,

Table 2. Taxonomic rates of the Ashgillian cephalopods based on Sepkoski (2002). Excluded "wastebasket-taxa" are e.g., *Michelinoceras*, *Geisonoceras*, and *Spyroceras*. Note how the exclusion of "wastebasket-taxa" reduces the survivor-rate.

	Number of cephalopod genera from Sepkoski (2002) without singletons		Number of cephalopod genera from Sepkoski (2002) without "wastebasket-taxa" and singletons	
originations	3	4%	3	4%
survivers	31	39%	21	30%
extinctions	48	61%	48	70%
total genera counted	79		69	

tarphyceridans, and in Kazakhstan proteoceridans occur freuently beneath oncoceridans. Endoceridans, actinoceridans, proteoceridans, and tarphyceridans lack completely in Porkuni. This fact is interpreted as an effect of the exceptional palaeoecological setting of the Porkuni outcrop in a shallow water inter-reef complex.

The reduced diversity of the Porkuni fauna may also reflect the exceptional time interval within the Hirnantian *Normalograptus extraordinarius* Biozone. However, highly diverse nautiloid faunas that commonly contain endoceridans and tarphyceridans are known from strata representing highest Richmondian in the Saluda and Whitewater Formations as well as from strata that directly overlay these formations (Robert C. Frey, personal communication 2006). It is not clear if these strata represent the *N. extraordinarius* Biozone making direct comparisons difficult. Nevertheless, the much more diverse North American nautiloid fauna at the end of the Ordovician suggests that the distinctive Porkuni fauna represents an exceptional palaeoecological setting.

Comparison of taxonomic rates

The taxonomic compendium of Sepkoski (2002) counts 110 cephalopod genera in the Ashgillian worldwide. When correcting this number by subtraction of "singletons" and "wastebasket-taxa" such as *Michelinoceras* Foerste, 1932, *Geisonoceras* Hyatt, 1884, *Kionoceras* Hyatt, 1884, or *Spyroceras* Hyatt, 1884, sixty-nine Ashgillian genera remain. 70% of these cephalopods became extinct at the end of the Ordovician whereas 30% survived (Table 2). Twelve genera are reported from the Siuge Member of Porkuni. Of these genera, only *Dawsonoceras* and *Strandoceras* are known from time intervals older or younger than Ashgillian. *Dawsonoceras* is a characteristic Silurian taxon, whereas *Strandoceras* is known only from the Ordovician. These genera together represent only 16% of the Porkuni cephalopod genera. The only survivor of the end-Ordovician event that occurs in Porkuni is *Dawsonoceras*; which is 8% of the Porkuni fauna in terms of genera richness. Worldwide, 30% of nautiloids are known to have survived the crisis. Thus, in contrast to the predictions deduced from evolutionary patterns of rugose corals (Webby 2004), the Porkuni cephalopods were not dominated by survivors of the end-Ordovician event or forms that became important in the Silurian. The cephalopods of Porkuni represent a highly endemic and stratigraphically very distinctive fauna.

Conclusion

The fossil association of the cherts of the Siuge Member of the Porkuni Regional Stage in Porkuni reflects a concentration of autochthonous cephalopods. The majority of Porkuni cephalopods are juvenile shells (many of them completely preserved) and small adults.

The taxonomic classification and comparison of the Porkuni cephalopods has difficulties, because in Porkuni, preferentially juvenile specimens and small taxa occur which are unknown from elsewhere. Thus, many of the discovered specimens can only be assigned to open nomenclature. Because of the excellent preservation, however, it is possible to distinguish between a variety of genera and species. The investigated fauna is stratigraphically and palaeogeographically very distinctive. Only two genera out of twelve are known from outside Baltoscandia. In contrast to my initial hypothesis, expressed in the introduction, the cephalopod fauna of Porkuni do not represent a fauna that is dominated by potential survivors of the end-Ordovician event or by nautiloid lineages that became important in the Silurian.

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References

Anstey, R.L., Pachut, J.F., and Tuckey, M.E. 2003. Patterns of bryozoan endemism through the Ordovician–Silurian transition. *Paleobiology* 29: 305–328.

Balashov, E.G. [Balašov, E.G.] 1953. Stratigraphic distribution of Nautiloidea in the Ordovician of the Baltic Area [in Russian]. *Trudy Vsesoûznogo Neftânogo Naučno-Issledovatel'skogo Geologo-Razvednonogo Instituta* 78: 197–216.

Balashov, E.G. [Balašov, E.G.] 1962. Order Ellesmeroceratida [in Russian]. *In*: V.E. Ružencev (ed.) *Osnovy Paleontologii*, 73–77, Isdatel'stvo Akademii Nauk SSSR, Moskva.

Barrande, J. 1865–74. *Système Silurien du centre de la Bohême, I.ère partie, Recherches Paléontologiques, vol. II, Classe de Mollusques, Ordre des Céphalopodes*. 804 pp. Charles Bellmann, Prague.

Barskov, I.S. 1972. *Posdneordovikskie i silurijskie golovonogie mollûski Kasachstana i Srednej Asii*. 109 pp. Izdatel'stvo Akademii Nauk SSSR, Moskva.

Brenchley, P. 2004. End Ordovician Glaciation. *In*: B. D. Webby, F. Paris, M.L. Droser, and I.G. Percival (eds.), *The Great Ordovician Biodiversification Event*, 81–83. Columbia University Press, New York.

Bruguière, J.G. 1789. Histoire naturelle des vers. Volume 1, part 1, *Encyclopedie methodique* 6: 1–757. Paris.

Chen, J.-Y., Liu G-Wu, and Chen T.-E. 1981. Silurian nautiloid faunas of central and southwestern China [in Chinese with English abstract]. *Memoirs of the Nanjing Institute of Geology and Palaeontology* 13: 1–104.

Cocks, L.R.M. and Torsvik, T.H. 2004. Major terranes in the Ordovician. *In*: B.D. Webby, F. Paris, M.L. Droser, and I.G. Percival (eds.), *The Great Ordovician Biodiversification Event*, 61–67. Columbia University Press, New York.

Dzik, J. 1984. Phylogeny of the Nautiloidea. *Palaeontologia Polonica* 45: 3–203.

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

Evans, D.H. 1993. The cephalopod fauna of the Killey Bridge Formation (Ordovician, Ashgill), Pomeroy, County Tyrone. *Irish Journal of Earth Sciences* 12: 155–189.

Flower, R.H. 1940. The superfamily Discosoridea (Nautiloidea). *Bulletin of the Geological Society of America* 51: 1969–1970.

Flower, R.H. 1941. Development of the Mixochoanites. *Journal of Paleontology* 15: 523–54.

Flower, R.H. 1946. Ordovician cephalopods from the Cincinnati region. Part 1. *Bulletins of American Paleontology* 29: 3–547.

Flower, R.H. 1962. Notes on the Michelinoceratida. *New Mexico Institute of Mining and Technology. State Bureau of Mines and Mineral Resources, Memoir* 10: 21–40.

Flower, R.H. and Kummel, B. 1950. A classification of the Nautiloidea. *Journal of Paleontology* 24: 604–616.

Foerste, A. F. 1928. Cephalopoda. *In*: W.H. Twenhofel (ed.), Geology of Anticosti Island. *Geological Survey of Canada, Memoir* 154: 257–321.

Foerste, A.F. 1932. Black River and other cephalopods from Minesota, Wisconsin, Michigan, and Ontario (Part 1). *Journal of Scientific Laboratories of Denison University* 27: 47–36.

Frey, R.C. 1995. Middle and Upper Ordovician nautiloid cephalopods of the Cincinnati Arch region of Kentucky, Indiana, and Ohio. *U.S. Geological Survey Professional Paper* 1066-P: 1–126.

Hints, L., Oraspõld, A., and Kaljo, D. 2000. Stratotype of the Porkuni Stage with comments on the Röa Member (Uppermost Ordovician, Estonia). *Proceedings of the Estonian Academy of Science, Geology* 49: 177–199.

Horný, R. 1965. *Corbuloceras* gen. n., nový onkoceroidní hlavonožec (Cephalopoda, Oncocerida) z českého siluru. *Časopis Narodního Muzea, oddíl přírodovědný* 134: 132–137.

Hyatt, A. 1883–84. Genera of fossil cephalopods. *Proceedings of the Boston Society of Natural History* 22: 253–338.

Hyatt, A. 1900. Cephalopoda. *In:* K.A. Zittel and C.R. Eastmann (eds.), *Textbook of Palaeontology. Volume 1*, 502–592, Macmillan and Co., Limited, London.

Jaanusson, V. 1976. Faunal dynamics in the Middle Ordovician of Balto-Scandia. *In*: M.G. Bassett (ed.), The Ordovician System. *Proceedings of a Palaeontological Association Symposium, Birmingham, September 1974*, 301–326. University of Wales Press, Cardiff.

Kiselev, G.N., Sinicyna, I.N. [Siničyna, I.N.], and Isakar, M.A 1990. *Atlas mollûskov verhnego ordovika i silura severo-zapada Vostočno-Evropejskoj platformy*. 80 pp. Izdatel'stvo Leningradskogo Universiteta, St. Petersburg.

Kröger, B. and Isakar, M. 2006. Revision of annulated orthoceridan cephalopods of the Baltoscandic Ordovician. *Mitteilungen aus dem Musem für Naturkunde in Berlin, Geowissenschaftliche Reihe* 9: 137–163.

Kröger, B. and Mapes, R.H. 2004. Lower Carboniferous (Chesterian) embryonic orthoceratid nautiloids. *Journal of Paleontology* 78: 560–573.

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

Kuhn, O. 1949. *Lehrbuch der Paläozoologie.* 326 pp. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Lindström, G. 1890. The Ascoceratidae and the Lituitidae of the Upper Silurian formation of Gotland. *Kungliga Svenska Vetenskaps-Akademiens Handlingar* 23 (12): 1–54.

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

Miller, A.K. 1932. The mixochoanitic cephalopods. *University of Iowa Studies, Studies in Natural History* 14 (4): 1–67.

Mjagkova, E.I. [Mâgkova, E.I.] 1967. *Silurijskie nautliloidei Sibirskoj platformy*. 56 pp. Izdatel'stvo Nauka, Moskva.

Münster, G., Graf zu 1840. Die Versteinerungen des Uebergangskalkes mit Clymenien und Orthoceratiten von Oberfranken. *Beiträge zur Petrefacten-Kunde* 3: 33–121.

Murchison, R.I. 1839. *The Silurian System Founded on Geological Researches in the Counties of Salop, Hereford, Padnor, with Descriptions of the Coal Fields and Overlying Formations*. 768 pp. John Murray, London.

Nestor, H. and Einasto, R. 1997. Ordovician and Silurian carbonate sedimentation basin. *In*: A. Raukas, and A. Teedumäe (eds.), *Geology and Mineral Resources of Estonia*, 192–204. Estonian Academy Publishers, Tallinn.

Oraspõld, A. 1975. On the lithology of the Porkuni Stage in Estonia [in Russian]. *Tartu Riikliku Ülikooli Toimetised Töid geoloogia alalt VII* (*Acta Commentatis Universitat Tartuensis*) 359: 33–75.

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

Salter, J.W. 1866. An Appendix on the Fossils, with Plates. *In*: A.C. Ramsay (ed.), The Geology of North Wales with Map and Sections. *Memoirs of the Geological Survey of Great Britain and the Museum of Practical Geology in London* 3: 239–381.

Schmidt, F. 1858. Untersuchungen über die Silurische Formation von Ehstland, Nord-Livland und Oesel. *Archiv für die Naturkunde Liv-, Ehst- und Kurlands, Serie 1 (Mineralogische Wissenschaften, nebst Chemie, Physik und Erdbeschreibung)* 2: 1–248.

Sepkoski, J.J. Jr. 2002. A compendium of fossil marine animal genera. *Bulletins of American Paleontology* 363: 1–560.

Shimizu, S. and Obata T. 1935. New genera of Gotlandian and Ordovician nautiloids. *The Journal of the Shanghai Science Institute, section 2*, 2: 1–10.

Strand, T. 1934. The Upper Ordovician cephalopods of the Oslo Area. *Norsk geologiske Tidsskrift* 14: 1–117.

Stridsberg, S. 1988. A Silurian cephalopod with a reinforced frilled shell. *Palaeontology* 31: 651–66.

Stumbur, H. 1956. Nautiloidea of the Kokhila Stage (Upper Ordovician of the Baltic Area) [in Russian]. *Tartu Riikliku Ülikooli Toimetised* 42: 176–185.

Sweet, W.C. 1958. The Middle Ordovician of the Oslo region of Norway. 10. Nautiloid cephalopods. *Norsk geologiske Tidsskrift* 31: 1–178.

Sweet, W.C.1964. Oncocerida. *In*: C. Teichert (ed.), *Treatise on Invertebrate Paleontology, Part K, Mollusca 3*, K277–K319, Geological Society of America and the University of Kansas Press, Boulder, Colorado.

Tanabe, K. and Uchiyama, K. 1997. Development of the embryonic shell structure in *Nautilus*. *Veliger* 40: 203–214.

Teichert, C. 1930. Die Cephalopoden-Fauna der Lyckholm-Stufe des Ostbaltikums. *Paläontologische Zeitschrift* 12: 264–312.

Teichert, C. 1964. Ellesmerocerida. *In*: C. Teichert (ed.), *Treatise on Invertebrate Paleontology, Part K, Mollusca 3*, K320–K342, Geological Society of America and the University of Kansas Press, Boulder, Colorado.

Troedsson, G.T. 1931. Studies on Baltic fossil cephalopods. I. On the nautiloid genus *Orthoceras*. *Lunds Universitets Årsskrift, NF 2*, 27 (16): 1–36.

Wahl, A. von 1923. Mitteilungen über die Geologie von Borkholm und seiner Umgebung. *Tartu Ülikooli juures oleva Loodusuurijate seltsi aruanded* 24 (for 1922): 23–29.

Webby, B.D., Elias, R.J., Young, G.A., Neumann, B.E.E., and Kaljo D. 2003. Corals. *In*: B.D. Webby, F. Paris, M.L. Droser, and I.G. Percival (eds.), *The Great Ordovician Biodiversification Event*, 124–146. Columbia University Press, New York.

Whiteaves, J.F. 1892. The Orthoceratidae of the Trenton limestone of the Winnipeg Basin. *Transactions of the Royal Society of Canada* 9: 77–90.

Yü, C.C. 1930. The Ordovician Cephalopoda of central China. *Palaeontologia Sinica, Series B* 1: 1–101.

Zhuravleva, F.A. [Žuravleva, F.A.] 1961. Some Paleozoic nautiloids from Podolia [in Russian]. *Paleontologičeskij žurnal* 1961 (4): 55–59.