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The Lyckholm acme of cephalopods – Review of the late Katian (Vormsi–Pirgu regional stages) Ordovician cephalopods of Estonia

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Abstract. A revision of more than 660 specimens of fossil cephalopods from the Vormsi–Pirgu regional stages (late Katian Stage), Ordovician Period, of Estonia, available from the Estonian palaeontological collections, reveals the extraordinarily high cephalopod-richness of this interval, termed "Lyckholm acme of cephalopods" herein. Ninety species can be distinguished, belonging to 35 genera, and 17 families. The high turnover between assemblages from the Vormsi and Pirgu stage strata is remarkable. Only 16 species range through both stages, where the former is dominated in abundance by tarphycerids and orthocerids, and the latter by multiceratoids, probably reflecting pronounced palaeo-environmental changes. Species abundance distributions from the main collection localities show differences in sampling practice and give evidence for potential problems in species delineation. Difficulties in the species delineation of, e.g., *Discoceras* exist because critical morphological details are commonly not preserved. A cluster analysis and comparison of the Estonian assemblage with assemblages of other regions reveals a high similarity with that of the Laurentia-palaeocontinent, a fact which suggests a possible connection of the Lyckholm-acme with the "Richmondian Invasion" of Laurentia. The revision, presented herein, is a first step toward an in-depth global-scale analysis of the spatiotemporal patterns of Katian cephalopod occurrences, in which this hypothesis could be tested. Four genera are new: *Gorbormoceras* gen. nov., *Hiiumoceras* gen. nov., *Hosholmoceras* gen. nov., *Saxbyoceras* gen. nov. 23 species are new: *Beloitoceras uuemoisense* sp. nov., *Cyrtorizoceras hariense* sp. nov., *Danoceras oviforme* sp. nov., *D. vohilaidense* sp. nov., *Deckeroceras balticum* sp. nov., *Discoceras paopense* sp. nov., *Dowlingoceras tornense* sp. nov., *Ephippiorthoceras vormsiense* sp. nov., *Gorbormoceras vohilaidense* gen. et sp. nov., *Hiiumoceras hiiuense* sp. nov., *Hosholmoceras ovalis* sp. nov., *H. triangulatum* sp. nov., *Kiaeroceras kaebliki* sp. nov., *K. ormsoense* sp. nov., *K. urgense* sp. nov., *Redpathoceras saxbyense* sp. nov., *Rizosceras teres* sp. nov., *Saxbyoceras kingpooli* gen. et sp. nov., *Striatocycloceras hosholmense* sp. nov., *Strandoceras kalevipoegi* sp. nov., *S. kohilense* sp. nov., *S. muhvi* sp. nov., *S. sulevipoegi* sp. nov. Six species are placed in new combinations: *Danoceras piersalense* (Teichert, 1930) comb. nov., *Isorthoceras luhai* (Stumbur, 1956) comb. nov., *Isorthoceras saaremense* (Balashov, 1959) comb. nov., *Gorbyoceras clathratoannulatum* (Roemer, 1861) comb. nov., *Richardsonoceras priscum* (Eichwald, 1860) comb. nov., *Schuchertoceras deformis* (Eichwald, 1860) comb. nov.

Keywords. Baltoscandia, Cephalopoda, diversification, fossil rank abundance, palaeoecology, palaeogeography.

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Introduction

Lyckholm is the historical Swedish name for today's Saaremõisa, a small village and former estate in western Estonia. Until the early 20th century, a limestone was quarried in the surroundings of the village, which was famous for its rich content of fossils. One of Estonia's classical stratigraphical units is named after it, the "Lyckholm'sche Schicht" of Schmidt (1858: 52, 134–135). In modern terms the Lyckholm strata comprise the late Katian Nabala to Pirgu regional stages of Baltoscandia (Jaanusson 1944; Hints & Meidla 1997a, 1997b).

In northern Estonia, where these strata crop out (Fig. 1), and where most of the macrofossils come from, the middle and upper parts of the Lyckholm form a bipartite, unconformity bounded unit. Its base forms a prominent karst-horizon at the top of the Saunja Formation, Nabala Regional Stage (Calner *et al.* 2010). The top is an unconformity below the onset of the Hirnantian strata of the Ärina Formation (Hints *et al.* 2005) (Fig. 2). In between these boundaries a lower argillaceous limestone layer represents the Vormsi Regional Stage and an upper pure limestone the Pirgu Regional Stage. The latter, locally contains small patch reefs.

Globally, the late Katian records a general trend of climatic cooling, although climate perturbations were drastic during this time (Melchin *et al.* 2013; Männik *et al.* 2021; Young *et al.* 2023). The climate change

Fig. 1. Map of the surface outcrop area of strata of Vormsi–Pirgu regional stages, Late Ordovician, Estonia (green area) and main sampling localities (red diamonds). Figure credits: Gennadi Baranov (Tallinn).

was associated with massive marine faunal shifts (Fortey & Cocks 2005; Stigall 2023) and eventually led to the major Hirnantian glaciations and extinction events (e.g., Finnegan *et al.* 2011; Zou *et al.* 2018; Hints *et al.* 2023).

In the Baltic region, the late Katian diversity signal shows an ambiguous pattern. The microphytoplankton-diversity peaks during the late Sandbian–early Katian stage (Keila Regional Stage) and gradually decreases toward the Hirnantian (Hints *et al.* 2010). The late Katian therefore also has been termed the "Katian prelude" (Kaljo *et al.* 2011), referring to the succeeding Hirnantian extinctions. In contrast, the diversity of brachiopods (Penny *et al.* 2022), conodonts (Kaljo *et al.* 2011), and scolecodonts (Hints *et al.* 2010) reached its peak during the latest Katian. Additionally, the interval saw a maximum expansion of metazoan dominated reefs, and carbonate mud mounds (Kröger *et al.* 2016; Levendal *et al.* 2019), and a pronounced facies differentiation on a developing carbonate platform, probably linked to the latter (Penny *et al.* 2022).

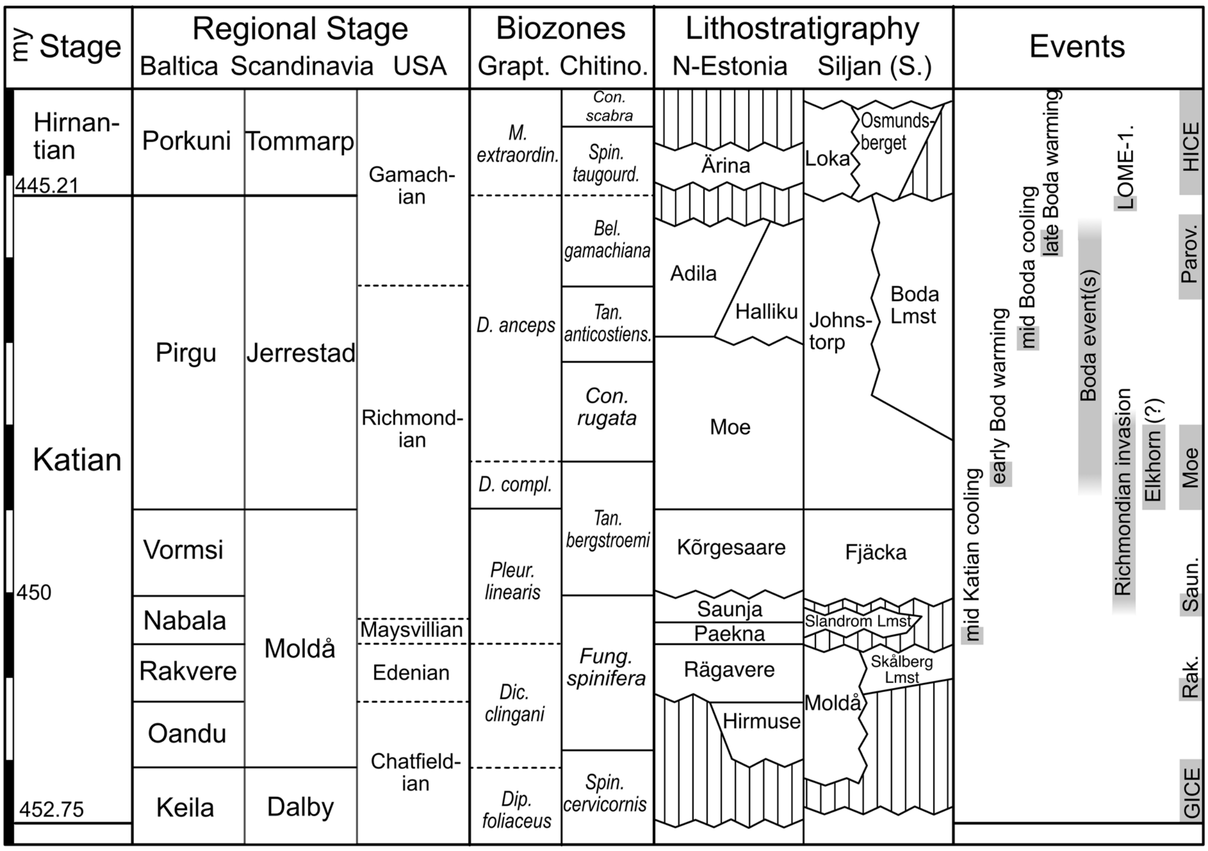


Fig. 2. Stratigraphy of the late Katian Stage, Late Ordovician Period and important events. Based on: Melchin *et al.* (2013), Goldman *et al.* (2020), McLaughlin *et al.* (2023), Meidla *et al.* (2023), Nielsen *et al.* (2023), Stigall (2023). Abbreviations: *anticostiens.* = *anticostiensis*; *Bel.* = *Belonechitina*; Chitino. = Chitonozoans; *compl.* = *complanatus*; *Con.* = *Conochitina*; *D.* = Dicellograptus; *Dic.* = *Dicranograptus*; *Dip.* = *Diplograptus*; *extraordin.* = *extraordinarius*; *Fung.* = *Fungochitina*; GICE = Guttenberg Isotopic Carbon Excursion; Grapt. = Graptoloids; HICE = Hirnantian Isotopic Carbon Excursion; Lmst = Limestone; LOME = Late Ordovician Extinction Event; *M.* = *Metabolograptus*; Moe = Moe Isotopic Carbon Excursion; my = million years ago; Parov. = Paroveja Isotopic Carbon Excursion; *Pleur.* = *Pleurograptus*; Rak. = Rakvere Isotopic Carbon Excursion; S. = Sweden; Saun. = Saunia Isotopic Carbon Excursion; Spin. = *Spinachitina*; *Tan.* = *Tanuchitina*; *taugourd.* = *taugourdeaui*.

The Katian eco-evolutionary dynamics of cephalopods during this time, however, are little understood despite the important ecological role of cephalopods as free-swimming, presumable top predators. This is also astonishing because the rich occurrence of cephalopods in the Lyckholm-limestone was already apparent when Karl Eduard von Eichwald described 29 species from these strata in his monumental "*Lethaia Rossica*" (Eichwald 1860). This was by then the most diverse cephalopod fauna known from Estonia. Curiously, this diverse fauna has never been described and revised systematically, and in its entirety. To date the most comprehensive overview of the Lyckholm-cephalopods remains the work of Teichert (1930), which was based on Teichert's own collections (kept in Frankfurt am Main and Berlin, Germany), and on collections in St Petersburg, Russia. The extensive collections of Estonian naturalists and geologists remained largely untouched, except for a few scattered descriptions of some species by Strand (1934), Stumbur (1956), and Balashov (1959).

Teichert (1930) and Strand (1934) emphasized the similarity between the Lyckholm-cephalopods and assemblages of North America and Greenland, a pattern which seems to be in contrast with, e.g., brachiopod palaeogeographic relationships of that time, which show a clear Avalonian affinity (Harper *et al.* 2013; Candela 2015).

A thorough taxonomic description provides the basis for use of cephalopods for further studies regarding the palaeogeographic and evolutionary dynamics of the Katian, and to better understand the differences and similarities among cephalopod groups. Here, based on a material of more than 600 specimens, collected by generations of Estonian geologists, including Friedrich Schmidt, Rein Einasto, Dimitri Kaljo, Heino Stumbur, Linda Hints, Mare Isakar, Gennadi Baranov, Ursula Toom, and the author, the cephalopods of the Vormsi and Pirgu regional stages are reviewed and described. A first analysis of their palaeogeographical relations and their diversity dynamics is presented herein to initiate further comparisons with other faunal groups. The large quantity of the material also allowed for an analysis of the completeness of the collection and possible collection biases.

Geological setting

The cephalopods described herein were exclusively collected in surface outcrops of limestone of the Vormsi–Pirgu regional stages of northern Estonia. These strata are part of the Lower–Middle Palaeozoic (Ediacaran–Devonian) sedimentary cover of the crystalline basement of the southern slope of the Fennoscandian Shield. They are generally affected by tectonic movements only to a very minor degree. As part of the Estonian Homocline, which is the dominant north Estonian to north Latvian tectonic structure, these strata have a generally very low (8–18°) southward dip (Puura & Vaher 1997), resulting in roughly west–east oriented outcrop belts. Accordingly, the Vormsi–Pirgu age strata form a ca 5–15 km wide outcrop belt extending over more than 250 km from northern Hiiumaa Island in the west to Lake Peipsi in the east (Fig. 1).

During the Late Ordovician this area was part of the Estonian Shelf of the Baltic palaeobasin (Meidla *et al.* 2023) on which relatively thick warm water to tropical carbonates were deposited (see, e.g., Nestor & Einasto 1997) accompanied by a widespread development of reefs (Kröger *et al.* 2016; Levendal *et al.* 2019). The sediments of the Vormsi Regional Stage are relatively homogenous throughout northern Estonia, ca 10–20 m thick, with a lower unit of argillaceous bioclastic limestone and an upper, partly glauconite rich, argillaceous limestone unit (Hints & Meidla 1997b).

The strata of the Pirgu Regional Stage form a relatively complex, up to 66 m thick (Hints & Meidla 1997a) palaeogeographic facies mosaic comprising nodular, argillaceous skeletal mud-wackestone, skeletal grainstone, patch reef structures and widespread areas with an algal rich micritic limestone (Hints *et al.* 2005). Drastic sea level drops during the Hirnantian caused widespread sedimentary hiati within the strata of the succeeding Porkuni Regional Stage (see, e.g., Ainsaar *et al.* 2015; Gul *et al.* 2021).

Material and methods

Repository

The material is deposited in the Geological Collections of Tallinn Technical University (TalTech) Department of Geology (collection acronym: GIT), the Geological Collections of the Tartu University Natural History Museum, Tartu University (collection acronym: TUG), and the Estonian Museum of Natural History, Tallinn (collection acronym: TAM). The metadata relating to the specimens, including images, are available through specimen numbers via the geoscience data platform SARV (https://geoloogia.info/). A list of all specimens and related stratigraphy and locality information is given in supplementary data 1–2, 6, and measurements taken from specimens are given in supplementary data 3–5 (Kröger 2025).

Sampling and preservation

All specimens were collected from limestone and are preserved as molds or with parts of the recrystallized, now calcitic, originally aragonitic shell. Most specimens preserve crucial details of the septal neck and connecting ring. The taphonomic compression of the specimens varies depending on the lithology. Typically, specimens, which originate from more argillaceous beds are more compressed than specimens originating from pure limestone.

A postmortem epifauna is common on the shells and consists of brachiopod attachment structures, cornulitids, tabulate corals, and abundant bryozoans, which grew partly inside the living chambers of the dead cephalopod shells. In several phragmocones imploded septa occur.

The material comprises 661 determined specimens (supplementary data 1), which were collected from 62 localities across northern Estonia. The geographic coordinates of all localities are given in the decimal degree (WGS84) coordinate system (supplementary data 2).

From most localities only few specimens are known. However, three outcrop areas were collected extensively by BK (Helsinki), Mare Isakar (Tartu), Ursula Toom (Tallinn), and Gennady Baranov (Tallinn) (Mõisaholm (Hosholm) shore, Mõisaholm (Hosholm) shore (tower locality), and Vohilaid shore) yielding assemblages large enough to compare relative abundances (Fig. 3, see below). At these localities we collected during the years 2021, 2022 systematically all cephalopod fragments, disregarding size, preservation, or taxon. The samples from all other localities are collections from multiple collectors, and from generations of scholars with different collection focuses and collection biases. The following three outcrop areas produced a major portion of the specimens, described herein:

Outcrops of Saxby shore, Vormsi Island (Fig. 3A)
The low cliff and shore near the lighthouse west of Saxby, Vormsi Island exposes 2–3 m of the upper parts of the Kõrgessaare Formation, Vormsi Regional Stage. The outcrop is the stratotype of the Vormsi Regional Stage (Rõõmusoks 1967).

The lithology and rich fossil content of the outcrop was first described in detail by Sauramo (1929), who listed a total of 46 taxa of anthozoans, brachiopods, bryozoans, mollusks, and trilobites from Saxby shore. Later, bivalves from Saxby shore were described by Isakar & Sinicyna (1985) and a rich (23 species) assemblage of ostracods was documented by Meidla (1983). Recently, Bicknell *et al.* (2024) described a cephalopod living chamber containing molted trilobite parts from Saxby shore.

Vormsi Island, and its western shores became easily accessible for Estonian geologists only since the second independence of Estonia in 1991. Since then, Saxby shore has been frequently visited by geologists and naturalists, including myself. This results in large collections from this site at SARV, amongst which those are 153 fragments of cephalopods determined herein.

Sauramo (1929) distinguished between the coastal outcrops Saxby shore (South) and Saxby shore (N), denoting a southern (S) and northern part (N). The distinction between Saxby (N) and Saxby (S) has been used ever since. Sauramo (1929) reported a total outcrop length of 2 km and an exposed thickness of 6 m. However, from Sauramo's short descriptions it is not clear where exactly the boundaries of Saxby (S) and Saxby (N) are, and how the thickness of 6 m was measured. Today, a practice has been established, in which the position of the parking spot and pier at 59.0248° N, 23.11747° E serves as the boundary between the northern and southern part of the outcrop (Fig. 3B). The Saxby lighthouse is near the northern end of the outcrop.

Until now only two sections have been published from the Saxby shore outcrop. These estimated the thickness at 1.6 m (Meidla 1983) and 2 m (Einasto 2012), respectively. Both publications distinguish between a lower more massive, and an upper more argillaceous part. Meidla (1983), based on ostracods, assigned the uppermost 0.2 m of the section to the Pirgu Regional Stage. However, it is not clear at which part of the section (S or N) this uppermost level was detected.

Jaak Nõlvak (pers. com.) sampled the uppermost part exposed at Saxby (N) near the lighthouse (probably equivalent with bed 8–9 in Fig. 4) and recovered among other microfossils *Acanthochitina barbata* Eisenack, 1931, indicative of the *A. barbata* chitonozoan-subzone, upper Vormsi Stage.

In Einasto (2012: fig. 5) a single prominent hardground was assigned as the boundary between the lower and upper parts of the section. This hardground is probably identical with the hardground at the top of bed 6, described herein (Fig. 4). The middle parts of the section, described herein (beds 4–6) are the most easily accessible (near to the parking lot) and best exposed (see also Bicknell *et al.* 2024).

Saxby (N) starts at a part of the shore ca 150 m north of the lighthouse at 59.02824° N, 23.11741° E, where the beds dip in a low angle of 2.5° toward southeast. There, the shore forms widely exposed bedding surfaces of bed 1 (Fig. 4) and the hardground at the top of bed 1. The greenish, argillaceous limestone is wavy bedded, and strongly bioturbated. At the bedding surfaces large and complex

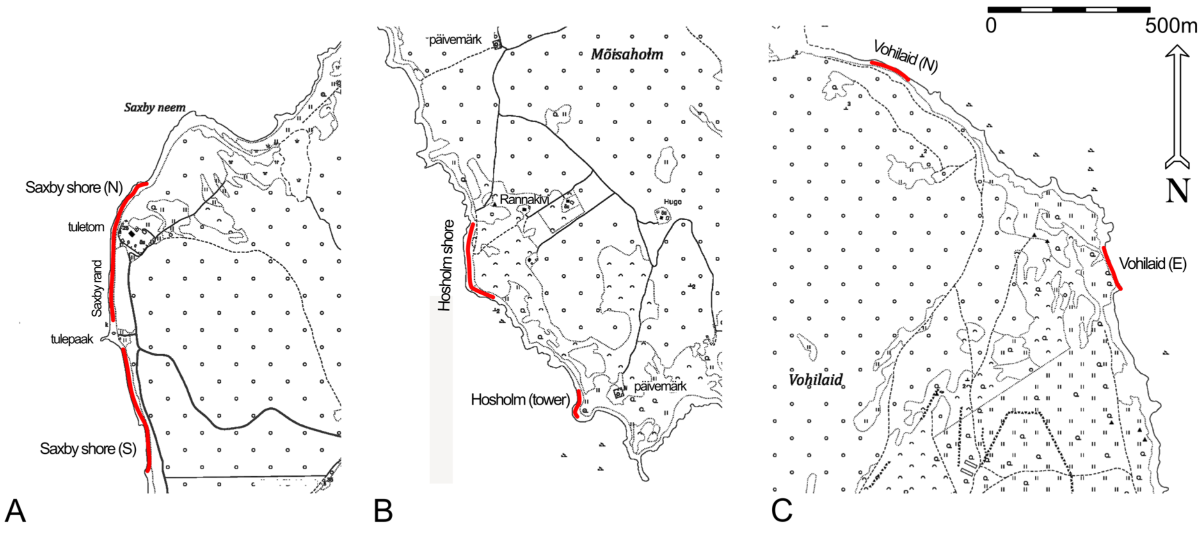


Fig. 3. Detailed localities. **A**. Saxby shore, Vormsi Island. **B**. Hosholm (Moisaholm) shore, Vormsi Island. **C**. Vohilaid shore outcrops, Vohilaid Island (marked in red). Maps are based on Estonian Basic Map 1:10 000, Estonian Topographic Database data, Estonian Land Board 2024 downloaded on 3 May 2024 from https://geoportaal.maaamet.ee/. A detailed map legend can be downloaded from https://geoportaal.maaamet.ee/docs/pohikaart/pk_legend.png

networks of *Thalassinoides* are common. On top of bed 1 four paracycles occur (beds 2–6) each with a several decimeter thick marly-silty base; becoming more massive, wavy bedded, bioturbated, greenish, argillaceous limestone toward the top, capped by a wavy to flat hardground. In the marly bases of the paracycles large lingulids (*Pseudolingula quadrata*) in life position are relatively abundant. Macrofossils (mollusks, rare tabulates, *Porambonites gigas*) are most abundant in the upper parts of the cycle, directly below the hardground surfaces. The hardgrounds are impregnated with iron and manganese, and partly heavily bored (*Trypanites sozialis*, U. Toom pers. com.). Beds 2–6 are best exposed directly below the lighthouse. From there, the two hardgrounds (top bed 5 and top bed 6) can be followed almost toward the southern end of Saxby (N). Cephalopods are most common in the upper part of bed 6. Above bed 6 a thick, wavey bedded limestone occurs with only a few inconspicuous omission surfaces. This limestone (beds 7–8) is more argillaceous and softer than the limestone-tops of the paracycles below. Pyrite-stained burrows are abundant. At ca 0.5 m above its base a several decimeter thick, almost platy bedded, marly interval occurs. Beds 7–8 continue toward the exposure of Saxby (S), but were not measured, because of poor outcrop conditions in this southern part of the outcrop. This part is generally less fossil rich, but tabulate corals and large stromatoporoids are more abundant in Saxby (S).

Outcrops of Mõisaholm (Hosholm) shore, Vormsi Island (Fig. 3B)
On the southwestern shore of the Mõisaholm peninsula (historically known under its Swedish name: Hosholm), west of Suuremõisa, Vormsi Island, the Adila Formation, Pirgu Regional Stage, is exposed in several low relief, nearly bedding-parallel outcrops. The patchiness and, generally, poor outcrop situation does not permit measurement of a section in these outcrops. Two main outcrop areas occur: a northern one, east of the Rannakivi houses, which is known in the SARV collections and in the literature (e.g., Rõõmusoks 1967) as "Hosholm shore", at 58.963019° N, 23.162005° E and a southern one near the southern tip of the peninsula west of the site of the Mõisaholmi landmark tower at 58.960617° N, 23.165817° E. The latter outcrop is termed "Hosholm tower outcrop", short Hosholm shore (tower), herein and in the SARV collections. At Hosholm tower, a thickness of less than 0.5 m is exposed, and at Hosholm shore a total thickness of not more than ca 1 m.

Fig. 4. Details of the lithological succession at Saxby (N) locality, Vormsi Island, Vormsi Regional Stage. Abbreviations: Fm = Formation; nr. = number.

The two outcrop areas have a geographic distance of ca 450–500 m, and, based on the approximate 2° N–NW dipping of the strata, they are stratigraphically ca 15 m apart within the Adila Formation. This is approximately the thickness of the Adila Formation in northwestern Estonia (up to 18 m according to Hints *et al.* 2005). The extreme southern outcrop at Hosholm shore (tower), therefore, represents the uppermost parts of the Pirgu Stage.

We (BK, Ursula Toom, and Mare Isakar) collected extensively during 2020, 2021, and 2022 at Hosholm shore and Hosholm shore (tower), concentrating on cephalopods, corals and stromatoporoids. Cephalopods were collected disregarding size, taxon, or aesthetics of the fragments. Cephalopods are most abundant at Hosholm shore (tower) where we collected and determined 92 cephalopod specimens, while corals and stromatoporoids are more common at Hosholm shore. From Hosholm shore a total of 57 cephalopod specimens could be determined.

Despite the relatively poor outcrop situation (strongly weathered bedding planes), and the lack of a detailed lithological analysis, the lithology appears to be almost identical in the two areas. It consists of a wavy bedded brownish argillaceous skeletal wackestone with weakly iron-manganese impregnated hardground surfaces, a lithology typical for the Adila Formation (see Hints *et al.* 2005). The rich and abundant tabulate-stromatoporoid assemblage from the two Hosholm localities will be described in a separate paper in the near future. Symbiotic associations between corals and cornulitids have been described from Hosholm shore samples by Vinn & Mõtus (2012) and Vinn & Wilson (2015).

Outcrops of the eastern shore of Vohilaid Island (Fig. 3C)

On Vohilaid Island, southeast of Hiiumaa, outcrops of Pirgu–Porkuni stage strata are historically known from small, now overgrown, quarries and from coastal outcrops (Stein 1937). Among the latter are two distinct outcrop areas with strata of latest Pirgu age. The northern one (point 2–3 in Stein 1937: fig. 129) (58.925267° N, 23.026817° E) is a low cliff, exposing less than one meter of a section of ca 0.3 m thick parasequences with argillaceous skeletal wackestone to skeletal grainstone lithologies and erosional tops, which are partly phosphatically to iron impregnated. The grainstone layers contain abundant brachiopods, turbid gastropods, bryozoan fragments, and trilobite carapace hash. Stein (1937) reported *Raphinesquina expansa* Holtedahl, 1916, *Platystrophia* sp., and *Chasmops eichwaldi* (Schmidt, 1881) from this northern outcrop. Rugose corals and massive colonies of tabulate corals, which will be described in a separate publication, are abundant and diverse. The occurrence of the high domical stromatoporoid *Aulacera vohilaidia* Jeon & Toom, 2024 is remarkable. *Discoceras antiquissimum* (Eichwald, 1842) and multiceratoid cephalopods occur. Based on the geological situation (Stein 1937) and the lithology the outcrop represents strata of the uppermost Pirgu to lowermost Porkuni regional stage (see also Hints & Rong 2024).

The southern outcrop area (point 8 in Stein 1937: fig. 129) is a bedding-parallel exposure of an argillaceous, wavy bedded skeletal wackestone on the shoreline, ca 900 m toward the southeast of point 2–3 (58.920072° N, 23.038717° E). Herein, this outcrop (point 8 in Stein 1937) is named Vohilaid (E). There, several areas, each forming patches of tens of meters in area, permit an extensive, nearly bedding-parallel collection of fossils. The strata contain a rich and abundant assemblage of mollusks (e.g., *Subulites*, *Maclurites neritoides*, cephalopods), domal bryozoan colonies, stromatoporoids, rugosans and tabulates. The occurrence of the giant brachiopod *Gasconsia gigantea* Hints & Rong, 2024 (Hints & Rong 2024) is remarkable. The latter, together with a unique microfossil assemblage recorded from Vohilaid (E), suggests that the strata exposed at Vohilaid (E) represent the terminal Pirgu Regional Stage (see Hints & Rong 2024).

Documentation, description, and measurement of specimens

In the Systematic Palaeontology section the Diagnosis paragraphs are followed by a short comment with reference. There, the term "adopted" refers to a diagnosis which is slightly reformulated from the original reference, the term "compiled" refers to a diagnosis which is a compilation from the original diagnosis, the description of the types and/or from illustrations of the type.

The measurements, when possible, were taken from taphonomically minimally deformed specimens or from dimensions parallel to the original bedding plane. Nevertheless, minor preservation effects could not be excluded and are thus part of the variability measurements.

The following measures were applied:

- The conch height index (CHI) is the conch height divided by the conch width. Note: this is the inverse proportional CWI of Pohle *et al*. (2022). Note also the typo in appendix 1 of Pohle *et al*. (2022: 49) where CWI should be correctly conch width divided by conch height.
- The relative body chamber length (RBL) is the mature body chamber length divided by the body chamber height at its base.
- The relative chamber length (RCL) is the chamber length divided by the chamber height.
- The relative siphuncle height (RSH) is the height of the septal foramen divided by the corresponding conch height (see also discussion in appendix 1 of Pohle *et al.* 2022: 53). The RSH is identical to the "relative siphuncle diameter" (rsd) used in Kröger & Aubrechtová (2017).
- The relative siphuncle position (RSP) is calculated as sv/(ch−fh) where sv = distance of the siphuncle from the ventral conch margin, ch = chamber height, and fh = height of the siphuncle at the septal foramen, following Pohle *et al.* (2022).
- The relative siphuncular shape (RSS) is the maximum height of the siphuncular segment divided by the corresponding fh.
- The siphuncle compression ratio (SCR) is the siphuncular height divided by the siphuncular length.
- The whorl expansion rate (WER) is calculated as $(d_{ml}/d_{ms})^2$, following Korn & Klug (2003), where d_{ml} = diameter of the conch, and d_{ms} = diameter 360° preceding d_{ml}.
- The whorl width index (WWI) is is the whorl width divided by the whorl height.

The descriptive terms and measures, if not otherwise stated, are taken from Pohle *et al.* (2022). For photography specimens were whitened with ammoniumchloride.

Taxonomy and systematics

The determination and delineation of species is difficult in some of the groups described herein. Against intuition, more material often reveals more transitional forms, which may blur the boundaries between species that were originally established on single specimens or a limited series (see also Guenser *et al.* 2022). This is especially relevant when few morphological characters (degrees of freedom) are available for comparison.

In some cephalopod genera described herein, such as *Beloitoceras* Foerste, 1924 and *Discoceras* Barrande, 1867, a large variability in conch shape is apparent and the available material does not permit statistical distinctions between previously clearly delineated morpho-groups. Here, a pragmatic approach to species delineation is followed. This is a compromise between determination effort (i.e., practicability) and maximum possible resolution (see discussion in the relevant taxon sections).

The difficulties with referring to species established by Eichwald (1860) have been previously noted (e.g., Teichert 1930, 1940). These difficulties arise because Eichwald's (1860) figures are often composites of several specimens, sometimes from different stratigraphic levels, and because the individual specimens representing the type series are incomplete and/or lost. Here, with a few exceptions (see below)

Eichwald's (1860) cephalopod species are generally disregarded for a species count. For a discussion of the unresolved species names, the reader is referred to Teichert (1930). The material, described herein, suggests that *Phragmoceras sulciferum* Eichwald, 1860 is a fragment of a phragmocone of a *Danoceras* Troedsson, 1926 or *Dowlingoceras* Foerste, 1928, and *Phragmoceras eximium* Eichwald, 1860, likely represents an indeterminate species of *Strandoceras* Flower, 1946.

Some late Katian Estonian species described in the Soviet-literature cannot be referred with certainty to other specimens than the types. This is the case for *Westonoceras estonicum* Balashov, 1959 from Vormsi–Pirgu level strata of Tapa, Estonia, which is a nearly straight fragment of a phragmocone with a widely expanded discosorid-like siphuncle. The mature body chamber and/or more apical conch parts with endosiphuncular deposits would be needed for a genus level determination and to provide sufficient features for a species level determination, because similar types of phragmocones occur in different species and genera (see below). The same is true for a specimen from late Katian strata from Vormsi described in Kiselev (1990: 47–48) as "*Cyrtogomphoceras paradoxum* (Eichwald, 1861)" [sic], which is a poorly preserved fragment of an endogastrically curved phragmocone with imploded chambers, a marginal siphuncle with slightly expanded segments and endosiphuncular bullettes. The specimen possibly represents a cyrtogomphoceratid, such as *Kiaeroceras* Strand, 1934 or *Strandoceras*, but a species level determination is impossible based on its fragmentary character. The specimen should be referred to as Multiceratoidea indet.

Species, which were previously described from Vormsi–Pirgu strata of Estonia, and which are not included in the descriptions herein because no additional material could be detected are: *Kiaeroceras* cf. *frognoyense* Strand, 1934, *Lyckholmoceras estoniae* Teichert, 1930; *Nybyoceras balticum* (Troedsson, 1926); *Orthoceras saksbyense* Teichert, 1930. A specimen of *L. estoniae* (TAM G1:365) was detected in the collections of TAM only when the main manuscript was already finished, it is the second specimen known from this species. The specimen has no locality information, and a figure is available from the SARV database (https://geoloogia. info/specimen/171547/). *Orthoceras saksbyense* (Teichert, 1930) by high probability belongs to *Geisonoceras* Hyatt, 1884 based on similar species, such as *Geisonoceras wegelini* (Angelin in Angelin & Lindström, 1880) known from the Boda limestone, Sweden. More material, preserving the external shell are needed to substantiate this suggestion.

Assemblage calculations and analyses

The diversities are estimated as coverage-extrapolated Hill numbers (species richness) using the function estimateD() of the R-Package "iNEXT" (ver. 3.01, 08/2022) (see Hsieh *et al.* 2016). There, the diversity estimates are extrapolated to double the reference sample sizes and based on the minimum coverage value (see iNext Documentation, Hsieh *et al.* 2016). Rarefaction–Extrapolation species richness curves were produced using the function iNext() of the R-Package "iNEXT".

The species abundance distribution was fit to log-series model distributions with the R-Package "sads" (ver. 0.6.3, 01/2024).

The comparison of the relative cephalopod abundance and richness among different assemblages is based on an order-level assignment that largely follows the systematic scheme of the *Treatise* (Moore *et al.* 1964) instead of the more up-to-date scheme of Pohle *et al.* (2022) (see supplementary data 1). The reason is pragmatic, because in Pohle *et al.*'s (2022) scheme a large fraction of brevicones, which are traditionally classified within the Oncocerida Flower, 1950 would be classified among the undifferentiated basal Multiceratoidea. Here, provisionally, we retain the Oncocerida (see also discussion in Pohle *et al.* 2022) for our quantitative analyses (but not in the systematic section) to better compare the differences among assemblages and only place species of the families Apsidoceratidae Hyatt, 1884, Bickmoritidae

Foerste, 1925, Plectoceratidae Hyatt, 1900, Sphyradoceratidae Foerste, 1926, Uranoceratidae Hyatt, 1900 into the wrapper "basal Multiceratoidea."

A cluster analysis of known species from different late Katian assemblages from Canada (Foerste 1928c, 1936; Sweet & Miller 1957; Nelson 1963; Holland & Copper 2008), Greenland (Troedsson 1926), Ireland (Evans 1993), Norway (Strand 1934), Sweden (Kröger 2013), and USA (Miller 1932; Foerste 1935a, 1935b; Flower 1946; Miller & Youngquist 1949) was performed using the function hclust() of the R-Package "Vegan" (ver. 2.5-7) with the "average" method (Oksanen *et al.* 2013). The clustering is based on dissimilarity indices, calculated with Vegan's function vegdist() using the Bray-Curtis index when the calculation is based on abundances (for order level clustering), and using the Raup-Crick index when the calculation is based on presence-absence data (for genus level clustering) (see Oksanen *et al.* 2013 for details of the method). The abundances (genera per order) per assemblage are normalized before clustering using the function decostand() of Vegan (i.e., their margins sum of squares is made equal to one, see Oksanen *et al.* 2013). The heatmaps were produced using the R-package ComplexHeatmaps (ver. 2.6.2) (Gu *et al*. 2016).

Results

Systematic palaeontology

Phylum Mollusca Linnaeus, 1758
Class Cephalopoda Cuvier, 1797
Subclass Endoceratoidea Teichert, 1933
Order Endocerida Hyatt, 1900
Family Endoceratidae Hyatt, 1884

Genus ***Cameroceras*** Conrad, 1842

Type species

Cameroceras trentonense Conrad, 1842, Middleville, New York, USA, Trenton Limestone, late Katian; by original designation.

Diagnosis

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. (Adopted from Teichert 1964a.)

Cameroceras hasta (Eichwald, 1857)
Figs 5A–B, 6

Endoceras hasta Eichwald, 1857: 194.
Endoceras magnum Stumbur, 1956: 182–183, pl. 3 figs 2–3, text-fig. 4.
Rossicoceras pirguense Balashov, 1968: 113, pl. 15 figs 3–4.
Endoceras novomagnum Greenfield, 2023: 1790.

Endoceras hasta – Eichwald 1860: 1247, pl. 46 fig. 7a–b.
Endoceras megastoma – Teichert 1930: 270, 273, pl. 5 fig. 1, text-fig. 2 (with synonymy).
Rossicoceras hasta – Balashov 1962a: pl. 4 fig. 4; 1968: 112, pl. 15 figs 1–2; 1974: 794, pl. 4 fig. 4. — Saladzius 1966: 36, pl. 6 fig. 2. — Dzik 1984: 35, text-fig. 7.32.
Endoceras magnum – Balashov 1968: 70.
Cameroceras hasta – Kröger 2013: 6–7, fig. 3.

Diagnosis

Smooth orthocones with a slightly depressed conch cross section; angle of expansion less than 5°; sutures directly transverse, seven or more chambers occur on a distance similar to the conch cross section; siphuncular diameter ca 0.5 of corresponding conch cross section; siphuncle slightly removed from conch wall; siphuncular segments slightly concave in lateral view; septal necks holochoanitic; endosiphocones form central spiculum. (Compiled from Balashov 1968.)

Material examined

ESTONIA • 2 specs; Hiiumaa Island, Kõrgessaare quarry; Vormsi Regional Stage; GIT 426-549, GIT 426-1111 • 4 specs; Paluküla quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-575, GIT 426-1102, 426-1104, GIT 878-127 • 1 spec.; Vormsi Island, Saxby old quarry; Kõrgessaare Formation, Pirgu Regional Stage; TUG 1745-240 • 1 spec.; Saaremõisa (Lyckholm); Kõrgessaare Formation, Vormsi Regional Stage; TUG 42-373 • 1 spec.; Vormsi Island, Saxby shore, Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-42 • 1 spec. from an unspecified locality at Vormsi Island, Kõrgessaare Formation, Vormsi Regional Stage; TUG 1650-1.

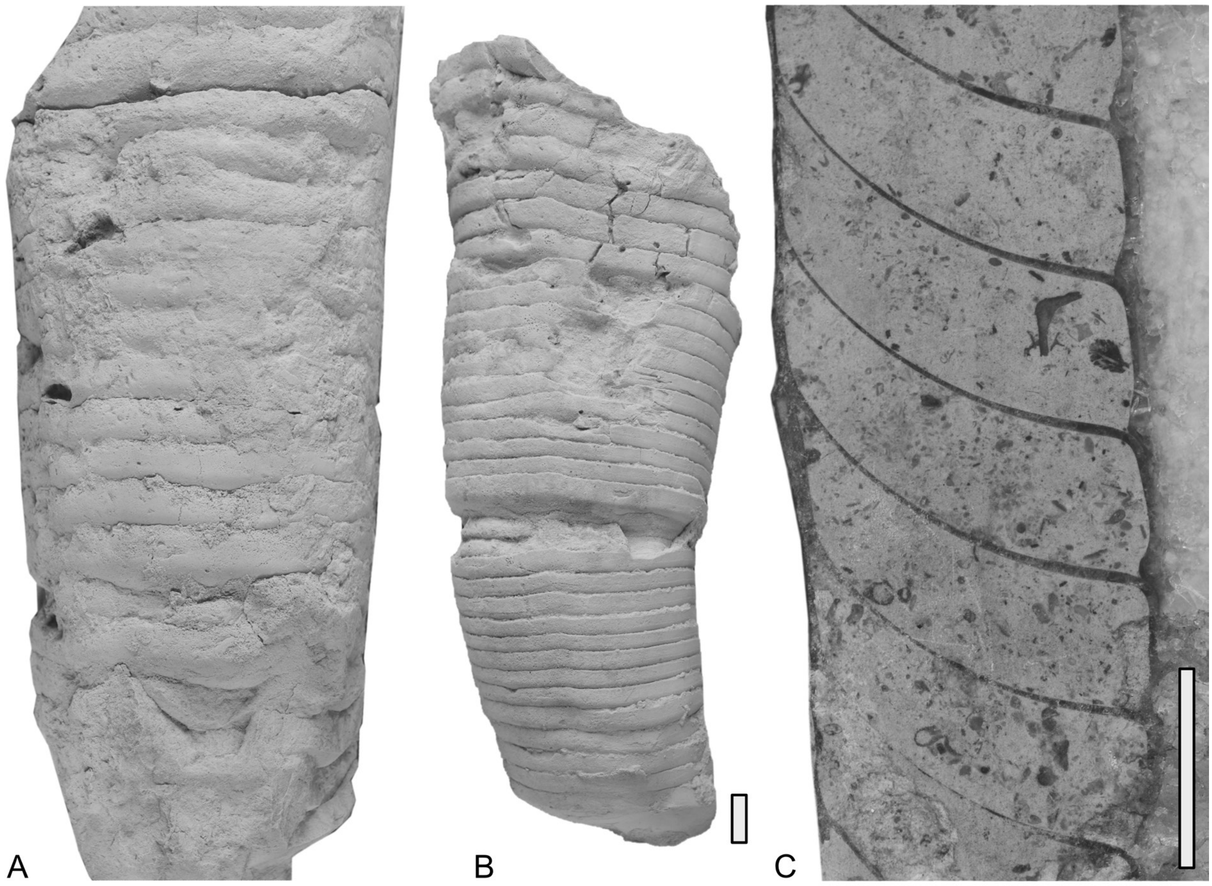


Fig. 5. Endocerida of the Vormsi–Pirgu regional stages, Estonia. **A–B**. *Cameroceras hasta* (Eichwald, 1857). **A**. Specimen TUG 42-373 from Saaremõisa (Lyckholm) old quarry, Vormsi Regional Stage, dorsal view. **B**. Dorsal view of the deformed specimen TUG 1745-240 from Saxby old quarry, Pirgu Regional Stage. **C**. *Cameroceras regulus* (Eichwald, 1860), polished median section of specimen TUG 939-75 from Nõmmeküla quarry, Vormsi Regional Stage. Scale bars = 10 mm for all figures, same scale in A–B.

Type locality and horizon

Saaremõisa (Lyckholm), N of Haapsalu, western Estonia; Kõrgessaare Formation, Vormsi Regional Stage, late Katian, Ordovician.

Description

Two specimens are relatively long, and well-preserved fragments of the phragmocone:

Specimen TUG 1745-240 (Fig. 5B) is a fragment of a phragmocone, which is slightly deformed and in which the outer shell is not preserved. The conch cross section was apparently circular. The conch height is 43–62 mm at a length of 125 mm (angle of expansion 9°). The sutures are narrowly spaced (at conch height 48 mm with chamber length of 4 mm, at conch height 62 mm with chamber length 5.5 mm, RCL = 0.08–0.09) and are directly transverse. At a conch height of 62 mm, the siphuncle is 7 mm from the conch margin, and 28 mm high (RSP = 0.21, RSH = 0.45). Where visible, the septal necks are holochoanitic. At a conch height of 45 mm, a symmetric endosiphocone is preserved, which has its tip at ca mid-height of the siphuncle, and which is ca 35 mm long. A similar symmetrical endosiphocone is preserved in specimen GIT 426-574 where the conch height is ca 50 mm, the siphuncular diameter is 21 mm. There, the cone is ca 45 mm long.

Specimen TUG 42-373 (Fig. 5A) is a well-preserved part of a phragmocone with a circular conch cross section and with parts of the smooth outer shell preserved. The conch has a diameter of 60–78 mm over a length of 110 mm (angle of expansion = 9°). The sutures are straight and directly transverse; at a conch height of 67 mm they are 8 mm apart (RCL = 0.12). The siphuncle is 33 mm heigh, where the conch height is 78 mm and positioned ca 15 mm from the conch margin (RSP = 0.33).

A compilation of measurements of the relative chamber length (RCL) and the relative siphuncular position (RSP) of the Estonian material shows the variability of respective values, resulting in a mean RCL of 0.09 (n= 10), and mean RSP of 0.24 (n = 7), respectively (Fig. 6).

Remarks

The species diagnosis given in Kröger (2013) was based on Balashov's (1968) description of the holotype, in which the latter states that in the holotype, seven chambers occur per distance similar to the conch

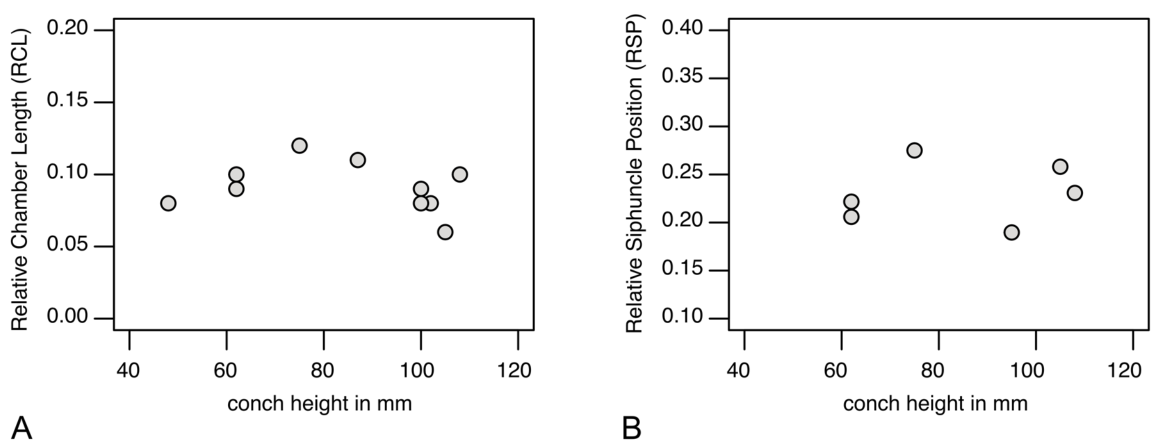


Fig. 6. Diagrams of morphological variability of specimens of *Cameroceras hasta* (Eichwald, 1857), Pirgu–Vormsi regional stages, Estonia. **A**. Relative chamber spacing (RCL). **B**. Relative siphuncle position (RSP).

cross section (RCL ca 0.14). This is in contradiction to the figured holotype (Balashov 1968: pl. 15, fig. 1), where the RCL can be measured as ca 0.11. The RCL of the measured holotype is larger than the mean of the RCL's from the material examined herein (RCL = 0.09) but still well within its variability (0.06–0.12). This applies also for the specimens assigned to *C. hasta* from the Boda Limestone, Sweden (Kröger 2013: 7). Accounting for this variability, the diagnosis given in Kröger (2013) is herein slightly emended with respect the relative chamber length.

Cameroceras regulus (Eichwald, 1860)
Fig. 5C

Endoceras regulus Eichwald, 1857: 177.
Orthoceras turris Angelin in Angelin & Lindström, 1880: 6, pl. 6 figs 14–15.
Endoceras iucundum Stumbur, 1956: 181, 182, pl. 1 fig. 4, pl. 2 fig. 1, text-fig. 3.

Endoceras regulus – Eichwald 1860:1248, pl. 46 fig. 8.
Cameroceras regulus – Balashov 1968: 70, 101, pl. 5 fig. 3. — Kröger 2013: 7–8.
Endoceras iucundum – Balashov 1968: 101.

Diagnosis

Orthocones with a slightly depressed conch cross section; angle of expansion less than 5°; ornamented with fine transverse striae; sutures directly transverse, ca seven chambers occur on a distance similar to the conch cross section; siphuncular diameter up to 0.5 of corresponding conch cross section; siphuncle marginal, in contact with shell wall; siphuncular segments slightly concave in lateral view; septal necks holochoanitic. (Adopted from Balashov 1968.)

Material examined

ESTONIA • 1 spec.; Harju County, Nõmmeküla quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 939-75.

Type locality and horizon

Kõrgesaare, Hiiumaa Island, Estonia; Kõrgessaare Formation, Vormsi Regional Stage, late Katian, Ordovician.

Description

Specimen TUG 939-75 is a fragment of a phragmocone with parts of the outer shell preserved. The conch surface is smooth. The conch cross section is circular. The conch has a height of 33–34 mm at a length of 46 mm (angle of expansion = 1.2°). At the conch height of 34 mm the chamber length is 7 mm (RCL = 0.21). The siphuncle is marginally positioned with a diameter of 16 mm where the conch height is 34 mm. The septal necks are holochoanitic and form siphuncular segments, which have in longitudinal view slightly concave outlines (Fig. 5C). The siphuncle is filled with a massive sparitic infill, which preserved no details of the internal structure of the endosiphuncular deposits.

Remarks

The specimen can be identified as a *C. regulus* based on its large marginal siphuncle and its holochoanitic septal necks.

Subclass Orthoceratoidea Teichert in Teichert & Yochelson, 1967
Order Actinocerida Teichert, 1933
Family Armenoceratidae Troedsson, 1926

Genus ***Nybyoceras*** Troedsson, 1926

Type species

Actinoceras (Nybyoceras) bekkeri Troedsson, 1926 from Niibi, Estonia, Pirgu Regional Stage, late Katian; by original designation.

Diagnosis

Slender straight shell, eccentric siphuncle; adnation areas broad ventrally on posterior side of segments; dorsally on adoral side; septal necks very short and adnate to adoral surface of septa, endosiphuncular canal system reticulate to curved, branching radial canals. (Compiled from Teichert 1964.)

Nybyoceras bekkeri Troedsson, 1926
Figs 7A, 8A–B

Actinoceras (*Nybyoceras*) *bekkeri* Troedsson, 1926: 106–107, pl. 63 figs 1–3.

Actinoceras bigsbyi Bronn aff. – Eichwald 1860: 1253–1255 (partim).
Nybyoceras bekkeri – Teichert 1930: 287–288, pl. 6 figs 7–8, pl. 7 fig. 19; 1933: 130, 149, 176; 1964a: K208, fig. 2a–c. — Foerste & Teichert 1930: 277, 279. — Strand 1934: 62. — Shimizu & Obata 1936: 119. — Balashov 1953a: 210 (faunal list only). — Teichert & Glenister 1953: 17–18. — Stumbur 1956: 176. — Flower 1957: 24. — Sweet 1958: 48. — Balashov & Zhuravlyeva 1962: 218, fig. 16, pl. 1 fig. 12. — Dzik 1984: 149, text-fig. 57.17. — Lehmann 1987: 193–194, pl. 3 figs 28–29.
Nybyoceras bekkei (sic) – Barskov 1972: 81.

Diagnosis

Nybyoceras with eccentric position of the siphuncle (RSP = 0.25), and with widely expanded siphuncular segments (SCR ca 2–2.5); incipient annuli grow in apical direction on the adoral surface of the septa; fully developed annuli are asymmetrically developed in longitudinal direction and are heavier on the ventral side. (Compiled from Teichert 1930.)

Material examined

ESTONIA • 1 spec.; Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; GIT 939-47 • 1 spec.; Vormsi Island, Saxby shore (N); Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-1129 • 1 spec.; Saaremõisa (Lyckholm); Kõrgessaare Formation, Vormsi Regional Stage; TUG 1745-227 • 1 spec.; Sutlepa quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 47-870 • 1 spec.; Paluküla quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-1107 • 1 spec.; Kasari, Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-1120. (see also supplementary data 1).

Type locality and horizon

Niibi, Estonia; Adila Formation, Pirgu Regional Stage.

Description

Specimen GIT 426-1107 (Fig. 8A) is a fragment of a phragmocone with a conch diameter of 66 mm, with a chamber length of 12 mm (RCL = 0.18) and a siphuncle, which is strongly expanded 24 mm in diameter (SCR = 2). The septal foramen is 7 mm wide. The connecting ring forms ventrally a wide (9 mm wide) area of adnation on the adoral surface of the septum and dorsally only a narrow (ca 3 mm wide) area of adnation on the adapical face of the septum. The septal necks are short and adnate. Incipient annuli grew in adapical direction and are more strongly developed on the ventral side of the conch.

Specimen GIT 426-1120 (Figs 7A, 8B) is a fragment of a phragmocone 125 mm long, and increasing in conch diameter 43–58 mm (angle of expansion= 7°), a circular conch cross section, a septal spacing with RCL of 0.2, and an RSP of 0.32. Specimen GIT 426-1129 is a fragment of a phragmocone 72 mm long, and increasing in conch diameter from 54–62 mm (angle of expansion= 6°), a septal spacing with RCL of 0.2, and an RSP of 0.23. Specimen TUG 1745-227 is a fragment of a phragmocone 78 mm long, and increasing in conch diameter 50–60 mm (angle of expansion= 7°), a septal spacing with RCL of 0.3, and an RSP of 0.33.

Remarks

The specimens assigned herein to *N. bekkeri* have an angle of expansion of 6–7°. This differs from the specimen figured in Teichert (1930: pl. 7 fig. 19), which expands with 12°. Because the angle of expansion is not known from the type-material (see Troedsson 1926), the diagnostic value of this character cannot be evaluated until more material from this species is known.

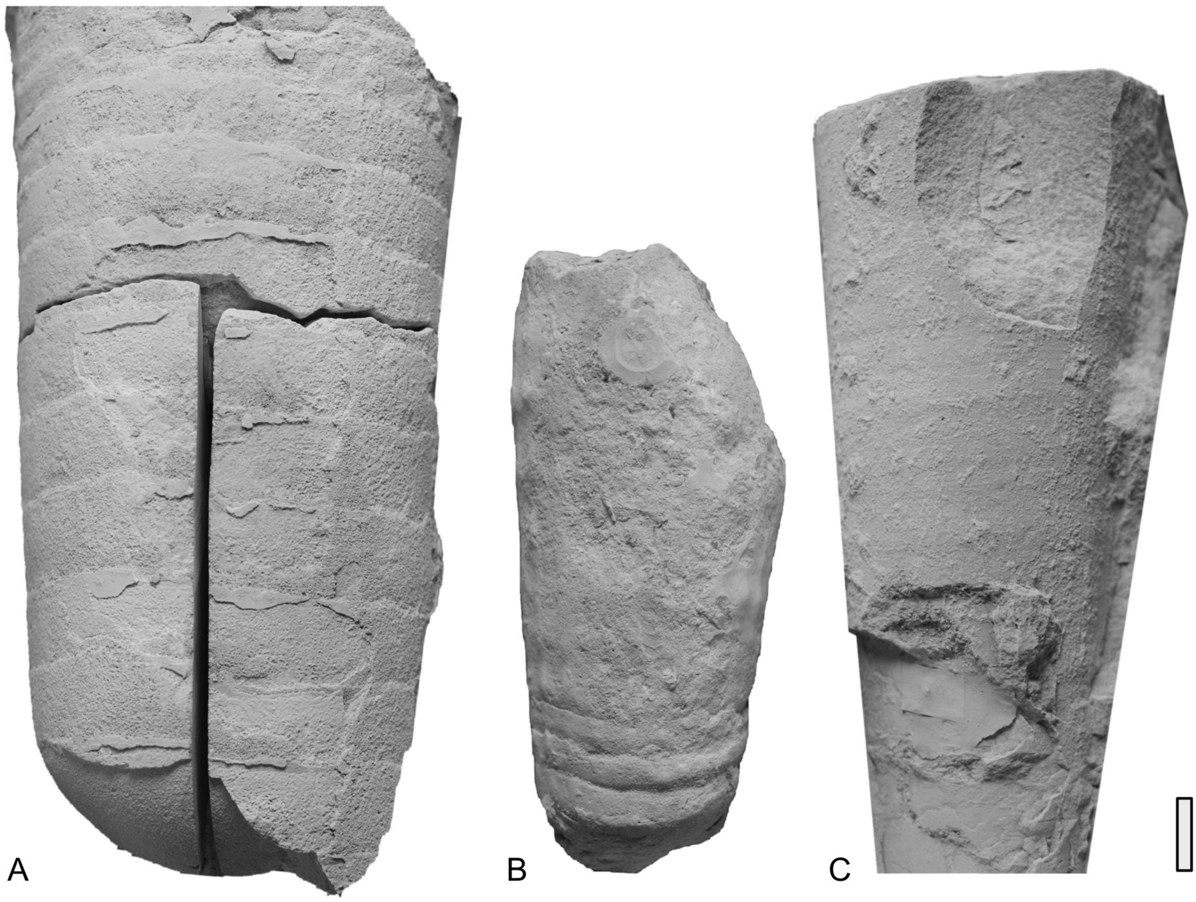


Fig. 7. Actinocerida Teichert, 1933 of the Vormsi–Pirgu regional stages, Estonia. **A**. *Nybyoceras bekkeri* Troedsson, 1926, specimen GIT 426-1120 from Kasari, Vormsi Regional Stage, dorsal view. **B**. *Gorbormoceras vohilaidense* gen. et sp. nov., holotype GIT 878-235, from Vohilaid shore (E), Vohilaid Island, Pirgu Regional Stage, lateral view. **C**. *Nybyoceras intermedium* Teichert, 1930, specimen TUG 939-49, from Moe stratotype outcrop, Pirgu Regional Stage, lateral view. Scale bar = 10 mm for all figures, same scale in A–C.

Nybyoceras intermedium Teichert, 1930
Figs 7C, 8C–D, G, 9A

Nybyoceras intermedium Teichert, 1930: 288, 290, pl. 7 fig. 22.

Nybyoceras intermedium – Foerste & Teichert 1930: 277. — Teichert 1933: 149. — Strand 1934: 63. — Balashov 1953a: 210; 1975: 63–64, pl. 5 fig. 10. — Stumbur 1956: 176. — Flower 1957: 24. — Saladzius 1966: tab. 1. — Barskov 1972: 81.

Emended diagnosis

Nybyoceras ornamented with fine, wavy longitudinal lirae, with subcentral to eccentric siphuncle position (RSP 0.3–0.5), with moderately expanded siphuncular segments (SCR ca 1.5–2); incipient annuli grow in adoral direction on the adoral surface of the septa; fully developed annuli are asymmetrically developed in longitudinal direction and are heavier on the ventral side. (Compiled from Teichert 1930.)

Material examined

ESTONIA • 1 spec.; Hiiumaa Island; Kõrgessaare quarry, Vormsi Regional Stage; TUG 939-50 • 1 spec.; Paluküla quarry; Kõrgessaare quarry, Vormsi Regional Stage; GIT 426-573 • 1 spec.; Moe stratotype; Moe Formation, Pirgu Regional Stage; TUG 939-49 • 1 spec.; Pahkla; Moe Formation, Pirgu Regional Stage; TUG 1745-293. (See also supplementary data 1)

Type locality and horizon

Niibi, Estonia; Adila Formation, Pirgu Regional Stage.

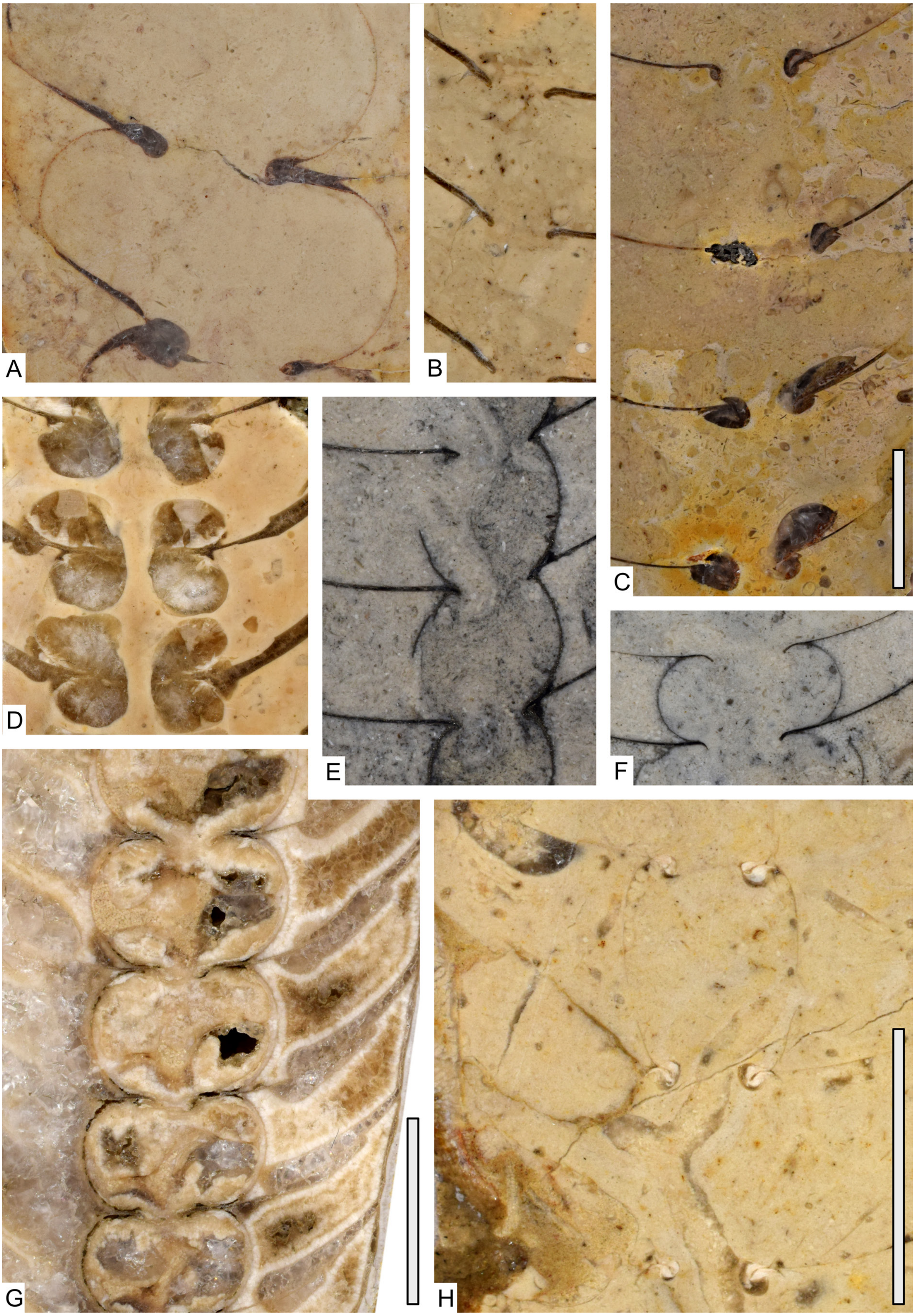
Description

Specimen GIT 426-573 is a fragment of a phragmocone, its conch diameter cannot be measured because of its incomplete preservation. The connecting ring is not preserved. The septal necks are short armenoceratoid, adnate. The septal foramen is 4–5 mm wide where the chamber length is 9.5 mm. Incipient endosiphuncular annuli are developed ventrally along the adoral surface of the septum (Fig. 8C).

Specimen TUG 939-49 is a 98 mm long fragment of a phragmocone with a diameter of 26–43 mm (angle of expansion = 10°) which has a well-preserved conch surface. The surface is ornamented with fine wavy longitudinal lirae; ca seven of them occur per millimeter. The lirae produce a fine Zigzag pattern (Fig. 9A).

Specimen TUG 1745-293 (Fig. 8G) is a fragment of a phragmocone 46 mm long and increasing in conch diameter 21–29 mm (angle of expansion = 10°). In this length, eight chambers occur (RCL: 0.23–0.24). The conch cross section is circular, and the surface is poorly preserved. The siphuncle is slightly eccentrically positioned (RSP: 0.45–0.46) and broadly expanded; where the conch diameter is 27 mm, one segment is 9.5 mm high and 6.2 mm long (SCR = 1.53) and the septal foramen has a diameter of ca 2 mm. The septal necks are short and adnate. The connecting ring forms wide adnate areas on the adapical surfaces of the septa. On the adoral surface of the septa the adnate area is only developed ventrally. Thick endosiphuncular deposits are present. These are more strongly developed on the adoral side of the septal foramen than the adapical side. Hypo- and episeptal cameral deposits are restricted to the ventral side of the siphuncle.

Specimen TUG 939-50 (Fig. 8D) is a fragment of a phragmocone with the internal characters preserved. Where the diameter is 23 mm, the chambers are 6 mm long (RCL = 0.26), the septal foramen is 2.8 mm in diameter, the connecting rings inflate to 9 mm in height (SCR = 1.5), and the septal necks are apparently short adnate. Thick, asymmetrically developed endosiphuncular annuli and thin mural, episeptal and hyposeptal deposits occur.


A
B
C
D
E
F
G
H

Remarks

Teichert (1930) distinguished *N. intermedium* from the two co-occurring species of *Nybyoceras* in the type locality Niibi by three features: (1) its narrower siphuncle (relative to the corresponding conch diameter), (2) its more centrally positioned siphuncle, and (3) unique growth pattern of the endosiphuncular annuli. The material available herein allows for a revision of Teichert's (1930) diagnosis:

(1) The relative siphuncular diameter of the type of *N. intermedium* is 0.31 compared to 0.55 in the specimen determined as *N. bekkeri* by Teichert (1930: pl. 7 fig. 19). However, often in actinocerids, complete conch cross sections are not available. Therefore, it is better to use the SCR for comparison, which is 1.6–1.9 in the type of *N. intermedium*, and 2.1–2.5 in the types of *N. bekkeri* (Troedsson 1926: pl. 63 figs 2–3).

(2) The figured specimens of the two species in Teichert (1930) differ only slightly in RSP with 0.30 in *N. intermedium*, and 0.26 in *N. bekkeri*. Two specimens, assigned here to *N. intermedium*, have subcentral siphuncle positions (TUG 939-49, 1745-293), where the conch diameter is between 20–29 mm. In the type specimen, the more eccentric siphuncular position occurs at diameters > 60 mm. This is interpreted here as an ontogenetic change in the siphuncular position, and it is included in the diagnosis of *N. intermedium*.

(3) Teichert (1930) distinguished *N. intermedium* from *N. bekkeri* based in the growth pattern of the endosiphuncular annuli. In *N. intermedium*, he found annuli, which initially grew toward the adoral side of the septal neck and septum. Little is known about the variability in the development of the annuli. When fully developed, the annuli of *N. bekkeri* and *N. intermedium* are virtually indistinguishable in dorsoventral median section as both exhibit stronger development the ventral adoral quadrant (compare Troedsson 1926: pl. 63 fig. 3). Additionally, the high potential for misleading interpretations of 3D-structures of endosiphuncular annuli have been described by Pohle *et al*. (2024) and Turek & Aubrechtová (2024).

In conclusion, the relative expansion of the siphuncle seems to be the most reliable character to distinguish between *N. bekkeri* and *N. intermedium*. Also included in the diagnosis is the ornamentation, which is now known from this species from specimen TUG 939-49.

Family Ormoceratidae Saemann, 1853

Genus ***Ormoceras*** Stokes, 1840

Type species

Ormoceras bayfieldi Stokes, 1840 from Niibi, Estonia; Adila Formation, Pirgu Regional Stage, late Katian; subsequent designation by Bassler (1915).

Fig. 8 (preceding page). Median sections of phragmocones of Actinocerida Teichert, 1933 of the Vormsi–Pirgu regional stages, Estonia. **A–B**. *Nybyoceras bekkeri* Troedsson, 1926. **A**. Specimen GIT 426-1107 from Paluküla quarry, Vormsi Regional Stage. **B**. Specimen GIT 426-1120 from Kasari, Vormsi Regional Stage. **C–D, G**. *Nybyoceras intermedium* Teichert, 1930. **C**. Specimen GIT 426-573 from Paluküla quarry, Vormsi Regional Stage. **D**. Specimen TUG 939-50 from Kõrgessaare quarry, Hiiumaa Island, Vormsi Regional Stage. **E**. *Ormoceras heckeri* Teichert, 1930, specimen TUG 1680-19 from Saxby shore, Vormsi Island, Vormsi Regional Stage. **F**. *Gorbormoceras vohilaidense* gen. et sp. nov., holotype GIT 878-235, from Vohilaid shore (E), Vohilaid Island, Pirgu Regional Stage. **G**. Specimen TUG 1745-293 from Pahkla, Pirgu Regional Stage. **H**. *Ormoceras* sp., specimen TUG 1745-239 from Salu, Pirgu Regional Stage. Scale bars = 10 mm for all figures, same scale in A–C, and in D–G.

Diagnosis

Medium-sized straight shells, circular or nearly so in cross section; siphuncle subcentral; segments almost globular; septal necks short cyrtochoanitic; endosiphuncular canal system moderately complex to simple, few radial canals. (Adopted from Teichert 1964a.)

Ormoceras heckeri Teichert, 1930
Fig. 8E

Ormoceras heckeri Teichert, 1930: 290, pl. 7 fig. 21.

Ormoceras heckeri – Balashov 1953a: 211. — Stumbur 1956: 176. — Flower 1957: 11.

Diagnosis

Straight shell with circular cross section; siphuncular position subcentral, siphuncular segments barrel-shaped, approximately as high as long (SCR ca 1); septal necks very short and adnate to adoral surface of septa (*Nybyoceras*-like).

Material examined

ESTONIA • 2 specs; Paope quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 1745-280, TUG 1745-281 • 1 spec.; Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; TUG 1680-19.

Type locality and horizon

Niibi, Estonia; Adila Formation, Pirgu Regional Stage.

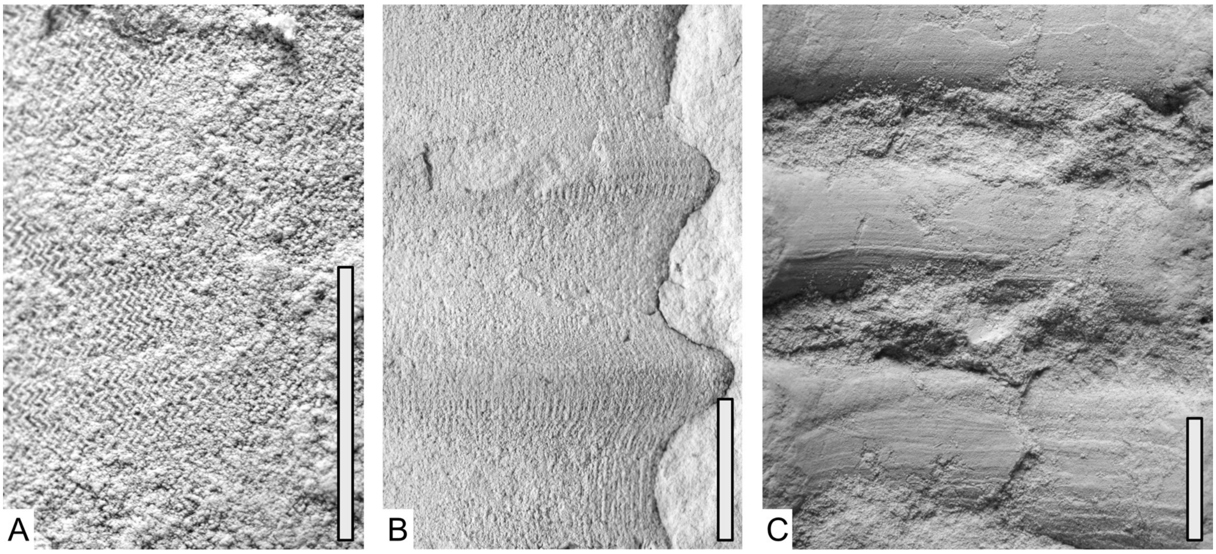


Fig. 9. Details of the conch surface of orthoconic cephalopods from the Vormsi–Pirgu regional stages, Estonia. **A**. *Nybyoceras intermedium* Teichert, 1930, specimen TUG 939-49, from Moe stratotype outcrop, Pirgu Regional Stage. **B**. *Palaeodawsonocerina senckenbergi* (Teichert, 1930), specimen GIT 878-53, from Saxby shore (N), Vormsi Island, Vormsi Regional Stage. **C**. *Striatocycloceras hosholmense* sp. nov., holotype GIT 878-297, from Hosholm shore, Vormsi Island, Vormsi Regional Stage, view of the inner surface of the outer shell. Scale bars = 5 mm for all figures. All figures with apertural side of specimens directed upward.

Description

Specimen TUG 1680-19 (Fig. 8E) is a short fragment of the phragmocone without external characters preserved, with circular conch cross section and a diameter of 36 mm, the septa are ca 7 mm apart (RCL = 0.19), and the siphuncle is eccentrically positioned (RSP = 0.34). The septal necks are short adnate and the connecting ring forms barrel-shaped segments with a height of 8 mm (SCR = 1.14).

Specimen TUG 1745-281 is a fragment of a phragmocone 28 mm long, and increasing in diameter 20–23.5 mm (angle of expansion = 7°). The conch surface is not preserved. The sutures are directly transverse and straight with an RCL of 0.26. The septal foramen is nearly centrally positioned (RSP = 0.48) and has a diameter of 2 mm where the conch diameter is 22 mm. The septal necks are very short adnate, the connecting ring is not preserved.

Remarks

The species was described in detail by Teichert (1930). The new data suggest an ontogenetic change of the position of the siphuncle from central in early growth stages to eccentric in later growth stages.

Ormoceras sp. A
Fig. 8H

Material examined

ESTONIA • 1 spec.; Salu; Pirgu Regional Stage; TUG 1745-239.

Description

Specimen TUG 1745-239 is a ca 113 mm long fragment of a phragmocone with a conch height of 23–45 mm (angle of expansion = 11°) which is slightly deformed. The conch surface is apparently smooth. The RCL varies between 0.23–0.24 and at a conch height of 27 mm the RSP is ca 0.3. The septal necks are short adnate, and the connecting ring forms barrel-shaped siphuncular segments with a height of 5.8 mm where the length is 6.5 mm (SCR = 0.89). Incipient, symmetric endosiphuncular annuli occur where the conch height is 25 mm.

Remarks

The specimen differs from *O. heckeri* in having a less expanded siphuncle (SCR = 0.89 in specimen TUG 1745-239 compared with SCR > 1 in *O. heckeri*) at comparable conch diameters. However, this single, fragmentarily preserved specimen does not allow for species level determination and detailed comparison with other, e.g., North American species of the genus.

Genus ***Gorbormoceras*** gen. nov.
urn:lsid:zoobank.org:act:923963A2-FF6F-4A62-8421-E6B8E2B10E76

Type species

Gorbormoceras vohilaidense gen. et. sp. nov., from Vohilaid shore (E), Vohilaid Island, Estonia; Adila Formation, Pirgu Regional Stage.

Diagnosis

Slightly exogastrically curved, nearly orthoconic longicones with a circular (or nearly so) conch cross section; ornamented with shallow annulation and distinct longitudinal lirae; sutures form shallow lateral lobes; ca five chambers occur at a length equal to corresponding conch cross section; siphuncle slightly eccentrically positioned; septal necks short or absent; siphuncular segments widely expanded with adnate areas at adoral and apical surfaces of septa; endosiphuncular and cameral deposits not known.

Etymology

Combination of the two genus names *Gorbyoceras* and *Ormoceras*, because the new genus, in a unique fashion, combines essential features of both genera.

Remarks

The new genus is provisionally assigned to the Ormoceratidae because of its subcentrally positioned, widely expanded siphuncle, and the very short recumbent or absent septal necks. Short or very short cyrtochoantitic to recumbent septal necks and widely expanded siphuncular segments are known from other ormoceratids, such as *Ormoceras* and *Orthonybyoceras* Shimizu & Obata, 1935.

Comparison

Troedssonoceras Foerste, 1928b is similar in having widely expanded siphuncular segments and a longitudinal ornamentation. In *Troedssonoceras*, the siphuncular shape is similar to *Deiroceras* (with cyrtochoanitic septal necks), and the connecting ring is not adnate (see, e.g., Flower 1946: 535). *Eskimoceras* Troedsson, 1926 has an annulated conch and widely expanded siphuncular segments. It differs from the new genus in having cyrtochoanitic septal necks and in lacking a longitudinal ornamentation.

Gorbormoceras vohilaidense gen. et. sp. nov.
urn:lsid:zoobank.org:act:820DB1BC-79F4-40A5-A0B0-19D08C785DD6
Figs 7B, 8F

Diagnosis

Same as for genus, by monotypy.

Etymology

The name refers to Vohilaid Island, the type locality.

Type material

Holotype

ESTONIA • Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage; GIT 878-235.

Description

The specimen is a slightly exogastrically curved mold of parts of a phragmocone and a body chamber. The conch cross section is apparently circular. At a conch diameter of 28–38 mm, the angle of expansion is 14°. At the base of the body chamber, the diameter is 31 mm. The preserved length of the body chamber is 60 mm. Although the outer shell is not preserved, traces of a relatively strong ornamentation with ca 20 longitudinal lirae around the circumference and a weak annulation are visible (Fig. 7B). Near the base of the body chamber, ca five annulations occur in a distance equal to the corresponding conch cross section.

The sutures form shallow lateral lobes and are slightly adorally shifted on the prosiphuncular side of the conch, the most adoral sutures are slightly crowded (chamber length 4.5 mm), at a conch height of 28 mm they are 6 mm distant (RCL = 0.21). The siphuncle is eccentrically positioned; near the apical end of the specimen, where the conch diameter is 31 mm, it is 10 mm distant from the conch margin and has a diameter of ca 3.3 mm (RSP = 0.36). The septal necks are short recumbent or achoanitic. The connecting ring is thin, and forms widely expanded segments with adnate areas at the adoral and apical septal surfaces (Fig. 8F). Where the septal foramen is 3.3 mm, and the chamber length is 4 mm, the segments expand toward a height of 8.6 mm (RSS = 2.15).

Remarks

This specimen is externally similar to *Cycloceras fenestratum* Eichwald, 1860 with regard to the general conch shape and its traces of the ornamentation (ca 20 longitudinal lirae and ca five annulations per distance equal to the corresponding conch cross section). However, it is larger (maximum diameter ca 25 mm in *C. fenestratum*) and has a larger angle of expansion (angle of expansion < 10° in *C. fenestratum*) (see e.g., Kröger 2013). Internally, the specimen is similar to species of *Ormoceras*.

Comparison

The widely expanded siphuncle and the ornamentation of the new species are most similar to *Troedssonoceras* (?) *obscuriliratum* Flower, 1946, from which it differs in having a more centrally positioned siphuncle and a weakly annulated conch. Another orthoconic species with a nodular ornamentation, comparable to *G. vohilaidense* sp. nov., is *Spyroceras* (?) *nodosum* Sweet & Miller, 1957, from which the internal characters are not known.

Order Orthocerida Kuhn, 1940
Family Orthoceratidae M'Coy, 1844

Genus ***Pleurorthoceras*** Flower, 1962

Type species

Orthoceras clarksvillense Foerste, 1924 from Clarksville, Ohio, USA, Waynesville Formation, latest Katian; by original designation.

Diagnosis

Slender, gradually expanding, smooth orthocones; circular in cross section with straight, transverse sutures; chamber distance between one-third to one half of the corresponding conch diameter (RCL = 0.3–0.5); siphuncle subcentral to central; siphuncular segments subtubular, slightly expanded within chambers; septal necks short, suborthochoanitic; endosiphuncular deposits unknown; mural cameral deposits well developed. (Adopted from Flower 1962.)

Pleurorthoceras sp.
Fig. 10, 11A, 12B

Material examined

ESTONIA • 1 spec.; Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-154 • 2 specs; same data as for preceding; TUG 1745-220, TUG 1837-81 • 1 spec.; Vormsi Island, Saxby shore (N); Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-18 • 1 spec.; Hiiumaa Island, Kõrgessaare quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-1110 • 1 spec.; same data as for preceding; TUG 1745-30 • 1 spec.; Paope quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-557 • 1 spec.; Saaremõisa (Lyckholm); Kõrgessaare Formation, Vormsi Regional Stage; TUG 1745-225 • 2 specs; Mõnuste quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 939-14, TUG 1745-31 • 1 spec.; Kersleti quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 44-42. (See also supplementary data 1.)

Description

The material comprises fragments of orthocones with an apparent or preserved smooth conch surface and a central to subcentral tubular siphuncle with orthochoanitic to suborthochoanitic septal necks and without endosiphuncular or cameral deposits. The material comprises two separate size classes of fragments (compare Figs 11A, 12B):

In the smaller fragments (conch diameters < 15 mm; specimens GIT 878-154, GIT 878-18, TUG 1745-220), the conch surface is smooth, the septal distance is relatively wide (RCL: 0.3–0.5; Fig. 10B); the septal curvature is 4 mm deep where the conch diameter is 12 mm (GIT 878-18); the sutures are directly transverse and straight; the siphuncle is nearly tubular (GIT 878-154: siphuncular height is 1.7 mm at mid-length between septa where the conch diameter is 13 mm, RSH = 0.13); and the septal necks are suborthochoanitic and ca 0.3 mm long (GIT 878-154).

In the larger fragments, the conch surface is not preserved but was apparently smooth. All larger fragments are deformed internal molds of phragmocones or fragmentary preserved in conch cross section. The largest specimen (GIT 426-557) has a maximum diameter of ca 66 mm with an RCL of ca 0.24. The RCL is in all specimens of the larger size class (> 30 mm) between 0.23–0.26 (Fig. 10B). The exact position of the siphuncle cannot be determined in these specimens because of poor preservation; it was apparently at a subcentral to central position. In specimen TUG 1745-31 (Fig. 11A) and TUG 939-14, the internal characters are preserved. The siphuncle is apparently tubular or nearly so and the septal necks are orthochoanitic to suborthochoanitic, 1 mm long where the septal distance is 13 mm, the conch diameter ca 50 mm, and the septal foramen is 5 mm in diameter.

Remarks

The two size classes of specimens with diameters < 15 mm and > 30 mm agree in apparent smooth conch surface, siphuncular position and siphuncular shape. However, no intermediate growth stages are known. Hence, the possibility exists that these represent two different species. However, despite the gap in size the resulting distribution (Fig. 10B) equally well could be interpreted as showing the ontogenetic trend in cameral depth seen in many other orthocerids and pseudorthocerids (i.e., rapid rise in early stages then decreasing more or less rapidly in later growth).

Because of the uncertainties in adult siphuncle position, ornamentation, and ontogentic trends of the angle of expansion, and other characters, the specimens are left in open nomenclature. The fragments differ from *P. osmundsbergense* Kröger, 2013, in having a lower angle of expansion (angle of expansion in *P. osmundsbergense* is ca 7°) and the conch is slightly curved. The American species of *Pleurorthoceras* differ in having a wider siphuncle (e.g., Frey 1995; Fig. 9B).

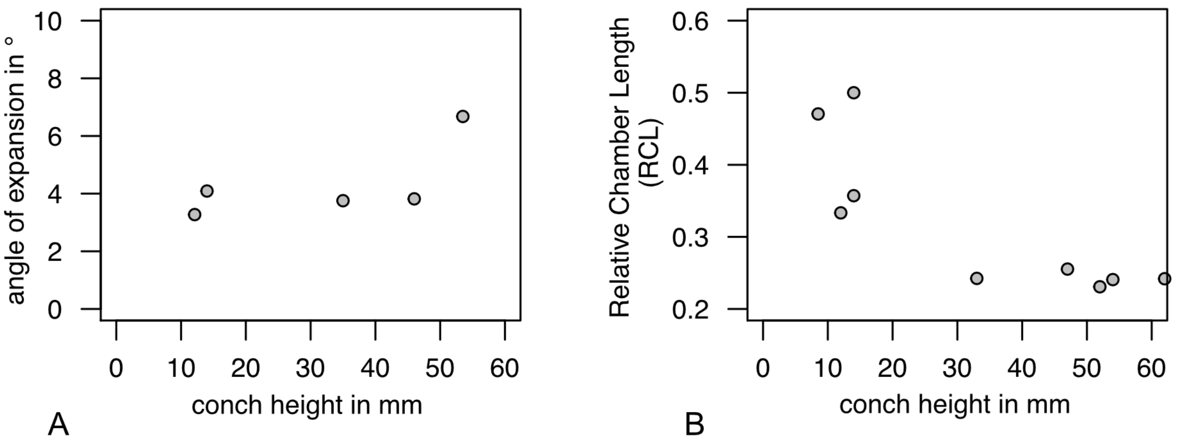


Fig. 10. Diagrams of morphological variability of specimens of *Pleurorthoceras* sp., Pirgu–Vormsi regional stages, Estonia. **A.** Angle of expansion. **B.** Relative siphuncle position (RSP). Note the decreasing RCL with increasing conch height.

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

Type species

Orthoceras undulostriatum Hall, 1847 from Middleville, New York, USA, Trenton Formation, late Katian; by original designation.

Diagnosis

Slender orthocones with circular or slightly compressed conch cross section, 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. (Adopted from Kröger & Isakar 2006.)

Comparison

Anaspyroceras Shimizu & Obata, 1935 differs from *Striatocycloceras* in having a fine longitudinal ornamentation. *Leurocycloceras* Foerste, 1928a is similarly ornamented to *Striatocycloceras* but differs in having long septal necks.

Striatocycloceras hosholmense sp. nov.
urn:lsid:zoobank.org:act:0530A9F0-1CC9-47F1-97C4-F5AB2352EE38
Figs 9C, 11E, G, 13B, D

Diagnosis

Annulated orthocones with circular conch cross section and nearly tubular conch at conch diameters >20 mm; ornamented with three to four annulations in a distance equal to the corresponding conch diameter; annulations straight transverse, regularly spaced and with sharp narrow crests; ornamented with ca 10–12 fine transverse growth lines or striae per cycle of annulation; suture lines in the troughs of the annulations and equally spaced to annulations; parallel sutures and annulations; RCL ca 0.25–0.3; siphuncle central, tubular to slightly expanded; septal foramen approximately one tenth of the diameter, septal necks orthochoanitic; shallow endosiphuncular deposits at position of septal necks; cameral deposits not known.

Etymology

Refers to the type locality, Hosholm shore, Vormsi Island.

Type material

Holotype

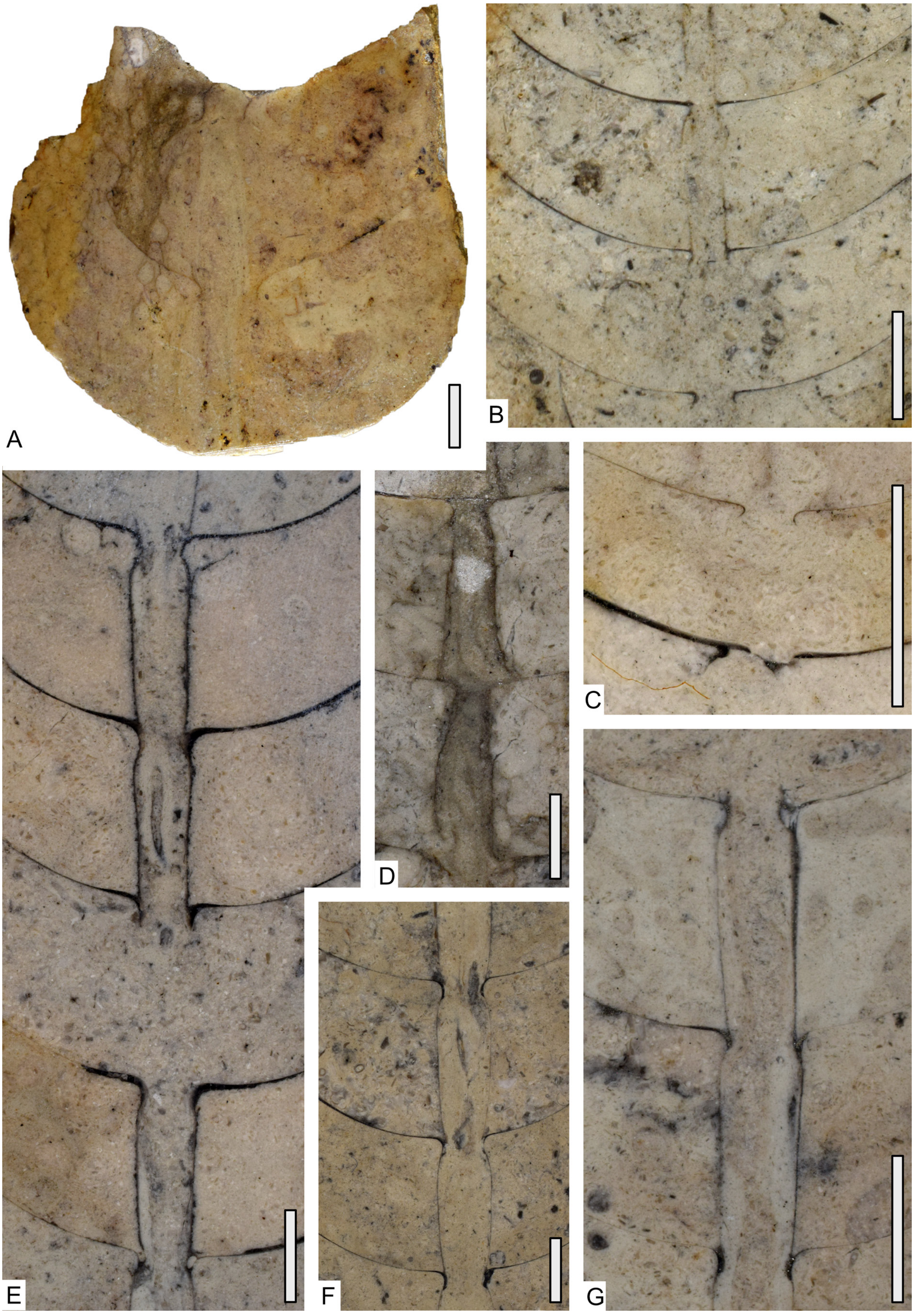
ESTONIA • Vormsi Island, Hosholm shore; Adila Formation, Pirgu Regional Stage; GIT 878-297.

Paratypes

ESTONIA • 5 specs; same collection data as for holotype; GIT 878-288, GIT 878-290, GIT 378-302, GIT 878-304, GIT 878-312 • 1 spec; same collection data as for holotype; TUG 1819-102.

Description

The holotype is an 81 mm long fragment of a phragmocone with a circular conch cross section, and a conch-diameter of 24–25 mm (Fig. 13B). Three to four annulations occur in a distance equal to the corresponding diameter. The entire fragment has 11 equally spaced, directly transverse annulations. The annulations have deep rounded troughs (1.5 mm deep) and sharp, and narrow crests. The conch surface is ornamented with ca 12 transverse growth-lines per annulation (Fig. 9C). The sutures are positioned


A
B
C
D
E
F
G

in the troughs of the annulations. The curvature of the septa is ca 3 mm deep with a slightly eccentric septal foramen, ca 2.5 mm in diameter. The siphuncle is nearly tubular, centrally positioned, slightly constricted at the position of the septal foramen. The septal necks are orthochoanitic, ca one millimeter long. At the position of the septal necks thin endosiphuncular annuli are developed (Fig. 11E). Cameral deposits are not developed.

A second specimen, GIT 878-312, is a fragment of a phragmocone with internal characters well-preserved. The fragment has a length of 68 mm, a diameter of 22–23 mm, and nine annulations and chambers (Fig. 13D). The siphuncle is nearly tubular with a diameter of ca 2.5 mm. The septal necks are orthochoanitic with a length of ca one millimeter, and thin endosiphuncular deposits are developed at the position of the septal necks. The siphuncle is nearly central. The angles of expansion of all specimens assigned to this species are less than 5° (Fig. 11G).

Remarks

The shell surface is poorly preserved in all specimens which are available for this study. The outer shell is commonly firmly attached to the matrix, covering the surface of the conch, obscuring fine detail of the ornamentation. Where the outer shell is visible, no longitudinal ornamentation is visible. However, it cannot be excluded that in this species very fine, sub-millimetre, longitudinal lirae are present on the shell surface. Therefore, *S. hosholmense* sp. nov. should also be compared with species of *Anaspyroceras* Shimizu & Obata, 1935 (see: Flower 1943b: 115, and Sweet 1964c: K230, for a genus diagnosis of *Anaspyroceras*). *Anaspyroceras* is an annulated orthocerid, which is internally similar to *Striatocycloceras* but has a fine longitudinal ornament.

Comparison

The holotype of this species shows great similarity to the specimen figured in Dzik (1984: pl. 35 fig. 4a–c); subsequently designated as the holotype of *Orthoceras clathrato-annulatum* Roemer, 1861 therein. However, inconsistencies between Roemer's (1861) figures and descriptions, and differences between Roemer's (1861) and Dzik's (1984) specimens indicate that Roemer's (1861) type material for *O. clathrato-annulatum* consisted of multiple species. The specimen figured in Dzik (1984) has no outer shell preserved and the internal characters remain unknown. Further study of Roemer's (1861) type material is needed to solve this problem (see also discussion under *Gorbyoceras clathratoannulatum*).

Striatocycloceras hosholmense sp. nov. differs from *S. undulatostriatum*, and *S. foerstei* (Teichert, 1930) in having a relatively wide annulation of three to four annuli per distance equal to the corresponding conch cross section, compared to more than four annuli in the latter two species. Additionally, endosiphuncluar annuli are not known from the latter two species. *S. romingeri* (Foerste, 1932) has a smaller adult size (only ca 10 mm) than *S. hosholmense*, and in *S. obliquum* (Eichwald, 1860), the annulation is oblique.

Fig. 11 (preceding page). Median sections of phragmocones of Orthocerida Kuhn, 1940 and Pseudorthocerida Flower & Caster, 1935 of the Vormsi–Pirgu regional stages, Estonia. **A**. *Pleurorthoceras* sp., specimen TUG 1745-31 from Mõnuste quarry, Vormsi Regional Stage. **B–C**. *Gorbyoceras clathratoannulatum* (Roemer, 1861) comb. nov. **B**. Specimen GIT 878-149, from Vohilaid shore (E), Vohilaid Island, Pirgu Regional Stage. **C**. Specimen GIT 840-138, from Hosholm shore, Vormsi Island, Vormsi Regional Stage. **D**. *Gorbyoceras textumaraneum* (Roemer, 1861), specimen GIT 878-299 from Vohilaid shore (E), Vohilaid Island, Pirgu Regional Stage. **E**. *Striatocycloceras hosholmense* sp. nov., holotype GIT 878-297, from Hosholm shore, Vormsi Island, Pirgu Regional Stage. **F**. *Striatocycloceras* cf. *hosholmense*, specimen TUG 939-20, from Hosholm shore, Vormsi Island, Pirgu Regional Stage. **G.** *Striatocycloceras hosholmense*, paratype GIT 878-312, from Hosholm shore, Vormsi Island, Pirgu Regional Stage. Scale bars = 5 mm for all figures.

Several species of *Anaspyroceras* are similar to *S. hosholmense* sp. nov. but differ in the following aspects: *A. anellus* (Conrad, 1843) and *A. paquettense* (Foerste, 1932) differ in having narrower annulations (ca 5–6 annulations per distance equal to the corresponding conch cross section) and in being ornamented with fine longitudinal lirae. *Anaspyroceras anzaas* Teichert & Glenister, 1953 has a low annulation and is ornamented with 26–33 longitudinal lirae. *Anaspyroceras cylindricum* Foerste, 1932 differs in having obliquely transverse annulations. *Anaspyroceras cumberlandense* Flower, 1946 has a narrower annulation and an irregularly nodose ornamentation. *Anaspyroceras williamsae* Flower, 1946 is ornamented with longitudinal lirae. The annulation of *A. obscurum* (Barrande, 1868) is less pronounced and narrower (>10 annulations at distance equal to the corresponding conch cross section).

Striatocycloceras* cf. *hosholmense
Figs 11F, 13C

Material examined

ESTONIA • 3 specs; Vormsi Island, Hosholm shore; Adila Formation, Pirgu Regional Stage; TUG 899-81, TUG 939-20, TUG 1745-233.

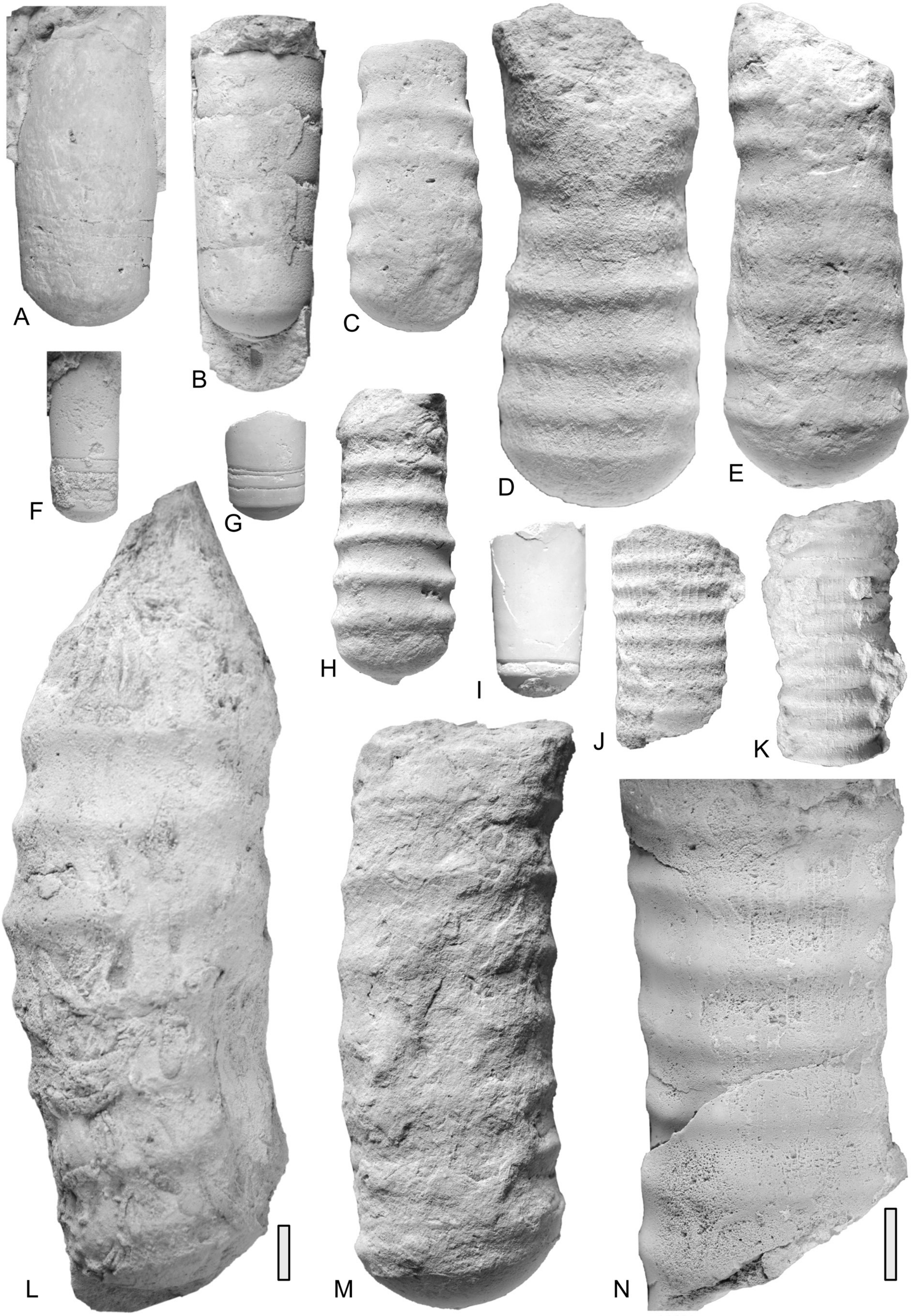
Description

Specimen TUG 939-20 is a fragment of a phragmocone, 38 mm long, with diameter 23–27 mm (apical angle 8.5°), and four chambers and annulations (Fig. 13C). The characters of the outer shell are not preserved. The annulations are directly transverse with deep troughs and sharply accentuated crests. The sutures are parallel to and positioned in the troughs of the annulations. The siphuncle is nearly centrally positioned and slightly expanded within the chambers. It is ca 2.5 mm wide at position of the septal foramen and 3.5 mm wide at mid-way between septa. The septal necks are orthochoanitic, 1.3 mm long (Fig. 11F). No cameral deposits are developed. Two additional specimens are in the Estonian collections which are similar in having a sharply crested annulations, ca three annulations per distance equal to the corresponding conch diameter and an apical angle of ca 10°.

Remarks

The specimens described as *Striatocycloceras* cf. *hosholmense* are in all aspect similar to *Striatocycloceras hosholmense* sp. nov. expect in having a distinctly larger apical angle at comparable conch diameters. However, none of the specimens has its outer shell preserved, making a comparison somewhat questionable. More material is needed to establish this group of specimens as a distinct species. Notably,

Fig. 12 (next page). Orthocerida Kuhn, 1940 and Pseudorthocerida Flower & Caster, 1935 of the Vormsi–Pirgu regional stages, Estonia. **A**. *Isorthoceras* sp. A, specimen GIT 878-128, Sutlema quarry, Vormsi Regional Stage. **B**. *Pleurorthoceras* sp., specimen GIT 878-154, from Saxby shore, Vormsi Island, Vormsi Regional Stage. **C**. *Gorbyoceras clathratoannulatum* (Roemer, 1861) comb. nov., specimen GIT 878-305, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage. **D–E**. *Gorbyoceras textumaraneum* (Roemer, 1861). **D**. Specimen GIT 878-143 from Vohilaid shore, Vohilaid Island, Pirgu Regional Stage. **E**. GIT 878-223, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage. **F**. *Isorthoceras* sp. C, specimen GIT 878-49, Saxby shore, Vormsi Island, Vormsi Regional Stage. **G**. *Isorthoceras* sp. B, specimen GIT 878-116, from Moe trench, Vormsi Regional Stage. **H**. *Gorbyoceras clathratoannulatum*, specimen GIT 840-265, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage. **I**. *Isorthoceras* sp. D, specimen GIT 878-114, Moe trench, Vormsi Regional Stage. **J**. *Gorbyoceras stumburi* (Kröger, 2013), specimen TUG 939-30, from Harilaid, Pirgu Regional Stage. **K**. *Palaeodawsonocerina* ? sp., specimen TUG 939-78, from Hosholm shore, Vormsi Island, Pirgu Regional Stage. **L–M**. *Gorbyoceras textumaraneum*. **L**. Specimen TUG 1745-193, from Mõnuste quarry, Vormsi Regional Stage, lateral view. **M**. Specimen GIT 878-306, from Vohilaid shore (E), Vohilaid Island, Pirgu Regional Stage. **N**. *Gorbyoceras* sp. A, specimen TUG 42-417, from Kohila, Vormsi Regional Stage, lateral view. Scale bars = 10 mm in all figures. Same scale in A–B, F–G, I, N, and in C–E, H, J, L.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a similar pair of species *A*. *anellus* and *A*. *paquettense* with low and high apical angles are known from Katian strata of North America (Foerste 1932: 104). This could indicate the presence of sexual dimorphism in this genus.

Striatocycloceras ? sp.
Fig. 13E

Material examined

ESTONIA • 1 spec.; Saaremõisa (Lyckholm); Kõrgessaare Formation, Vormsi Regional Stage; TUG 42-414.

Fig. 13. Annulated Orthocerida of the Vormsi–Pirgu regional stages, Estonia. **A**. *Palaeodawsonocerina senckenbergi* (Teichert, 1930), specimen TUG 939-81, from Saxby shore (N), Vormsi Island, Vormsi Regional Stage. **B, D**. *Striatocycloceras hosholmense* sp. nov., holotype GIT 878-297, from Hosholm shore, Vormsi Island, Pirgu Regional Stage. **C**. *Striatocycloceras* cf. *hosholmense*, specimen TUG 939-20, from Hosholm shore, Vormsi Island, Pirgu Regional Stage. **E.** *Striatocycloceras* sp., specimen TUG 42-414, from Saaremõisa (Lyckholm), Vormsi Regional Stage. Scale bars = 10 mm for all figures, same scale in A, C–E.

Description

The specimen is a nearly complete body chamber of an adult specimen, ca 60 mm long, with a conch diameter at the position of the last septum of 16 mm and at the aperture of 13.5 mm. The conch diameter decreases rapidly in the adapical half of the body chamber and in its adoral half remains nearly constant at ca 14 mm. The conch cross section is circular. In longitudinal direction the conch is (probably taphonomically) slightly curved. Annulations are regular, directly transverse and with ca four annulations in a distance equal to the corresponding conch diameter. The troughs of the annulations are widely rounded, and the crests narrow and sharp. Very fine growth lines or striae, 20 per annulation are present parallel to the annulation.

The single preserved septum is three millimeter deep and positioned in the trough of an annulation. The suture line is parallel to the annulation. The septal foramen is central with a diameter of ca 2 mm.

Remarks

The specimen was collected by F. Schmidt (1832–1908) and originally determined as "*Orthoceras anellus*" [sic]. *Orthoceras anellum* Conrad, 1843, is the type species of *Anaspyroceras*, which is ornamented with fine longitudinal lirae. Fine lirae are not visible in specimen TUG 42-414 despite a well-preserved conch surface. Details of the septal neck and siphuncular shape are not preserved in this specimen, making a genus determination questionable. Herein, the specimen is questionably assigned to *Striatocycloceras* because of the apparent absence of longitudinal elements in the ornamentation. The spacing of the annulation of this specimen is similar to *S. undulatostriatum*, from which it differs in having a smaller adult size (the conch diameter of the latter reaches 30 mm, see Kröger & Isakar 2006: 150). The specimen differs from specimens assigned to *S. foerstei* (Teichert, 1930) in having a wider annulation (in *S. foerstei* six to seven annulations occur in a distance equal to the conch cross section). More material is needed for a species-level determination.

Family Dawsonoceratidae Flower, 1962

Genus ***Palaeodawsonocerina*** Kröger & Isakar, 2006

Type species

Spyroceras senckenbergi Teichert, 1930, Saaremõisa (Lyckholm), N of Haapsalu, Kõrgessaare Formation, Vormsi Regional Stage; by original designation.

Diagnosis

Straight or slightly cyrtoconic, circular or subcircular shell, with prominent, narrowly spaced annulations, growth lines, and numerous subordinate filiform longitudinally raised lines, producing a fine reticulate pattern; siphuncle central or slightly eccentric, slightly expanded, with achoanitic to very short orthochoanitic septal necks; apex blunt, slightly cyrtoconic, annulated. (Adopted from Kröger & Isakar 2006.)

Palaeodawsonocerina senckenbergi (Teichert, 1930)
Figs 9B, 13A, 14

Spyroceras senckenbergi Teichert, 1930: 280, pl. 5 figs 3–4.
Spyroceras saxbyense Stumbur, 1956: 180, pl. 1 fig. 1.

Spyroceras sp. A – Strand 1934: 21, pl. 3 fig. 7.
Gorbyoceras duncanae – Balashov 1975: 68, pl. 1 figs 3–6.
Spyroceras senckenbergi – Dzik 1984: 122, 125, pl. 35 fig. 5, text-figs 48a, 49.20.

Gorbyoceras? *senckenbergi* – Kiselev 1991: 92, pl. 1 fig. 2.
Palaeodawsonocerina senckenbergi – Kröger & Isakar 2006: 154–156, figs 8a, 10i, 12d–e. — Kröger 2013: 34–36, figs 12a, 13ca. — Pohle *et al*. 2022: fig. 2.

Diagnosis

Slightly compressed orthocones with very low apical angle of approximately 1°–2°; adult dorsoventral diameter approximately 25 mm; ornamented with five to six annulations in a distance that equates to the corresponding shell diameter in adult specimens; annulations straight or very slightly oblique to the normal of the conch axis and regularly spaced; very fine growth lines, about 50 per cycle of annulations; very fine longitudinal striae or raised lines, about five to seven per mm; suture line at the ridges of the annulations; parallel sutures and annulations; siphuncle central, slightly expanded within the chamber; septal foramen about 0.07 of the shell diameter. (From Kröger & Isakar 2006.)

Material examined

ESTONIA • 1 spec.; Aulepa quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 895-150 • 3 specs; Harilaid; Vormsi–Pirgu regional stages; TUG 1745-241 to TUG 1745-243 • 1 spec.; Hosholm shore; Adila Formation, Pirgu Regional Stage; TUG 939-78 • 1 spec.; Kersleti quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 1745-17 • 2 specs; Kõrgessaare quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-30, GIT 426-49 • 5 specs; Moe trench; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-103, GIT 878-105, GIT 878-110, GIT 878-111, GIT 878-112 • 1 spec.; Mõnuste quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-8 • 4 specs; Paluküla quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-62, GIT 426-65, GIT 426-87, GIT 426-88 • 2 specs; same data as for preceding; TUG 1745-20, TUG 1745-21 • 3 specs; Paope quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-29, GIT 426-563, GIT 426-564 • 1 spec.; same data as for preceding; TUG 1745-18 • 1 spec.; Saaremõisa (Lyckholm); Kõrgessaare Formation, Vormsi Regional Stage; TUG 1745-283 • 4 specs; same data as for preceding; GIT 878-119 to GIT 878-121, GIT 878-124 • 2 specs; Saxby old quarry; Moe Formation, Pirgu Regional Stage; TUG 1745-218, TUG 939-28 • 30 specs; Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; TUG 939-28, TUG 1745-264, TUG 1666-12, TUG 1745-226, TUG 1745-251, TUG 1745-255, TUG 1745-256, TUG 1745-261 to TUG 1745-272, TUG 1745-321, TUG 1837-82, TUG 38-815, TUG 39-777, TUG 39-792, TUG 939-17, TUG 939-19, TUG 939-27, TUG 939-73, TUG 939-81, TUG 939-82 • 4 specs; same data as for preceding; GIT 426-96 to GIT 426-99 • 16 specs; Saxby shore (N); Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-1125, GIT 426-1126, GIT 426-1131, GIT 426-24, GIT 426-42, GIT 426-43, GIT 878-32 to GIT 878-35, GIT 878-37, GIT 878-51, GIT 878-53, GIT 878-54, GIT 878-72, GIT 878-81 • 2 specs; Sutlema quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-134, GIT 878-162 • 1 spec.; Urge quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 939-18 • 1 spec.; Vormsi Island; Kõrgessaare Formation, Vormsi Regional Stage; TUG 42-283.

Type locality and horizon

Saaremõisa (Lyckholm), N of Haapsalu; Kõrgessaare Formation, Vormsi Regional Stage.

Remarks

Previous descriptions of this common species in the Vormsi Regional Stage strata of Estonia focused on well-preserved features of mature specimens, including the siphuncle, septal necks (Kröger & Isakar 2006), and ornamentation (Kröger 2013). Here, new data about the variability of the angle of expansion, and ornamentation (Figs 9B, 13A) complement this knowledge, permitting the synonymy of *Spyroceras* sp. A of Strand (1934) with *P. senckenbergi*, because of its general similarity in conch shape and ornamentation. Also, based on the new data, and in contrast to previous lists of synonymies, *Spyroceras senckenbergi* in Dzik (1984) is synonymised with *P. senckenbergi*.

The data show that the angle of expansion tends to decrease with increasing conch size, being almost tubular in adult stages and up to 4–5° in juvenile growth stages (Fig. 13A). The largest specimen in the collection, specimen GIT 878-112, is a short fragment of a body chamber with a diameter of 30 mm. Only three specimens (GIT 878-53, GIT 878-112, TUG 1745-263) of the total collection (n= 89) have a diameter of more than 26 mm. This suggests an approximate adult size of the species of ca 25–30 mm.

It has been observed that the relative spacing of the annulation in *P. senckenbergi* decreases with conch size although it was not possible to substantiate quantitatively (Kröger & Isakar 2006). Here, based on measurements from 22 specimens, it can be shown that there is no ontogenetic trend in relative annulation distance in *P. senckenbergi* (Fig. 14B–C). The spacing of the annulation varies between 1–6 mm in all specimens, it is widest in fragments of mature specimens (Fig. 14B).

Palaeodawsonocerina ? sp.
Fig. 12K

Material examined

ESTONIA • 1 spec.; Hosholm shore; Adila Formation, Pirgu Regional Stage; TUG 939-78.

Description

The specimen is a ca 39 mm long, 18–20 mm high, orthoconic fragment (angle of expansion 3°) of a phragmocone with well-preserved shell sculpture. The conch cross section is slightly deformed. The conch is annulated with ca four annulations in a distance equal to the corresponding conch cross section. The annulations are directly transverse. The conch is ornamented with ca 60 fine longitudinal lirae around the circumference and subordinate transverse growth lines or lirae, producing a reticulate pattern (ca 10 transverse lirae per annulation). The septa are only partially preserved, the siphuncle and septal necks are not preserved. The sutures are positioned in the troughs of the annulations and are directly transverse parallel to the annulations.

Remarks

The finely reticulate ornamentation and the general conch shape of this specimen is similar to other species assigned to *P. senckenbergi*. It differs from the latter in having a wider spacing of its longitudinal lirae (1 mm and 60 lirae around circumference versus five to seven lirae per mm in *P. senckenbergi*).

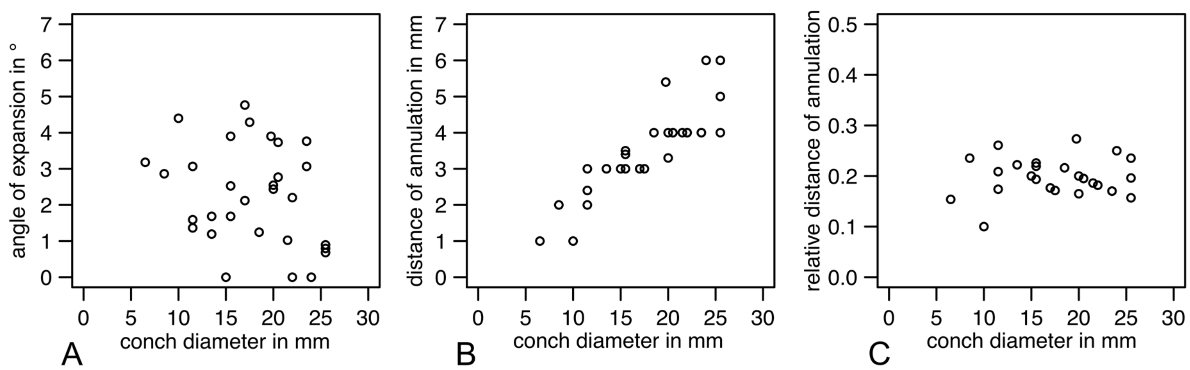

Fig. 14. Diagrams of morphological variability of specimens of *Palaeodawsonocerina senckenbergi* (Teichert, 1930), Pirgu–Vormsi regional stages, Estonia. **A**. Angle of expansion. **B**. Absolute distance of annulation. **C**. Distance of annulation relative to conch diameter. Note the constant relative distance of annulation throughout growth.

The fragmentary preservation of the internal characters leaves the genus level determination questionary because a similar fine reticulate ornamentation is known from *Anaspyroceras*, and *Gorbyoceras* (see e.g., Flower 1943b). Possibly, the specimen belongs to the same species as a specimen described by Strand (1934: 21) under *G. clathratoannulatum*, also ornamented with ca 60 longitudinal lirae.

Order Pseudorthocerida Flower & Caster, 1935
Family Proteoceratidae Flower, 1962

Genus ***Ephippiorthoceras*** Foerste, 1924

Type species

Orthoceras formosum Billings, 1857, from English Head, Anticosti Island, Quebec, Canada, English Head formation, zone 3 or 4 (Foerste 1928c) (= Vauréal Formation, see Achab *et al.* 2011), late Katian; by original designation.

Diagnosis

Orthocones with circular to slightly compressed conch cross section; smooth or ornamented with fine transverse and / or longitudinal striae and lirae or coarse oblique plications; sutures form distinct broad lateral lobes; siphuncle subcentral to central, cyrtochoanitic septal necks; siphuncular segments expanded slendering adorally, parietal endosiphuncular deposits occur. (Compiled from Flower 1962, and Sweet 1964c.)

Remarks

Flower (1962: 33) assigned *Ephippiorthoceras* into his newly erected Proteoceratidae and justified it, without being more specific, among other arguments with the comment "other material indicates adoral slendering of the segments of the siphuncle." Sweet (1964c: K256) assigned the genus with question into the Proteoceratidae and remarked that: "Details of the interior are not known in the type-species […] *Ephippiorthocras* is probably a pseudorthoceratid rather than a proteoceratid." The material described herein suggests that Flower's (1962) original evaluation was correct. In the Estonian specimens, a clear tendency for proteoceratid-like "slendering" is apparent. Moreover, the position of the siphuncle becomes more eccentric in later growth stages (see below).

Ephippiorthoceras vormsiense sp. nov.
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Figs 15A–C, 16A–B, 17

Diagnosis

Faintly exogastrically curved longicones to orthocones with an angle of expansion of up to 9°; lateral sutural lobes shifted slightly adorally at venter; mature conch height ca 38–40 mm, with maximum height reached near the base of the mature body chamber or at adoral-most part of the mature phragmocone; mature body chamber ca 90 mm long and constricted; siphuncular position subcentral in early growths stages, eccentric in latest growth stages; siphuncle fusiform, expanded in early growth stages and nearly tubular in latest growth stages with septal necks changing from cyrtochoanitic to suborthochoantic during ontogeny.

Etymology

Refers to the type locality, Vormsi Island.

Type material

Holotype

ESTONIA • Vormsi Island, Hosholm shore (tower locality), Adila Formation, Pirgu Regional Stage; GIT 878-192.

Paratypes

ESTONIA • 2 specs; same collection data as for holotype; GIT 878-195, GIT 878-228 • 2 specs; Vohilaid Island, Vohilaid shore (E), Adila Formation, Pirgu Regional Stage; GIT 878-193, GIT 878-194 • 2 specs; same data as for preceding; TUG 1745-28, TUG 1743-75.

Description

The holotype (GIT 878-192) (Fig. 15A) is the largest specimen, it reaches a conch height of 40 mm ca 25 mm adapically of the last septum on phragmocone. There, the conch width is 33 mm (CHI = 1.21).

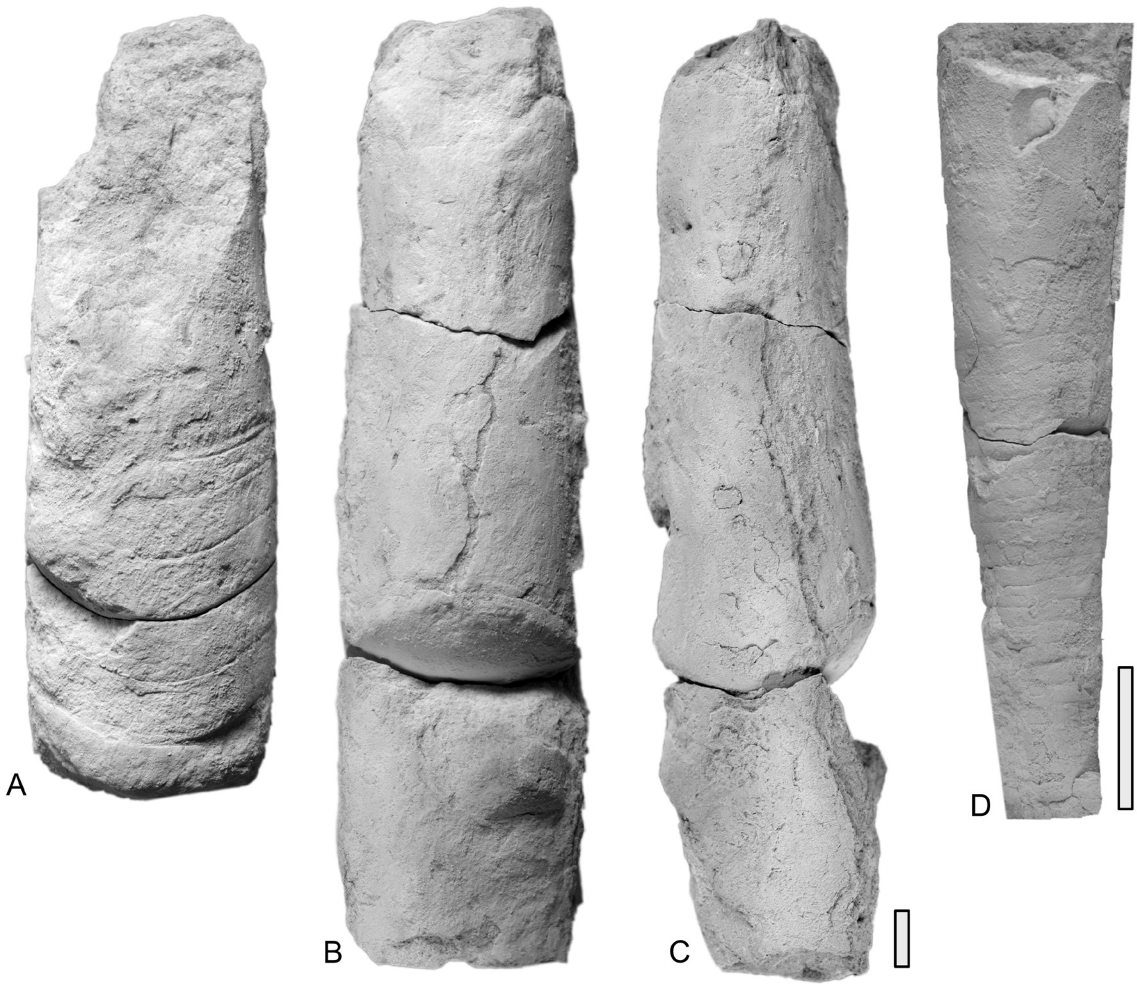

Fig. 15. Pseudorthoceratidae Flower & Caster, 1935 of the Vormsi–Pirgu regional stages, Estonia. **A–C**. *Ephippiorthoceras vormsiense* sp. nov. from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage. **A**. Specimen GIT 878-192, lateral view. **B–C**. Specimen GIT 878-228. **B**. Lateral view. **C**. Ventral view. **D**. *Isorthoceras saaremense* (Balashov, 1959) comb. nov., specimen GIT 878-41, from Saxby shore (N), Vormsi Island, Vormsi Regional Stage. Scale bar = 10 mm in all figures, same scale in A–C.

The phragmocone decreases in height and width toward 39 mm, 32 mm, respectively at the base of the body chamber. Only the basal ca 60 mm of the body chamber are preserved, they indicate a decreasing height toward the aperture. The sutures form a marked lateral lobe and have a distance of 7 mm (the adoralmost chamber) to 9 mm (RCL up to 0.23). The septal foramen is subcentral with a RSP of 0.39 at a conch height of 39 mm.

The mature body chamber is preserved in three specimens (GIT 878-192, GIT 878-194, GIT 878-228). Specimen GIT 878-228 (Fig. 15B) is a fragment of a phragmocone and a nearly complete mature body chamber, which is slightly deformed. At the base of the body chamber, the height and width are 35 mm, 37 mm respectively (CHI 0.95). The body chamber has a length of 90 mm and continuously decreases in diameter toward the aperture, where the width is 33 mm. The adapical ca 5 mm are constricted and apparently a ca 15 mm deep hyponomic sinus occurs on the prosiphuncular side. The adoralmost chamber of the phragmocone has a length of 4 mm, further adapicallly the sutures are 7 mm distant (RCL = 0.19). The sutures form a deep lateral lobe and are slightly more adorally located on the prosiphuncular side (the side with the hyponomic sinus) than on the opposite side. The preserved part of the phragmocone has an angle of expansion of 3° at a width of 35–37 mm. The septal foramen is nearly centrally positioned.

Specimen GIT 878-194 is a mold of a mature body chamber with a conch height and width at its base of 36 mm, 28 mm respectively (CHI = 1.29) and a preserved length of 70 mm. The height and width decrease adorally until at a point ca 45 mm from the base, the height is 31 mm. Further toward the aperture the height increases slightly, resulting in a body chamber outline with concave margins. The septal foramen at the last septum is subcentral (RSP = 0.33).

Specimen TUG 1743-75 is a slightly curved fragment of a phragmocone with heights of 23–31 mm and an angle of expansion of 9°, The sutures form distinct lateral lobes and are 5 mm apart at a conch height of 23 mm and 7 mm at a conch height of 30 mm (RCL: 0.22–0.23).

Measurements of the position of the septal foramen indicate a slight marginal shift of the siphuncle during growth with an RSP of 0.43 at a conch height of 23 mm (TUG 1745-286), toward and RSP of 0.38–0.39 at a conch height of 38–39 mm (GIT 878-192, GIT 878-193). The details of the siphuncle and septal neck are preserved in specimens GIT 878-192, GIT 878-193, and TUG 1745-28 (Fig. 16A–B). They reveal that the septal necks are cyrthochoanitic at earlier growth stages (conch heights < 33 mm) and suborthochoanitic near maturity (conch height 36–39 mm). The siphuncular segments are expanded fusiform in early growth stages and nearly tubular in later growth stages (Table 1).

Comparison

Ephippiorthoceras vormsiense sp. nov. has a smooth, or nearly so, conch surface, which differs from species which have a wrinkled or lirate ornamentation such as *E. laddi* Foerste, 1935b, *E. formosum*, *Ephippiorthoceras plicatuloides* Strand, 1934 (see also below), *E. plicatulum* Foerste in Twenhofel, 1928, *E. schucherti* Foerste, 1928c, *E. tenuistriatum* Foerste, 1935b. *Ephippiorthoceras altocameratum* Foerste, 1928c, and *E. sieboldi* (Billings, 1866) reach larger adult sizes (conch heights more than 55 mm

Fig. 16 (next page). Median sections of phragmocone of cephalopods of the Pirgu Regional Stage, Estonia. **A–B**. *Ephippiorthoceras vormsiense* sp. nov. **A**. Holotype (GIT 878-192), from Hosholm shore (tower), Vormsi Island. **B**. Specimen TUG 1745-28, from Vohilaid shore (E), Vohilaid Island. **C–D**. *Danoceras piersalense* (Teichert, 1930) comb. nov. **C**. Specimen TUG 80-510, from Piirsalu quarry. **D**. Specimen TUG 1745-296, from Pirgu River outcrop. **E**. *Dowlingoceras kallholnense* Frye, 1987, from GIT 878-247, from Hosholm shore, Vormsi Island. **F**. *Danoceras piersalense* specimen GIT 840-271, from Hosholm shore, Vormsi Island. **G**. *Beloitoceras* cf. *sinuoseptatum* (Roemer, 1861), specimen GIT 426-2 from Hosholm shore, Vormsi Island. Scale bars = 5 mm in all figures, same scale in A–G.

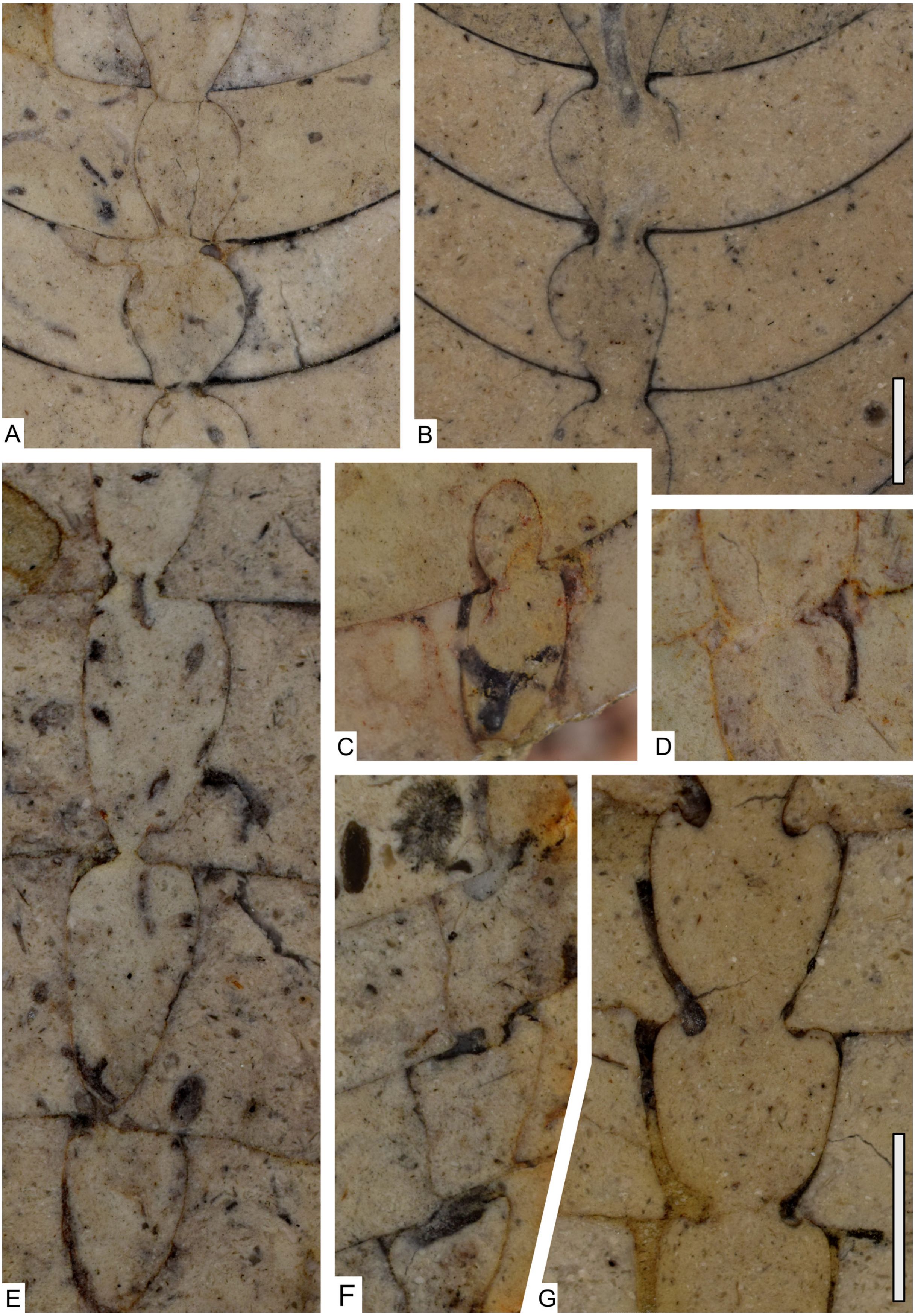
A
B
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Table 1. Shape of the siphuncular segments of *Ephippiorthoceras vormsiense* sp. nov., measured at specimens GIT 878-192, GIT 878-193, and TUG 1745-28.

Septal foramen height in mm	siphuncular segment height in mm	chamber length in mm	conch height in mm	RSS	SCR
2.5	3.5	8	39	1.4	0.44
2.3	5.3	6.7	30	2.3	0.79
2.5	5	7	26	2	0.71

at base of mature body chamber) (Foerste 1928c). *Ephippiorthoceras compressum* Foerste, 1928b differs in having strongly obliquely sloping sutures and a very low angle of expansion. *Ephippiorthoceras decorum* Teichert & Glenister, 1953 differs in having cameral and endosiphuncular deposits and a clearly more eccentrically positioned siphuncle. The siphuncle of *E. modestum* Troedsson, 1926 is more centrally positioned.

Strand (1934) described two species of *Ephippiorthoceras* from late Katian strata of Norway (*E. plicatuloides* Strand, 1934, *E. frognoyense* Strand, 1934). Details of the siphuncle and septal necks are unknown for either species. The two species are similar to *E. vormsiense* sp. nov. in size and suture shape but differ in having more narrowly spaced chambers (RCL = 0.13–0.14 in *E. frognoyense*) and have conspicuously wrinkled conchs (*E. plicatuloides*). Both species are known from one or two specimens only, making comparisons with the Estonian material difficult. The narrow chamber spacing could be interpreted as an effect of maturity, but the wrinkled surface is known from other species of the genus (see above). A synonymy of *E. vormsiense* with one of the Norwegian species is therefore unlikely.

Genus ***Gorbyoceras*** Shimizu & Obata, 1935

Type species

Orthoceras gorbyi Miller in Miller & Faber, 1894, from Franklin County, Indiana, probably Saluda Formation, latest Katian, USA; by original designation.

Diagnosis

Slender, circular or slightly compressed orthocones with symmetrically curved septa and straight transverse sutures; sutures parallel to annulations in each groove of the annulations; annulations with

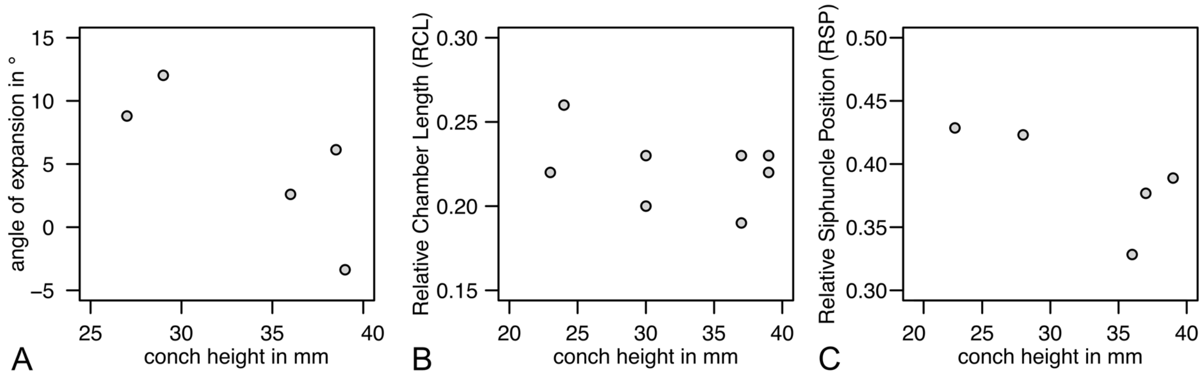


Fig. 17. Diagrams of morphological variability of specimens of *Ephippiorthoceras vormsiense* sp. nov., Pirgu Regional Stage, Estonia. **A**. Angle of expansion. Note the decreasing conch width (negative angle of expansion) at mature growth stages. **B**. Relative chamber length. **C**. Relative siphuncle position.

fine transverse ornament or growth lines; annulations more prominent in adult growth stages; distinct irregularly spaced longitudinal ridges that may form nodes at the ridges of the annulations; siphuncle subcentral, expanded in early growth stages, with short cyrtochoanitic septal necks, nearly tubular in later growth stages, with suborthochoanitic septal necks; mural cameral deposits developed much farther anteriorly than endosiphuncular deposits. (Adopted from Kröger 2013.)

Remarks

Gorbyoceras and *Dawsonoceras* share many similarities. Following the diagnosis in the *Treatise* (Sweet 1964c), both are slender, annulated, orthocones with a transverse and longitudinal ornamentation; in both genera species with curved mature growth stages occur; in both genera the siphuncle is centrally positioned or nearly so, and tubular to slightly expanded; and in both genera the septal necks are very short, varying between achoanitic to suborthochoanitic to very short cyrtochoanitic, and small endosiphuncular annuli occur. The asserted difference between the two genera is the shape of the siphuncle and its ontogenetic change (Flower 1946; Sweet 1964c). In *G. gorbyi* and closely related species, such as *G. grossi* Flower, 1946, the siphuncle is clearly expanded (Flower 1946: 146). Flower (1946: 144–145) emphasized the ontogenetic variability of the siphuncular segments of species of *Gorbyoceras*. In several of them, "in general the outline of the segments becomes gerontically simplified, approaching an orthochoanitic condition […]" (Flower 1946: 145). Therefore, *Gorbyoceras* is placed within the Proteoceratidae of the Pseudorthocerataceae in the *Treatise* (Sweet 1964c: K256). In contrast, Frey (1995: P63) stated that no evidence exists for an ontogenetic change of siphuncular segments from expanded barrel-shape to subcylindrical in *Gorbyoceras*, and thus questioned the classification of *Gorbyoceras* within the Proteoceratidae.

The siphuncular segments of the *Dawsonoceras* are described as subcylindrical, and as "abruptly constricted at septal foramina" (Sweet 1964c: K238). Therefore, in the *Treatise*, *Dawsonoceras* as type of the Dawsonoceratida is placed within the Orthocerataceae (Sweet 1964c: K238). However, the shapes of the siphuncle and septal necks are not known from the type-species *D. hyatti* (see Foerste 1928a: 273–276, and Foerste 1928b: 28–29). In the *Treatise*, the illustrated details of the siphuncle and septal necks of *Dawsonoceras* are taken from Flower (1946: fig. 11), which is a generalized scheme not attributable to a specific species. The concept of *Dawsonoceras* in Sweet (1964c) was largely adopted by Kröger & Isakar (2006) and in later publications (Kröger 2007, 2013), placing the Late Ordovician *Cycloceras fenestratum* Eichwald, 1860 into *Dawsonoceras*.

However, Sweet (1964c) and Kröger & Isakar (2006) were not aware of, or ignored, Horny's (1956) revision of *Dawsonoceras*. In this revision, a much narrower concept of *Dawsonoceras* was suggested, restricting the genus to annulated forms with a frilled ornamentation (Horny 1956: 462). Furthermore, Horny (1956: pl. 3 figs 2–4) described and illustrated the details of the well-preserved siphuncle and septal necks of specimens closely related to the Silurian type of *Dawsonoceras* (*D. hyatti*), and type material of *D. annulatum* (Sowerby, 1816) from the British Wenlock. The siphuncle of these specimens is tubular, slightly expanded into the chambers, and adnate to the septa, and the septal necks are very short achoanitic or cyrtochoanitic. Hence, the ornamentation and the internal details of Ordovician species attributed to *Dawsonoceras*, such as *Cycloceras fenestratum* Eichwald, 1860 (Kröger & Isakar 2006: fig. 8b; Kröger 2013: fig. 13a) differ considerably from the Silurian material described by Horny (1956) and are outside of his diagnosis of *Dawsonoceras*.

Accepting Horny's (1956) diagnosis has consequences for recent approaches to classifying *Dawsonoceras* and *Gorbyoceras* (Pohle *et al.* 2022), which were based on descriptions of specimens assigned to *C. fenestratum* and *G. textumamareum* (Roemer, 1861) by Kröger & Isakar (2006) and Kröger (2013). Therein, *Gorbyoceras* was placed within the Dawsonoceratidae (Pohle *et al*. 2022).

Here, Horny's (1956) diagnosis is accepted. Therefore, *C. fenestratum* (probably together with the similarly ornamented *D. gregarium* Kröger *et al*., 2011) need to be assigned to a genus other than Dawsonoceras (a task beyond the scope of this paper). Moreover, the Estonian material studied herein, supports Flower's (1946) opinion that the siphuncle of *Gorbyoceras* changes from an expanded barrel shape towards subcylindrical (see Remarks chapter of *G. textumamareum*) during ontogeny, and hence the genus is best classified within the Proteoceratidae as suggested earlier (e.g., Sweet 1964c).

Gorbyoceras clathratoannulatum (Roemer, 1861) comb. nov.
Figs 11B–C, 12C, H, 18

Orthoceras clathrato-annulatum Roemer, 1861: 57–58, pl. 7 figs 4a–b.

Orthoceras clathrato-annulatum – Roemer 1885: 52, 67, fig. 10a–b, pl. 3 fig. 10. — Rüdiger 1889: 51–52, 85. — Sauramo 1929: 8, 10. — Dzik 1984: pl. 35 fig. 4a–c.
Spyroceras clathrato-annulatum – Teichert 1930: 278, 280, pl. 5 fig. 5. — Balashov 1953a: 212.
Spyroceras cf. *clathrato-annulatum* – Strand 1934: 21 (partim).

Diagnosis

Annulated orthocones with circular conch cross section; adult conch diameter ca 20 mm; mature body chamber with decreasing conch diameter toward aperture and slightly bent against adapical conch part; ornamented with three to four annulations in a distance equal to the corresponding conch diameter; annulations straight transverse or very slightly oblique and slightly irregularly spaced; ornamented with ca 30 fine longitudinal and subordinate transverse lirae, about 10–15 transverse lirae per cycle of annulations; suture lines located in the troughs of the annulations and equally spaced as annulations; parallel sutures and annulations; siphuncle central, barrel-shaped, expanded in early growth stages, nearly tubular in late growth stages; septal foramen approximately one tenth of the diameter, septal necks short cyrtochoanitic to suborthochoanitic, endosiphuncular and cameral deposits not known.

Material examined

ESTONIA • 1 spec.; Vormsi Island, Hosholm shore; Adila Formation, Pirgu Regional Stage; GIT 840-138 • 3 specs; same data as for preceding; TUG 899-80, TUG 1445-232, TUG 1745-14 • 7 specs; Vormsi Island, Hosholm shore (tower locality); Adila Formation, Pirgu Regional Stage; GIT 840-265, GIT 840-266, GIT 878-285 to GIT 878-287, GIT 878-298, GIT 878-305 • 1 spec.; Vohilaid Island; Vohilaid outcrop 8 (8 after B. Stein), Pirgu Regional Stage; GIT 878-149.

Type locality and horizon

Zawidowice by Oleśnica, Poland; erratic boulder, Vormsi–Pirgu regional stages ("Lyckholm Stufe" of Teichert 1930).

Description

Nine specimens with mature body chambers are in the Estonian collections (GIT 840-265, -266, GIT 878-149, -285, -286, -287, -298, -305, TUG 899-80, TUG 1445-232, TUG 1745-14) (Fig. 12H). Amongst these specimens' the conch diameter at the base of the body chamber varies between 18–22 mm (mean = 20.1 mm). At the position of the base of the mature body chamber the conch is slightly curved. In specimen GIT 878-149, the body chamber deviates ca 10° against the adapical part of the conch; it is ca 45 mm long and decreases from 22 mm at its base to a diameter of 19 mm at ca 30 mm from the base, indicating maturity. Adorally, toward the mature aperture, the diameter again increases to 20 mm, forming an irregular constriction with one or two shallower and irregularly spaced annuli. Similar body chamber modifications occur in the other specimens.

The conchs are annulated with ca three to four annulations in a distance equal to the corresponding conch cross section (mean RCL = 0.28, n = 16). There is no ontogenetic trend of decreasing or increasing relative distance of the annulations (Fig. 18B). The conch surface is poorly preserved in all specimens, but where visible, ca 28–30 shallow longitudinal lirae occur around the circumference.

The maximum apical angle measured in a juvenile specimen is ca 8° (specimen GIT 840-138). The angle of expansion decreases with increasing conch diameter (Fig. 18A). The septa are equally spaced as the annulations, are invariably positioned within the troughs of the annulations, and like the annulations, are directly transverse. The position of the siphuncle is central or nearly so. In specimen GIT 840-138, the septal foramen is ca 1 mm in diameter where the conch diameter is 10 mm and in specimen GIT 878-149, the septal foramen is 1.5 mm where the conch diameter is 22 mm. The septal necks are short cyrtochoanitic in early growth stages (specimen GIT 840-138, Fig. 11C) and suborthochoanitic in late growth stages (specimen GIT 878-149, Fig. 11B). The shape of the siphuncle accordingly varies from an expanded barrel shape in early growth stages to subtubular in late growth stages.

Remarks

Roemer's (1861) original description of *O. clathrato-annulatum* is based on material, which very likely represents multiple taxa of annulated orthocones. The original description emphasized the reticulate pattern (with finer transverse than longitudinal lirae), and the decreasing conch diameter of the mature body chamber as diagnostic characters of this species (Roemer 1861: 58). No explicit information regarding the number of longitudinal lirae was provided by Roemer (1861). The only illustrated specimen has 22 longitudinal lirae in lateral view (suggesting a total of ca 40–45 lirae), and ca three to four annulations in a distance similar to the conch diameter (Roemer 186: pl. 7 fig. 4).

Roemer (1861: 58) distinguished *O. clathrato-annulatum* from the similar *O. textum-araneum* by the position of the siphuncle (central in the former), the adult size (much larger in the latter), and the shape of the mature body chamber (curved in the latter).

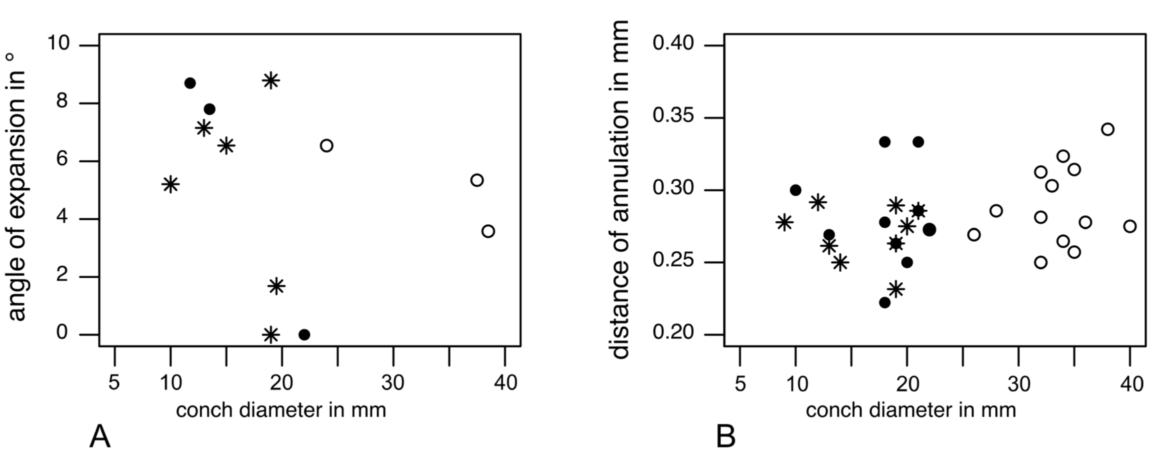


Fig. 18. Diagrams of morphological variability of specimens of *Gorbyoceras* Shimizu & Obata, 1935 from Vormsi–Pirgu regional stages, Estonia. **A**. Angle of expansion. Note the low values (nearly mature specimens of *G.* sp. and *G. stumburi* Kröger 2013). **B**. Distance of annuli relative to corresponding conch height. A species distinction of specimens smaller ca 15–20 mm is not possible based on angle of expansion and relative chamber distance. Circles = *G. textumaraneum* (Roemer, 1861); filled circles = *G. clathratoannulatum* (Roemer, 1861) comb. nov.; stars = *G.* sp., and *G. stumburi*.

However, Dzik (1984: pl. 35 fig. 4a–c) figured a fragment of a phragmocone as holotype of *O. clathrato-annulatum* with no traces of the fine reticulate pattern described in the original description, leaving some uncertainty about the ornamentation of this species. Moreover, this specimen has great similarities to specimens described herein under *Striatocycloceras hosholmensis* sp. nov. The internal characters and details of ornamentation of this specimen, however, remain unknown.

Teichert (1930), followed Roemer's (1861) concept of *O. clathrato-annulatum* (i.e., reticulate ornamentation, relatively small mature body chamber with decreasing conch diameter), and distinguished two, roughly similar species in the strata of Lyckholm, Estonia: a large-sized *Spyroceras textum-araneum* and a smaller *Spyroceras clathrato-annulatum*. A reinvestigation of Roemer's (1861) type material is needed to clarify if Teichert's (1930) interpretation of *O. clathrato-annulatum* is consistent with the types or if this species needs a radical reinterpretation (i.e., if *S. hosholmensis* sp. nov. is a subjective junior synonym of *O. clathrato-annulatum* and if the species described herein under G. *clathratoannulatum* represents a new species).

For the time being, the diagnosis, given herein, follows Teichert's (1930) interpretation. Details of the ornamentation of *O. clathrato-annulatum*, and of the siphuncle and septal necks, which are missing in Roemer (1861) and Teichert (1930), are appended to the diagnosis, based on the new Estonian material.

Strand (1934) described several specimens from the Late Ordovician "Gastropod Limestone" of Norway under *Spyroceras* cf. *clathrato-annulatum.* The Norwegian specimens, ornamented with ca 40 longitudinal lirae, and described under this taxon, probably belong to *G. textumaraneum* or *Gorbyoceras*? *stumburi* (Kröger 2013) (see below). The specimen described by Strand (1934: 21), ornamented with ca 60 longitudinal lirae and an apical angle of 7–8° at conch diameters up to 21 mm, is certainly not a *G. clathratoannulatum*, because at this size, this species has a nearly tubular conch or is decreasing in diameter, as well as possessing a smaller number of longitudinal lirae. It can probably be synonymized with specimen TUG 939-78, described herein as *Palaeodawsonoceras*? sp. A.

Gorbyoceras stumburi (Kröger, 2013)
Figs 12J, 18

Dawsonoceras stumburi Kröger, 2013: 32–34, figs 16e, 17b.

Dawsonoceras sp. – Kröger & Isakar 2006: 157, figs 10e, j, 12h.

Diagnosis

Annulated orthocones with angle of expansion of ca 5° and circular cross section; ca five relatively shallow annulations occur in a distance similar to conch diameter; approximately 40 longitudinal lirae occur around shell circumference, more than 10 pronounced transverse striae occur per cycle of annulations; septal necks achoanitic; siphuncle subcentral, fusiform, expanded within chambers. (Adopted from Kröger 2013.)

Material examined

ESTONIA • 1 spec.; Vormsi Island, Hosholm shore; Adila Formation, Pirgu Regional Stage; TUG 1745-47 • 1 spec.; Harilaid; Vormsi–Pirgu regional stages; TUG 939-30 • 1 spec.; Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; TUG 939-21.

Type locality and horizon

Kallholn, Siljan District, Sweden; Boda Limestone, Boda Core Member, late Katian, Ordovician.

Description

Specimen TUG 1745-47 is a slightly curved fragment of a mature body chamber with a length of ca 35 mm and a maximum diameter of 20 mm. Approximately five annulations occur in a distance similar to the conch diameter. The surface is ornamented with ca 40 longitudinal lirae around the circumference and fine growth lines. At its base, the fragment has a diameter of 19 mm and a chamber of the phragmocone is preserved with two septa which are 5 mm distant. The septa are located in the troughs of the respective annulations and are directly transverse, parallel to the annulations. The septal foramen is poorly preserved but apparently slightly eccentric in position and located toward the convex side of the conch curvature.

Specimen TUG 939-30 (Fig. 12J) is a nearly tubular fragment of a body chamber with relatively well-preserved conch surface showing ca 40 longitudinal lirae across the circumference and fine transverse lirae or raised growth lines (ca 10–12 per cycle of annulation). The spacing of the annulation is relatively narrow with 5–6 cycles of annulations per distance similar to the corresponding conch cross section.

Remarks

No new data on the internal characters of this species can be added with the Estonian material. The species was originally placed within *Dawsonoceras*. However, based on the similarity of the known characters from this species with other species of *Gorbyoceras* and following the more restricted genus diagnosis of *Dawsonoceras* of Horny (1956), followed herein (see above), a placement within *Gorbyoceras* is suggested, herein.

Gorbyoceras textumaraneum (Roemer, 1861)
Figs 11D, 12D–E, L–M, 18

Orthoceras textum-araneum Roemer, 1861: 58–59, pl. 7 fig. 3a–b.

Orthoceras textum-araneum – Rüdiger 1889: 52–53.
Spyroceras textum-araneum – Teichert 1930: 280, pl. 5 fig. 6.
Spyroceras cf. *clathrato-annulatum* – Strand 1934: 21 (partim).
Spyroceras textum-aranaceum [sic] – Balashov 1953a: 212; 1955: 98–99, pl. 45 fig. 3; 1962b: 108, pl. 48 fig. 1.
Gorbyoceras textumaraneum – Dzik 1984: 121, text-fig. 49.15, pl. 35 fig. 6. — Kröger & Isakar 2006: 158–159, figs 8c, 10c–d, 12a–b. — Pohle *et al*. 2022: fig. 2.

Diagnosis

Slightly compressed orthocones with curved mature body chamber; adult conch diameter ca 40 mm; ornamented with three to four annulations in a distance equal to the corresponding conch diameter; annulations straight or very slightly oblique to the normal of the conch axis and slightly irregularly spaced; fine growth lines, about 15 per annulation; additionally ornamented with fine longitudinal lirae; suture lines in the troughs of the annulations and equally spaced with the annulations; parallel sutures and annulations; siphuncle eccentric in juvenile, subcentral in more adult growth stages; septal foramen approximately one tenth of the diameter. (Compiled from Roemer 1861 and Kröger & Isakar 2006.)

Material examined

ESTONIA • 1 spec.; Haapsalu holm; Adila Formation, Pirgu Regional Stage; TUG 1745-238 • 1 spec.; Vormsi Island, Hosholm shore; Adila Formation, Pirgu Regional Stage; TUG 1743-77 238 • 5 specs; Vormsi Island, Hosholm shore (N); Adila Formation, Pirgu Regional Stage; GIT 878-223, GIT 878-224, GIT 878-282 to GIT 878-284 • 1 spec.; Mõnuste quarry; Kõrgessaare Formation, Vormsi Regional

Stage; TUG 1745-193 • 1 spec.; Paluküla quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 225-968 • 5 specs; Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage; GIT 878-143, GIT 878-299 to GIT 878-301, GIT 878-306.

Type locality and horizon

Zawidowice by Oleśnica, Poland; erratic boulder, Vormsi–Pirgu regional stages ("Lyckholm Stufe" of Teichert 1930).

Description

The largest specimen of this species in the Estonian collections is TUG 1745-193 from Mõnuste quarry, Vormsi Regional Stage (Fig. 12L). The specimen is a nearly complete internal mold of a slightly curved body chamber and one chamber of the phragmocone with maximum conch height of 37 mm and conch width 41 mm at the adoral end of the preserved part of the body chamber. The body chamber is ca 100 mm long with conch height ca 32 mm and conch width ca 35 mm at its base, and with eight directly transverse annulations. The five adapical annulations of this specimen are regularly spaced, 10–12 mm apart, with widely rounded troughs and more sharper ridges. The three adoral annulations are less well pronounced and irregularly spaced with distances between 12–16 mm. On the adoralmost part of the specimen, traces of distinct irregularly spaced longitudinal lirae are preserved, which are ca 3–4 mm apart, and which would amount to ca 40 around the entire circumference. The two septa preserved at the adapical end of the specimen are 11 mm apart and are positioned in the mid-troughs of the respective annulation. Traces of the septal foramen and siphuncle are not preserved.

Seven specimens with adult body chambers are preserved (GIT 878-143, GIT 878-224, GIT 878-223, GIT 878-282, GIT 878-283, TUG 1745-193, TUG 1745-238) with conch heights at their bases ranging from 32–35 mm (mean = 33 mm); all are slightly curved and have in the adoral third, a section with irregularly spaced, less well pronounced, annulations (Fig. 12L–M).

The internal characters are preserved in GIT 878-299, a slightly curved fragment of a phragmocone with a diameter of 29–32 mm. There, the septal foramen has a diameter of ca 2.8 mm, is eccentric on the convex side of the conch curvature 12 mm from the conch margin at its adapical end. The septal necks are poorly preserved, but apparently suborthochoanitic, and the siphuncle is slightly expanded to nearly tubular in shape (Fig. 11D).

Remarks

The information available for this species regarding the number of longitudinal lirae across the circumference is confusing. Roemer (1861: 59) counted 22–24 lirae, but in the original illustration (Roemer 1861: pl. 7 fig. 3) 17–18 lirae are visible in lateral view, suggesting a total of ca 35 lirae. There is no evidence that the number of lirae changed during ontogeny. Therefore, Kröger & Isakar (2006: 158) included number of "approximately 35 irregularly spaced longitudinal ridges" in their species diagnosis of *G. textumaraneum*.

In contrast, a photograph of the lectotype of *G. textumaraneum* in Dzik (1984: pl. 35 fig. 6) supports the 22–24 lirae count of Roemer (1861: pl. 7 fig. 3). The specimens described by Kröger & Isakar (2006) under *G. textumaraneum* have ca 40 lirae. The only Estonian specimen with surface characters preserved (specimen TUG 1745-193) also has ca 40 longitudinal lirae around the circumference. More well-preserved material is needed to evaluate the diagnostic value of this character (i.e., the number of longitudinal lirae) for *G. textumaraneum*. Strand (1934: 21) described annulated specimens (with three and a half annulations per length equal to diameter), ornamented with ca 40 longitudinal lirae from the Late Ordovician "Gastropod Limestone" under *Spyroceras* cf. *clathrato-annulatum*, which can be synonymized with the material described herein.

Additionally, growth stages of *G. textumaraneum* with conch diameters < ca 20 mm are poorly known. The species most conspicuous features are confined to the mature body chamber and a smaller species with similar general conch shape and ornamentation exists (*G. stumburi*). Fragments with diameters smaller than the adult diameter of *G. stumburi* (ca 20 mm) therefore cannot be assigned to either *G. stumburi* or *G. textumaraneum*. Five specimens (TUG 1745-275, 1745-300, 1745-301, TUG 1819-85, TUG 1827-61) with an ornamentation of the aspect of *G. stumburi* and G. *textumaraneum* and diameters > 20 mm and assigned to *Gorbyoceras* sp. are included in the measurements to illustrate the morphological variability of the entire cohort (Fig. 18A–B) (see measurements in supplementary data 3).

Gorbyoceras sp. A
Fig. 12N

Material examined

ESTONIA • 1 spec.; Kohila quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 42-417.

Description

The specimen is a ca 75 mm long fragment of a curved body chamber with external sculpture partly preserved. The original diameter was larger than 35 mm. The fragment is annulated with ca 4–5 regularly spaced annulations per distance equal to the corresponding conch diameter. The annulations are relatively shallow. Additionally, the conch is ornamented with numerous fine longitudinal lirae and subordinate transverse growth lines, producing a reticulate pattern. The longitudinal and transverse lirae are ca 1 mm distant.

Remarks

The ornamentation of this fragment is similar to other species of *Gorbyoceras*. Its curved, relatively large body chamber (conch diameter > 35 mm) is similar to *G. textumaraneum*, from which it differs by its fine reticulate ornamentation. The fragmentary preservation of this specimen does not permit a species level determination.

Genus ***Isorthoceras*** Flower, 1962

Type species

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

Diagnosis

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 to cyrtochoanitic; endosiphuncular annuli grow forward and backward, joining those of adjacent segments to form continuous parietal lining of uniform thickness throughout segments; mural to episeptal cameral deposits. (Compiled from Flower 1962 and Frey 1995.)

Isorthoceras luhai (Stumbur, 1956) comb. nov.
Figs 19A–C, F, 20–21

Orthoceras luhai Stumbur, 1956: 179–180, text-fig. 1, pl. 1 figs 2–3, pl. 2 fig. 4, pl. 3 fig. 1.
Michelinoceras dnestrovense Balashov, 1975: pl. 2 figs 7–8.
Isorthoceras dalecarlense Kröger *et al.*, 2011: 45, fig. 9c, g.

Isorthoceras dalecarlense – Kröger 2013: 58–59, figs 4b, 26.

Diagnosis

Smooth, nearly straight *Isorthoceras* with circular cross section and comparatively low angle of expansion of 6°, chamber distance 0.3 of corresponding cross section, depth of septal curvature ca 0.26 of corresponding cross section; adult size > 35 mm in cross section; siphuncle eccentric in early, subcentral in later growth stages, siphuncular segments slightly expanded within chambers with diameter ca 0.1 of conch cross section; septal necks short, bordering between cyrtochoanitic and suborthochoanitic; in apical parts of siphuncle thin parietal deposits, that ventrally fuse forming irregular endosiphuncular lining in extreme apical part of conch; cameral deposits not known. (From Kröger *et al.* 2011.)

Material examined

ESTONIA • 1 spec.; Haapsalu holm; Adila Formation, Pirgu Regional Stage; TUG 2-359 • 1 spec.; Vormsi Island, Hosholm shore (tower outcrop); Adila Formation, Pirgu Regional Stage; GIT 878-291 • 1 spec.; Jootma ditch; Moe Formation, Pirgu Regional Stage; GIT 426-577 • 1 spec.; Kohila; Kõrgessaare Formation, Vormsi Regional Stage; TUG 939-1 • 1 spec.; Paluküla quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-1108 • 1 spec.; Saksi manor; Kõrgessaare Formation, Vormsi Regional Stage; TUG 1745-215 • 2 specs; Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; TUG 80-474, TUG 895-24 • 4 specs; Vormsi Island, Saxby shore (N); Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-1124, GIT 878-30, GIT 878-45, GIT 878-60 • 1 spec.; same data as for preceding; TUG 1745-222.

Type locality and horizon

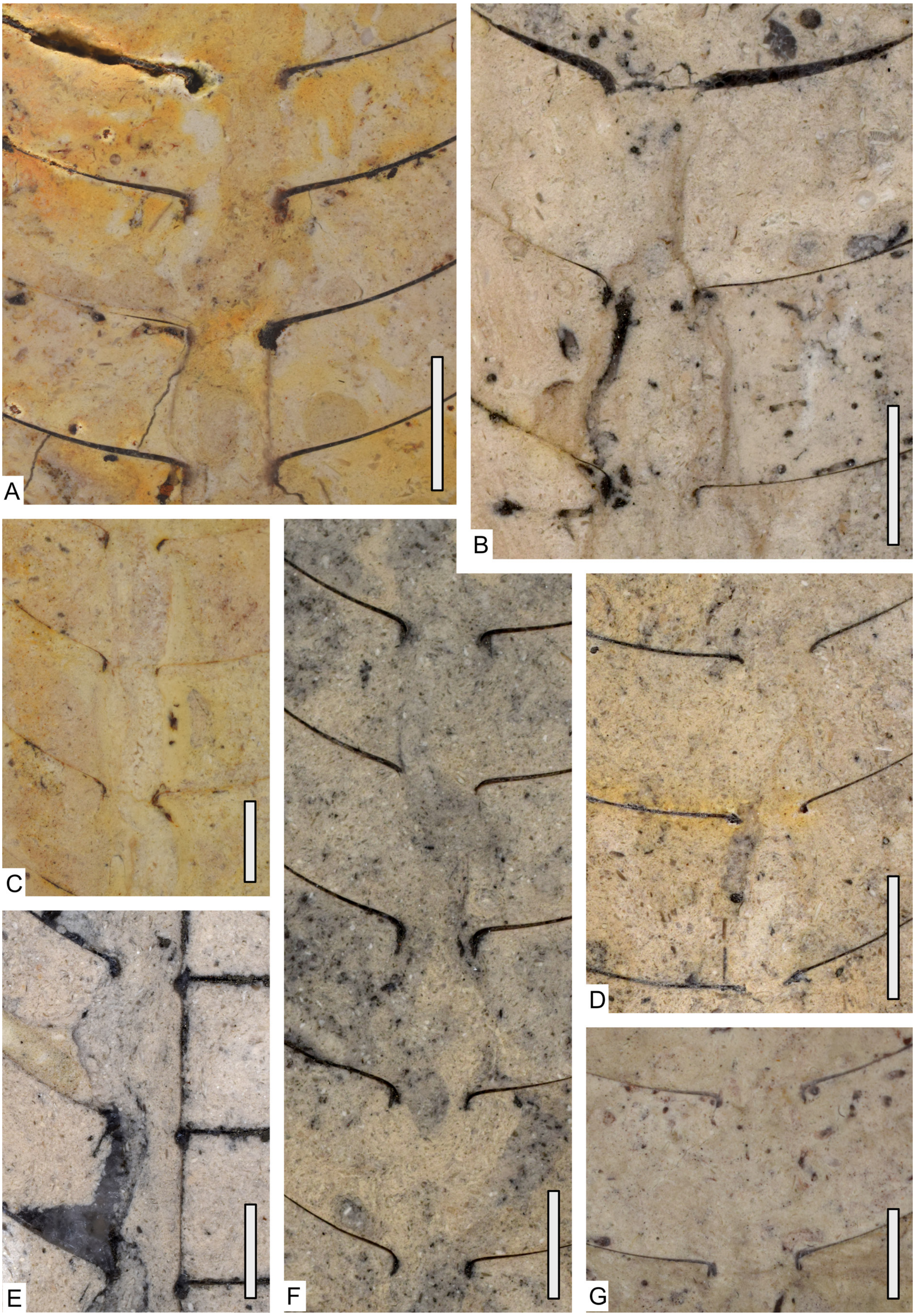
Kohila, Estonia; Vormsi Regional Stage.

Description

This species was described in detail as *I. dalecarlense* in Kröger *et al.* (2011) and Kröger (2013). Here, new data regarding the variability of the angle of expansion, the relative chamber length and the relative siphuncle position can be added – especially for specimens with diameters larger than 20 mm (Figs 20–21). The data show that the apical angle decreases from a maximum of 8° at conch diameters 16–20 mm (specimen TUG 80-474) to a minimum of 3° at conch diameters 29–32 mm (specimens GIT 426-1108, GIT 878-30) (Fig. 20A). Similarly, the relative chamber length decreases in growth stages greater than 16 mm in diameter, reaching maximum values at ca 16 mm with an RCL of 0.32 (specimen TUG 895-24) and minimum values of an RCL of less than 0.2 at conch diameters larger than 24 mm (specimens GIT 426-1108, GIT 878-60, GIT 878-291) (Fig. 20B). The position of the siphuncle changes during ontogeny from RSP 0.32 (specimen TUG 2-359) at a conch diameter of 12 mm toward a central position in specimens with diameters larger than 30 mm (specimen GIT 878-30) (Fig. 20C).

The septal necks are short suborthochoanitic with a siphuncle that appears to be more expanded, barrel-shaped in earlier growth stages and more tubular in later growth stages (Fig. 19A–C, F). Endosiphuncular

Fig. 19 (next page). Median sections of phragmocones of *Isorthoceras* Flower, 1962 of the Vormsi–Pirgu regional stages, Estonia. **A–C**. *Isorthoceras luhai* (Stumbur, 1956) comb. nov. **A**. Specimen GIT 426-1108 from Paluküla quarry, Vormsi Regional Stage. **B**. Specimen GIT 838-30 from Saxby shore, Vormsi Island, Vormsi Regional Stage. **C**. Holotype TUG 939-1, from Saxby shore, Vormsi Island, Vormsi Regional Stage. **D**. *Isorthoceras saaremense* (Balashov, 1959) comb. nov., specimen GIT 878-20, from Saxby shore, Vormsi Island, Vormsi Regional Stage. **E**. *Isorthoceras* sp. E, GIT 426-1132, from Saxby shore, Vormsi Island, Vormsi Regional Stage. **F**. *Isorthoceras luhai*, specimen GIT 426-1108, from Paluküla quarry, Vormsi Regional Stage. **G**. *Isorthoceras saaremense*, TUG 1745-305, from Kersleti old quarry, Vormsi Regional Stage. Scale bars = 5 mm in all figures.


A
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G

and cameral deposits are absent in the specimens which were cut and polished at median position. These have diameters larger than ca 15 mm.

Remarks

The species was established based on a single, poorly preserved specimen (holotype: GIT 939-1, Fig. 19C). With the nine specimens, described herein, the range of variation of this species becomes apparent (measurements are available in supplementary data 3). The new data reveal that the type-material of *I. dalecarlense* Kröger *et. al.*, 2011 is, at comparable growth stages, well within the known range of variation of the shell features of *I. luhai* (Fig. 20). Therefore, *I. dalecarlense* must be interpreted

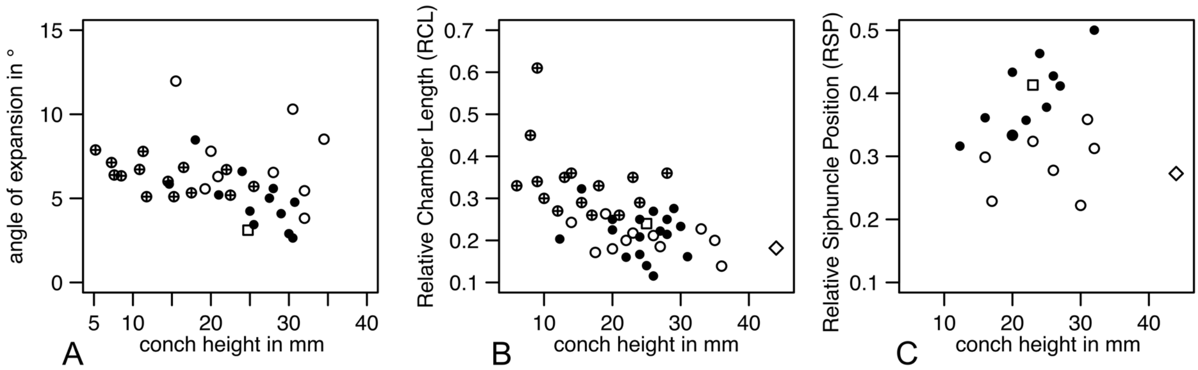


Fig. 20. Diagrams of morphological variability of specimens of *Isorthoceras luhai* (Stumbur, 1956) comb. nov. and *Isorthoceras saaremense* (Balashov, 1959) comb. nov. from Vormsi–Pirgu regional stages, Estonia. **A**. Angle of expansion. **B**. Relative chamber length. **C**. Relative siphuncle position. Explanation of symbols: circle = *I. saaremense*; filled circle = *I. luhai*; circle plus = types of *I. dalecarlense* Kröger *et al.*, 2011; diamonds = type of *Hedstroemoceras saaremense* Balashov, 1959; squares = type of *Michelinoceras dnestrovense* Balashov, 1975. Note the difference in siphuncle position between *I. luhai* and *I. saaremense.*

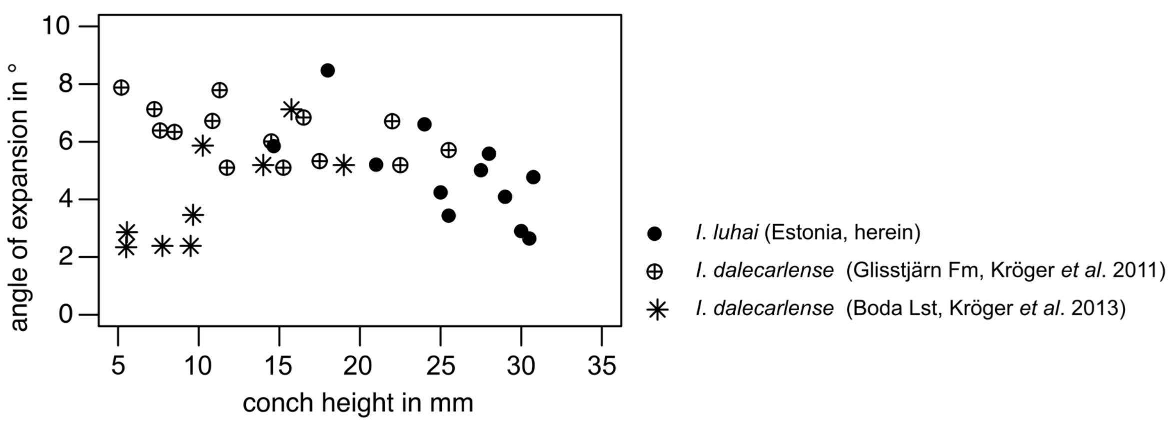


Fig. 21. Diagram of the variation in angle of expansion in specimens assigned to *Isorthoceras dalecarlense* Kröger *et al.* 2011, and *Isorthoceras luhai* (Stumbur, 1956) comb. nov. Abbreviations: Fm = Formation; Lst = Limestone. Explanation of symbols: black circles = *I. luhai* (herein); circle plus = types of *I. dalecarlense* in Kröger *et al.* 2011; stars = *I. dalecarlense* in Kröger 2013. Note the divergent angle of expansion in specimens assigned to *I. dalecarlense* in specimens < 10 mm. See text for discussion.

as subjective junior synonym of *I. luhai*. The same can be said for *Michelinoceras dnestrovense* Balashov, 1975 from late Katian strata of Podolia, Ukraine (see Fig. 20).

The Estonian fragments are on average larger in diameter than the types of *I. dalecarlense* from the Glisstjärn Formation, Hirnantian, Sweden (Kröger *et al.* 2011). Together with the Swedish material described as *I. dalacarlense* from the Boda Limestone, Sweden, this now permits an evaluation of the ontogenetic changes of the angle of expansion, of the RCL, and the RSP from juvenile stages to near maturity (Figs 20–21).

As a result, divergent trajectories in early growth stages for the angle of expansion between the samples of *I. dalecarlense* from the Glisstjärn, and from that of the slightly older Boda Formation, Sweden (see Kröger 2013: fig. 26) are evident. The specimens assigned to *D. dalecarlense* from the Boda Formation initially have a low angle of expansion, which increases toward a diameter of ca 15 mm. The Glisstjärn material, in contrast, shows a continuously decreasing angle of expansion throughout ontogeny (Fig. 21) (Note: in Kröger 2013: fig. 26, correctly the grey dots represent the type-material and the dots with black circles the Boda material, compare Kröger *et al.* 2011: fig. 10). This difference could be interpreted as an intraspecific variability within *I. luhai* or, alternatively as evidence for the presence of two different species, one in the Boda Formation and another in the Glisstjärn Formation. Additional specimens of the smaller size fraction from Estonia are needed to test if the Estonian *I. luhai* follows the early ontogeny trajectory of the *I. dalecarlense*-type material from the Glisstjärn Formation or that of the Boda Formation. The latter case would open the possibility to distinguish between *I. luhai* with a low juvenile angle of expansion and *I. dalecalense* with a high juvenile angle of expansion. Until more material is known, the most parsimonious solution to the problem is followed, which is to synonymize the three samples under *I. luhai*, which has priority.

Comparison

Isorthoceras luhai differs from the co-occurring *I. saaremense* (Balashov, 1959) in having a smaller angle of expansion at comparable growth stages (Fig. 20A) and in having a less eccentric siphuncle position (mean RSP is 0.4, compared with 0.3 in in *I. saaremense*, Fig. 20C).

Isorthoceras saaremense (Balashov, 1959) comb. nov.
Figs 15D, 19D, G

Hedstroemoceras saaremense Balashov, 1959: 42, pl. 5 fig. 11.

Hedstroemoceras saaremense – Balashov & Zhuravlyeva 1962: pl. 13 fig. 2; 1974: pl. 13 fig. 2.

Emended diagnosis

Isorthoceras with circular conch cross section; smooth shell surface; weakly curved growth axis with siphuncle slightly eccentric (RSP = 0.29) on concave side of curvature; angle of expansion of up to ca 12°; mature body chamber with maximum diameter more than 40 mm; siphuncular segments pyriform to fusiform; with weakly developed endosiphuncular deposits; septal necks short, suborthochoanitic to orthochoanitic.

Material examined

ESTONIA • 1 spec.; Kersleti quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 1745-305 • 1 spec.; Paluküla quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-570 • 1 spec.; Paope quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 939-2 • 1 spec.; Salutaguse quarry; Moe Formation, Pirgu Regional Stage; GIT 878-138 • 4 specs; Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; TUG 1743-4, TUG 1745-223, TUG 1745-246, TUG 1745-259 •

4 specs; Vormsi Island, Saxby shore (N); Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-1133, GIT 878-40, GIT 878-41, GIT 878-20 • 1 spec.; Sutlema quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-128.

Type locality and horizon

Tapa, Estonia; Vormsi–Pirgu regional stages.

Description

Specimen GIT 878-41 is a 155 mm long fragment of part of a body chamber and phragmocone with a diameter of 19–39 mm (angle of expansion = 7.4°). The preserved part of the body chamber is 61 mm long with a conch diameter of 33 mm at its base. The conch cross section is circular or slightly compressed. The conch is slightly curved. Where preserved, the conch surface is smooth. The sutures are directly transverse and 5.5 mm distant at a corresponding conch diameter of 32 mm and 4.5 mm at a conch diameter of 24 mm. The septal foramen is located 10 mm from the margin of the conch at the convex side of the conch curvature, and has a diameter of 2.3 mm where the conch height is 31 mm.

The complete set of measurements available reveals a decreasing angle of expansion from 12° at corresponding conch diameters of ca 15 mm toward 9°–4° in more mature specimens (Fig. 20A). The relative cameral length decreases.from ca 0.25 to less than 0.15 (mean RCL = 0.21, n = 10).

The details of the internal characters are preserved in specimens GIT 878-40, GIT 878-20, TUG 939-2, TUG 1745-246, 1745-259, and TUG 1745-305, These represent fragments of the phragmocone with diameters between 19–37 mm (Fig. 19D, G). In all specimens the shape of the siphuncle is slightly expanded, barrel-shaped with greatest widths at ca mid-length of the siphuncular segments, and the septal necks are short orthochoanitic to suborthochoanitic. The position of the siphuncle varies between RSP 0.2–0.3 with no apparent ontogenetic trend (mean RSP = 0.3, n= 7).

Remarks

This species was originally classified within the Middle Ordovician genus *Hedstroemoceras* Foerste, 1930a, without explicit justification, probably based on its eccentric siphuncle. It has been originally described from a single poorly preserved small fragment of a phragmocone. The outer shell in the holotype is not preserved. The specimen can be identified, based on its siphuncular position and septal neck features, as an *Isorthoceras*. It has an eccentric siphuncle position (RSP = 0.27) at a conch diameter of 44 mm, and an apparently a very low angle of expansion. In the context of the additional material, the holotype can be interpreted as an adoral fragment of a phragmocone of a near mature specimen with a low angle of expansion, and, in contrast to *I. luhai*, an eccentric siphuncle during late ontogeny.

Comparison

This species is in almost all aspects like *I. wahlenbergi* from the Boda Limestone, Late Katian, Sweden. It differs from the latter in its larger size. *Isorthoceras wahlenbergi* reaches an adult size of ca 30 mm, which is documented in numerous specimen (Niko 2008; Kröger 2013: fig. 26). Immature specimens of *I. saaremense* can be distinguished from *I. wahlenbergi* by their more central siphuncular position: the mean RSP is 0.22 in *I. wahlenbergi* (Kröger 2013: 66), it is 0.29 in *I. saaremense*.

Isorthoceras **sp. A**
Fig. 12A

Material examined

ESTONIA • 1 spec.; Sutlema quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-128.

Description

The specimen is a ca 45 mm long fragment of parts of a mature body chamber and three phragmocone chambers with a circular conch cross section. The maximum diameter of the specimen is 16 mm at ca mid-length of the body chamber. The body chamber is at least 34 mm long and at its base 15 mm in diameter. At ca 15 mm from its base, the body chamber has a wide, shallow constriction occurs. The three preserved chambers of the phragmocone decrease in length from 4 mm to 3.2 mm, to 2 mm in adoral direction. The septal foramen is well-preserved at 3.7 mm from the conch margin, where the conch cross section is 15 mm in diameter (RSP = 0.27), and it has a diameter of 1.2 mm. The conch surface is apparently smooth, although fine details of the ornamentation are not preserved.

Remarks

This specimen can be related to *I. heroyense* (Strand, 1934), and *I. angelini* Kröger, 2013, with respect to the mature conch size, position of the siphuncle and general conch shape. However, because the nature of the conch surface is uncertain, a species level determination is impossible.

Isorthoceras sp. B
Fig. 12B

Material examined

ESTONIA • 1 spec.; Moe trench; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-116.

Description

Specimen GIT 878-116 is a ca 12 mm long internal mold of parts of a mature body chamber and three phragmocone chambers with a circular conch cross section. The maximum diameter of the specimen is 10 mm at its adoral end. At the base of the body chamber the diameter is 9.8 mm and the adapicalmost chamber has a diameter of 9.6 mm (angle of expansion 2.5°). The three preserved chambers of the phragmocone decrease in length from 2.4 mm to 1.5 mm, to 0.5 mm adorally. The septal foramen is well preserved at 1.7 mm from the conch margin, where the conch cross section is 9.6 mm in diameter (RSP = 0.18), with a diameter of 1.1 mm (RSH = 0.11). The conch surface is apparently smooth, although fine details of the ornamentation are not preserved.

Remarks

This specimen can be related to *I. junceum* (Hall, 1847) with respect to the mature conch size, position of the siphuncle, and general conch shape. However, because the crucial details of the conch surface are not preserved, a species level determination is not possible.

Isorthoceras sp. C
Fig. 12F

Material examined

ESTONIA • 1 spec.; Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-49.

Description

This specimen is a fragment of a body chamber and four chambers of the phragmocone with a nearly tubular circular conch with a diameter of 9.2–9.5 mm and an angle of expansion of ca 1°. The preserved part of the body chamber is 16 mm long, the septa are ca 1.8 mm apart, respectively (RCL = 0.19), and the septal foramen is eccentric with an RSP of 0.28. The septa are directly transverse. The conch surface is not preserved.

Remarks

This specimen can be compared with *Isorthoceras* sp. B, but its lower angle of expansion at smaller conch diameters indicates an even smaller adult size (ca 10 mm) of this species. The lack of external shell prohibits any species level determination. However, based on the small adult size, conch shape and siphuncular position the species can be related to *I. junceum*. Another small species known from Late Ordovician strata of Sweden, *I. curvilineatum* Kröger, 2013, differs in having a central siphuncle.

Isorthoceras sp. D
Fig. 11I

Material examined

ESTONIA • 2 specs; Moe trench; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-114, GIT 878-125 • 1 spec.; Paluküla quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-433 • 2 specs; Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-44, GIT 878-83 • 2 specs; same data as for preceding; TUG 939-3, TUG 939-4.

Description

Specimen GIT 878-114 (Fig. 11I) is a fragment of a body chamber and one chamber of the phragmocone. The body chamber is slightly deformed and does not permit measurement of the angle of expansion. The conch cross section at the base of the body chamber is circular with a diameter of 10 mm. The preserved two septa are 1.8 mm apart (RCL = 0.18) and the septal foramen is nearly centrally positioned (RSP = 0.46) with a diameter of ca 1 mm. The outer shell is not preserved. Specimen TUG 939-4 is a fragment of a body chamber and seven chambers of the phragmocone with a circular conch cross section. The septal distance varies between 2.5–3.5 mm (RCL = 0.23–0.39) and is most distant at smaller diameters (9 mm) and decreases toward the base of the body chamber at the base of the body chamber 11 mm. The angle of expansion of the specimen is ca 3°. The siphuncle is nearly central (RSP = 0.45), its shape is nearly tubular, and the septal necks are very short suborthochoanitic to orthochoanitic. The largest specimen is a fragment of a 28 mm long body chamber with a maximum diameter of ca 13 mm (GIT 878-83).

Remarks

The adult size of this species is indicated by mature septal crowding occurring in specimens TUG 939-4, and GIT 878-114 at conch diameters of ca 10–11 mm. The maximum adult diameter at the aperture was probably not much more than 13 mm. These specimens are assigned to *Isorthoceras* based on their similarity with other small orthocerids known from the Late Ordovician of Baltoscandia, and because of their short suborthochoanitic septal necks. They differ from *I.* sp. E in having a central siphuncle. Better preserved material is needed for a species level determination.

Isorthoceras sp. E
Fig. 19E

Material examined

ESTONIA • 1 spec.; Vormsi Island, Saxby shore, Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-1132.

Description

The specimen is a 110 mm long, 27–32 mm high fragment of a phragmocone (angle of expansion ca 4°) with 16 chambers preserved (RCL 0.21–0.31), and with a circular cross section. The outer shell is not preserved. The siphuncle is eccentric (RSP = 0.31) and, where preserved, with a straight, tubular connecting ring. The septal necks are short (ca 0.8 mm long) orthochoanitic-suborthochoanitic and shallow endosiphuncular annuli occur.

Remarks

This specimen is unique among the larger *Isorthoceras* fragments in having a combination of relatively low angle of expansion (comparable to *I. luhai* at similar conch heights) and a relatively eccentric siphuncle position (comparable to *I. saaremense* at similar conch heights). Additionally, the siphuncle is more tubular than compared to the other species of *Isorthoceras* known from Estonia, and shallow endosiphuncular deposits occur. More material is needed with external characters preserved to allow for a species level determination.

Subclass **Multiceratoidea** Mutvei, 2013

Remarks

Herein, the classification of Pohle *et al*. (2022) is followed. The order Oncocerida Flower in Flower & Kummel, 1950 is rejected (but see supplementary data 1, and remarks in Methodology section), because it represents a paraphyletic group (Pohle *et al.* 2022). Below, families, previously classified within the Barrandeocerida or Oncocerida are listed alphabetically, without assigning them to an existing order.

Family Apsidoceratidae Hyatt, 1884

Genus ***Charactoceras*** Foerste, 1924

Type species

Trochoceras (?) *baeri* Meek & Worthen, 1866, Richmond, Indiana, USA, Whitewater Formation, late Katian, Ordovician; by original designation.

Diagnosis

Closely coiled, rapidly expanding conchs with dorsally impressed whorl cross section, with flattened venter and rounded sides that converge towards the dorsum; sutures essentially straight laterally but forming broad ventral and dorsal lobes; surface with transverse growth lines that form distinct hyponomic sinus on venter, and transverse ribs in early stages only; siphuncle between center and venter, with cyrtochoanitic septal necks, empty; segments expanding slightly within camerae.” (Adopted from Sweet 1964a.)

Charactoceras estonicum Strand, 1934
Fig. 22A

Charactoceras estonicum Strand, 1934: 28–29, pl. 2 fig. 5, pl. 7 fig. 1.

Charactoceras estonicum – Balashov 1953b: 266, pl. 11 figs 1–2; 1962c: pl. 7 fig. 1. — Stumbur 1962: 136. — Dzik 1984: 44, 154, text-figs 12.30, 59.5.

Diagnosis

Charactoceras with smooth, rapidly expanding conch (WER ca 3–4), and adult diameter of ca 140 mm; whorl cross section with rounded venter and rounded umbilical margins, and with deeply impressed dorsal furrow, moderately compressed with WWI ca 1.1–1.3 with greatest width in the dorsal half; sutures with broad and shallow ventral lobes and ventro-lateral saddles; siphuncle close to ventral conch margin. (Adopted from Strand 1934.)

Material examined

ESTONIA • 2 specs; Vormsi Island, Hosholm shore; Adila Formation, Pirgu Regional Stage; TUG 939-68, TUG 1745-274 • 5 specs; Vormsi Island, Hosholm shore (tower locality); Adila Formation, Pirgu

Regional Stage; GIT 878-216 to GIT 878-220 • 2 specs; Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage; GIT 878-198, GIT 878-229.

Type locality and horizon

Piirsalu, Estonia; Moe Formation, Pirgu Regional Stage.

Description

The species has been described in detail by Strand (1934). Additional measurements, taken from the Estonian specimens, contribute to the knowledge on its variability in WWI and WER. The measurements show that WER and WWI are nearly constant throughout different growth stages, with a mean WWI = 2.16 (1st quartile 1.14–3rd quartile 1.26, n = 10,) and a mean WER = 3.44 (1st quartile 3.27–3rd quartile 3.45, n = 5). Also, the shape of the whorl cross section does not change significantly at different growth stages with rounded venter and flanks and greatest width located in the dorsal half of the whorl.

The most complete specimen in the collection (apart from the holotype TUG 939-68, which has been described in detail by Strand 1934 and Balashov 1953b), is GIT 878-229. This specimen is a fragment of a phragmocone consisting of two whorls, and has a maximum diameter of 72 mm. The preceding whorl has a diameter of 40 mm (WER = 3.24). At a conch diameter of 44 mm, the next whorl has a diameter of 24 mm (WER = 3.36). The WWI is 1.13 at a conch width of 36 mm, 1.20 at a conch width of 24 mm, and 1.1 at a conch width of 11 mm. The septa are 8 mm apart at the venter where the whorl height is 32 mm. The septal foramen is located 3 mm from the ventral conch margin and has a diameter of 3 mm where the conch height is 28 mm (RSH = 0.11, RSP = 0.12).

Remarks

The diagnosis is adopted from Strand (1934: 28). Here, the WER and WWI are used to describe the relative conch dimensions and are included in the diagnosis; their values are based on the type specimen.

Comparison

Charactoceras estonicum is apart from the Laurentian palaeocontinent known only from Baltica (see Foerste 1926, 1928b, 1935a, 1935b; Troedsson 1926; Strand 1934; Wilson 1961; Nelson 1963; Frye 1982). Species of *Charactoceras* are differentiated by whorl cross section shape, ornamentation, and expansion rate. All four species of *Charactoceras* described by Frye (1982) from the Boda Limestone, late Katian, Sweden, differ in being annulated.

Charactoceras estonicum is one of the species of *Charactoceras* with a smooth, non-annulated shell. Among those smooth species, *C. laddi* Foerste, 1935a, *C. manitobaense* Nelson, 1963 differ in having a flattened venter, and *C. eximium* (Sweet & Miller, 1957) and *C. triangulum* Frye, 1982 differ in having a trapezoidal whorl cross section. An elliptically depressed whorl cross, but with smaller WWI than in *C. estonicum*, have: *C. baeri* (WWI = 1.4–1.5, Foerste 1924), *C. hercules* (Billings, 1857) (WWI = 1.8 at whorl height 53 mm, Nelson 1963: 102), *C. normale* Wilson, 1961 (WWI = 3.6 at whorl height of 18 mm, Wilson 1961), and *C. warranae* Nelson, 1963 (WWI = 2 at whorl height of 45 mm). The two species which are most similar to *C. estonicum* with respect to whorl cross section and ornamentation are *C. rotundum* Troedsson, 1926 and *C. schucherti* Foerste, 1928b; they differ in having a smaller expansion rate (*C. rotundum*: WER = 2.3 at conch diameter 107 mm, Troedsson 1926), and (*C. schucherti*: WER = 2.5 at conch diameter of 47 mm, Foerste 1928b), respectively.

Charactoceras sp. A
Fig. 22C, E

Material examined

ESTONIA • 1 spec.; Vormsi Island, Hosholm shore; Adila Formation, Pirgu Regional Stage; GIT 878-215.

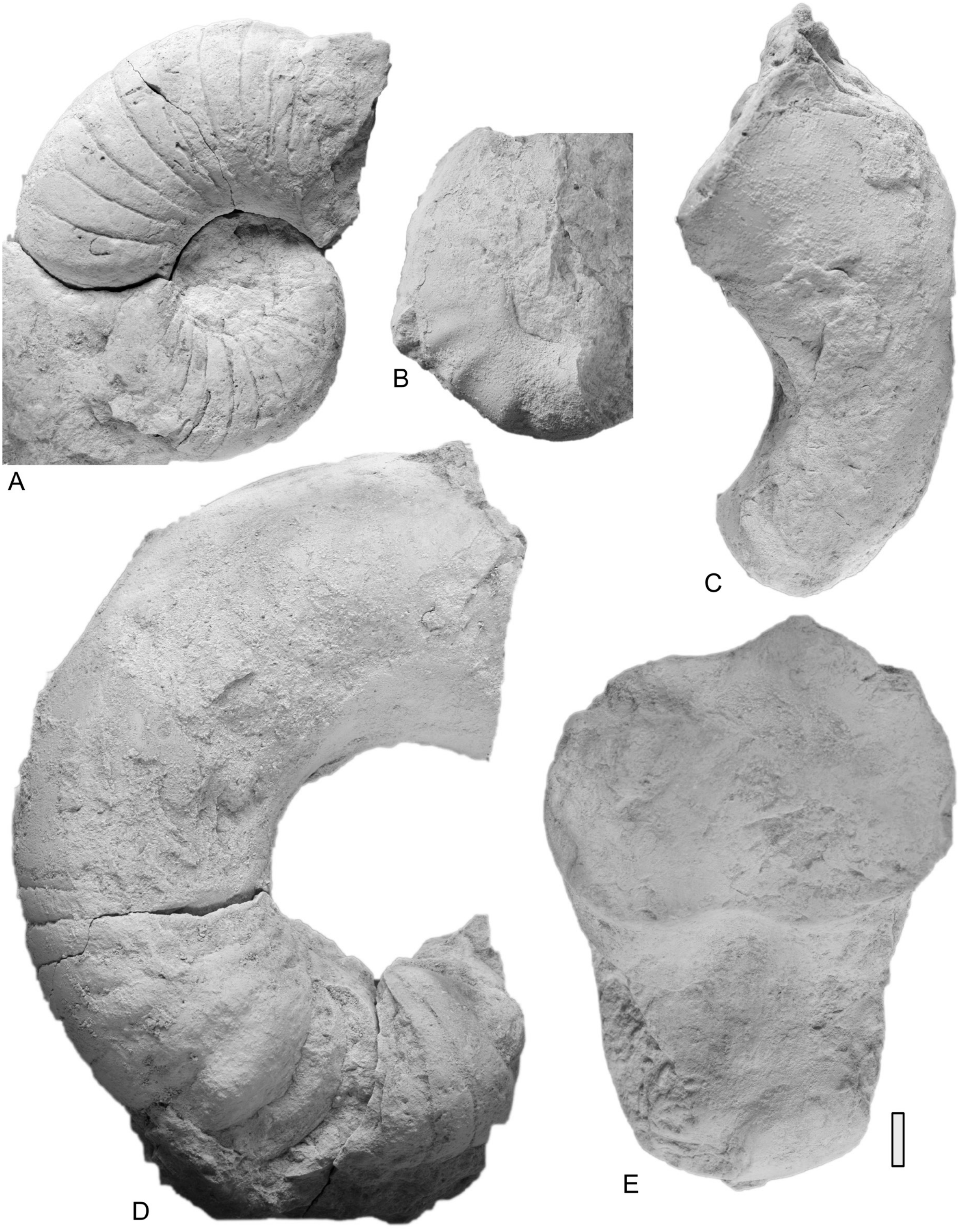


Fig. 22. *Charactoceras* Foerste, 1924 from the Pirgu Regional Stage, Estonia. **A**. *Charactoceras estonicum* Strand, 1934, specimen GIT 878-229, from Vohilaid shore (E), Vohilaid Island. **B**. *Charactoceras* ? sp., specimen TUG 1006-13, from Paope quarry. **C**. *Charactoceras* sp. A, specimen GIT 878-215, from Hosholm shore (tower), Vormsi Island. **D**. *Charactoceras* sp. B, specimen GIT 878-222, from Hosholm shore (tower), Vormsi Island. **E**. Same specimen as in C, dorsal view. Scale bar = 10 mm, same scale in A–E.

Description

The specimen is a fragment of a nearly complete body chamber and one chamber of the phragmocone with a wide, reniform whorl cross section; it is 36 mm high at the aperture and 57 mm wide. At the base of the body chamber, it measures 24 mm in height and 41 mm in width. The body chamber measures ca 90–100° in length. Throughout its entire length, the greatest width of the whorl is reached between mid-flank and dorsum. On the broadly rounded ventral side, a distinct, broad, U-shaped hyponomic sinus is preserved, which has a width of 35 mm and a depth of 20 mm. Around the aperture patches of the outer shell remain, these are smooth, with distinct narrowly and irregularly spaced growth lines.

The two septa at the base of the body chamber are 6 mm distant, and a septal foramen located a few millimeters from the venter is apparent, but is not well enough preserved to measure.

Remarks

This single fragment does not permit species level determination. The position of the siphuncle and the shape of the body chamber, and its aperture show, however, that this specimen is a fragment of a *Charactoceras*. Its relatively large WWI of 1.71 (see Fig. 22E) distinguishes the specimen from *C. estonicum* and suggests a comparison with *C. hercules* (Billings, 1857) from late Katian strata of Anticosti Island, Quebec (e.g., Foerste 1928c). However, with the available material a detailed comparison is impossible as the more apical parts of the phragmocone are not known.

Charactoceras sp. B

Fig. 22D

Material examined

ESTONIA • 1 spec.; Vormsi Island, Hosholm shore; Adila Formation, Pirgu Regional Stage; GIT 878-222.

Description

The specimen is a fragment of a complete body chamber and an additional 14 chambers of the phragmocone. The body chamber is ca 90° long with an unconstricted aperture with a wide U-shaped hyponomic sinus. The total fragment has a conch diameter of 113 mm, and the diameter of the preceding whorl is 83 mm. At its base, the width of the body chamber is 48 mm and the height 39 mm (CHI = 0.81), at the aperture it measures 60 mm in width and 45 mm in height (CHI = 0.75). The septal distance at the base of the body chamber is 6 mm at the venter. There is no sign of mature septal crowding. The sutures run straight and transverse over flanks and venter. At a position where the whorl height is 33 mm, the septal foramen of the siphuncle is ca 2.5 mm in diameter and is located ca 6 mm from the ventral conch margin (RSP = 0.20).

Remarks

The fragment does not permit species level determination because the more juvenile growth stages are not preserved. These are critical for species determination because many species of *Charactoceras* are differentiated by the extent of the annulation of the early growth stages. The WER of 1.85 of this specimen is lower than that of comparable growth stages of the type of *C. estonicum* (WER > 3.5, compare Fig. 22A, D) and of other known species of *Charactoceras*. The species of *Charactoceras* with lowest known expansion rate is *C. rotundum* (WER: 1.9–2.4) from late Katian Strata of northern Greenland (Troedsson 1926). However, this latter species differs in having a siphuncle that is located more distantly from the ventral conch margin.

Charactoceras ? sp.
Fig. 22B

Material examined

ESTONIA • 1 spec.; Paope quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 1006-13.

Description

The specimen is a ca 120° long fragment of a body chamber with a broad elliptical whorl cross section. The dorsal part of the whorl is not preserved. The fragment has a shallow annulations, which run nearly directly transverse over the umbilical margin, ca 19–20 annulations occur per volution. A shallow U-shaped hyponomic sinus is apparent both from faint growth lines preserved on the mold and the shape of the annulations. The preserved part of the conch has a maximum diameter of 52 mm, and the diameter of the preceding whorl is 33 mm (WER = 2.48); at its adoral end the whorl width is 18 mm and the corresponding whorl height is 16 mm (WWI = 1.13).

Remarks

The conch shape and ornamentation of this fragmentary specimen is similar to annulated species of *Charactoceras*, such as *C. kallholnense* Frye, 1982 or *C. suecicum* Frye, 1982, However, the siphuncle including the septal foramen are not preserved, making a genus determination uncertain, and the fragmentary character of this specimen does not permit species level determination.

Genus ***Saxbyoceras*** gen. nov.
urn:lsid:zoobank.org:act:F9537354-5080-41CB-9ADF-D443823ECEAD

Type species

Saxbyoceras kingpooli gen. et sp. nov., from Saxby shore, Kõrgessaare Formation, Vormsi Island, Estonia; Vormsi Regional Stage.

Diagnosis

Slightly endogastrically curved brevicone with smooth (or nearly so) conch surface; conch cross section circular or slightly compressed; mature body chamber slightly curved, not (or only very slightly) constricted; sutures are nearly straight and directly transverse; siphuncle eccentrically positioned toward the concave side of the conch with widely expanded segments; septal necks very short or achoanitic; endosiphuncular or cameral deposits not known.

Etymology

From Saxby, Vormsi Island, Estonia, the type locality of the type species of this genus.

Remarks

The new genus is best compared with *Siljanoceras* Kröger, 2013, from which it differs in having a much smaller angle of expansion (33° in *Siljanoceras*) and an endogastrically curved conch.

Saxbyoceras kingpooli gen. et sp. nov.
urn:lsid:zoobank.org:act:569E3891-BA40-49E8-A7BA-C29851D45C19
Fig. 23A–B

Diagnosis

Same as for genus, by monotypy.

Etymology

Refers to Kingpool, the tallest of the three figures in Eno Raud's (1928–1996) children-book series "Naksitrallid".

Type material

Holotype

ESTONIA • Vormsi Island, Saxby shore, Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-25.

Paratype

ESTONIA • 1 spec.; same data as for holotype; TUG 1745-245.

Description

The holotype is a fragment of a slightly endogastrically curved conch consisting of a phragmocone and a mature body chamber. The external shell is partially preserved (Fig. 23A). The conch surface appears smooth but possesses faint narrowly spaced growth lines. In lateral view the body chamber is slightly curved with a straight margin on the prosiphuncular side and a convex margin on the antisphuncular side. It has a height of 78 mm at its base, and 89 mm at its aperture, and a maximum length of 48 mm. The peristome is too fragmentarily preserved to describe its complete outline but a shallow hyponomic sinus is visible on the prosiphuncular side. A faint ca 10 mm wide constriction occurs a few millimeters from the apertural conch margin.

The phragmocone expands from a height of 65 mm to 78 mm at a length of 41 mm (angle of expansion 18°). At a conch height of 65 mm, a conch width of ca 60 mm can be estimated (CHI = 1.1). The sutures are nearly straight transverse or with a shallow lateral lobe and are 10 mm apart where the conch height is 70 mm (RCL = 0.14). The septal foramen has a diameter of 12 mm and is located ca 17 mm from the concave conch margin where the conch height is ca 60 mm (RSH = 0.20, RSP = 0.35). The connecting ring is thick, the septal necks are short recumbent or achoanitic and no endosiphuncular deposits occur.

The second specimen is preserved only as two isolated phragmocone chambers with a conch height of 63–70 mm and a septal distance of 12 mm and 10 mm, respectively (RCL: 0.14–0.19). The sutures are directly transverse. The depth of the curvature of the septa is 14 mm where the conch height is 63 mm. The septal foramen is located in a distance of 20 mm from the conch margin with a diameter of 7 mm where the conch height is 63 mm (RSH = 0.11, RSP = 0.36). At a conch height of ca 60 mm, the siphuncular segments are expanded into the chambers with a rounded, convex shape in longitudinal section and with a maximum diameter of 11 mm where the chamber length is 8 mm (RSS = 1.38) and where the septal foramen is 3 mm. The segments have narrow circular adnate areas on the adoral and adapical surfaces of the septa (ca 2 mm wide). The connecting ring is thick, the septal necks are short recumbent or achoanitic and no endosiphuncular deposits occur.

Remarks

The specimens described above superficially, and with respect of the position and size of the septal foramen, are similar to specimens described by Eichwald (1860) under *Orthoceras declive* Eichwald, 1860. However, because this species apparently combines type material of different taxa from the Middle Ordovician (collected in Tallinn) and from Katian strata (collected in Lyckholm) (Eichwald 1860: 1206–1207) the species name cannot be used until the original material is revised.

Cyrtoceras substriatum Eichwald, 1860, collected from Hohenholm (= Kõrgessaare; Hiiumaa) is probably related to *S. kingpooli* sp. nov., because of its similar conch shape and nearly central siphuncle (compare Teichert 1930: 271) but differs in having a transverse ornamentation.

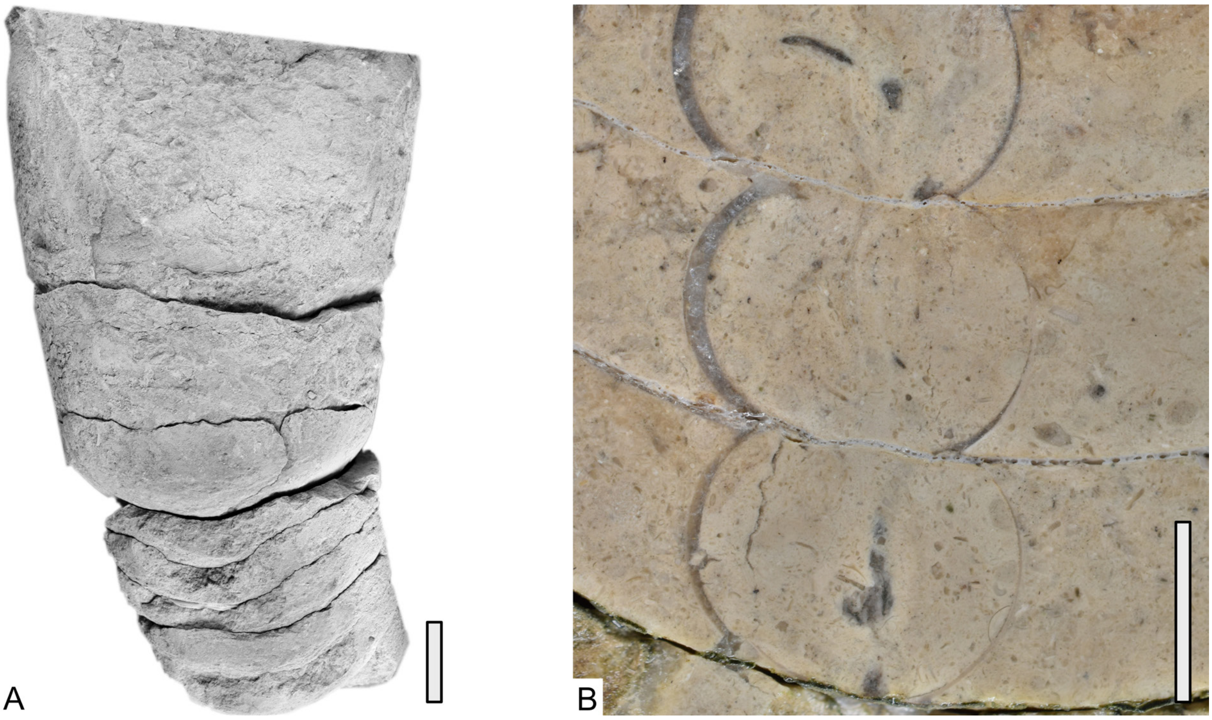


Fig. 23. *Saxbyoceras kingpooli* gen. et sp. nov., holotype GIT 878-25 of the Vormsi Regional Stage, from Saxby shore, Vormsi Island, Estonia. **A**. Lateral view. **B**. Median section of the phragmocone with details of the siphuncle and connecting ring. Scale bars: A = 20 mm; B = 5 mm.

Another species, which is possibly related to *S. kingpooli* sp. nov. is *Faberoceras demshinense* Balashov, 1975 from late Katian strata (Molodovskii horizon) of Podolia, Ukraine, which is a cyrtocone with a nearly central, widely expanded siphuncle. This species differs from *S. kingpooli* in having a more strongly curved conch and a transversely annulated ornamentation.

Family Diestoceratidae Foerste, 1926

Genus ***Danoceras*** Troedsson, 1926

Type species

Danoceras ravni Troedsson, 1926, Cape Calhoun, northern Greenland, Cape Calhoun series, Late Ordovician; by original designation.

Diagnosis

Slender diestoceratids with straight or slightly curved shell, and compressed conch cross section with narrow venter and / or dorsum; mature body chamber with widest height and width near its base, with simple constriction close to mature aperture, with apertural widening and shallow hyponomic sinus; siphuncle positioned near conch margin, cyrtochoanitic; necks recumbent, segments elongate, subtrapezoidal in longitudinal section; thin annulosiphonate deposits with distinctive irregular linear processes, which extend adapically and adorally without fusing from segment to segment. (Compiled from Strand 1934, and Sweet 1964b.)

Danoceras breve Strand, 1934
Fig. 24B

Danoceras breve Strand, 1934: 81–82, pl. 11 fig. 6, pl. 13 fig. 1.

Danoceras breve – Flower 1946: 420. — Dzik 1984: 67, text-fig. 18.11.

Diagnosis

Danoceras with compressed elliptical to oval conch cross section (CHI = 1.3–1.4); mature body chamber with maximum conch height near its base with height of ca 42 mm; apical angle of the phragmocone ca 25°; conch surface, with distinct constriction near peristome and amphora-like apertural opening.

Material examined

ESTONIA • 1 spec.; Haapsalu holm; Adila Formation, Pirgu Regional Stage; GIT 426-988.

Type locality and horizon

Vestre Svartøy, Ringerike, Norway; Bønsnes Formation, late Katian.

Description

The specimen is a slightly deformed fragment of a phragmocone and the mature body chamber. The maximum conch height of the specimen (41 mm) is at the base of the body chamber. There, the conch width is 30 mm (CHI = 1.37). The preserved part of the body chamber is 27 mm long.

The phragmocone increases in conch height from 23 mm to 40 mm at a length of 38 mm (angle of expansion 25°). At the adoral end of the phragmocone, the chamber length is 6 mm (RCL = 0.15). Traces of a weak longitudinal striation are preserved on the surface of the internal cast of the phragmocone. The conch surface is not preserved. The conch is very slightly curved with a thin (ca 3 mm in diameter) siphuncle preserved near the conch margin at the convex side of the conch curvature.

Remarks

This specimen is very similar in dimensions and conch shape to the types of *Danoceras breve* and although details of the siphuncle are not examined, the thin marginal siphuncle is indicative of a species of *Danoceras*.

Danoceras oviforme sp. nov.
urn:lsid:zoobank.org:act:8DCABC85-83A4-4DAA-9B32-91D58875FB3F
Fig. 24A, C

Diagnosis

Danoceras with compressed oval conch-cross section (CHI = 1.2); mature body chamber with maximum conch height near its base with height of ca 36 mm and height to length ratio of ca 0.9; maximum conch heigh near adoral end of mature phragmocone.

Etymology

Refers to the egg-like conch form of mature specimens.

Type material

Holotype

ESTONIA • Moe trench, Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-108.

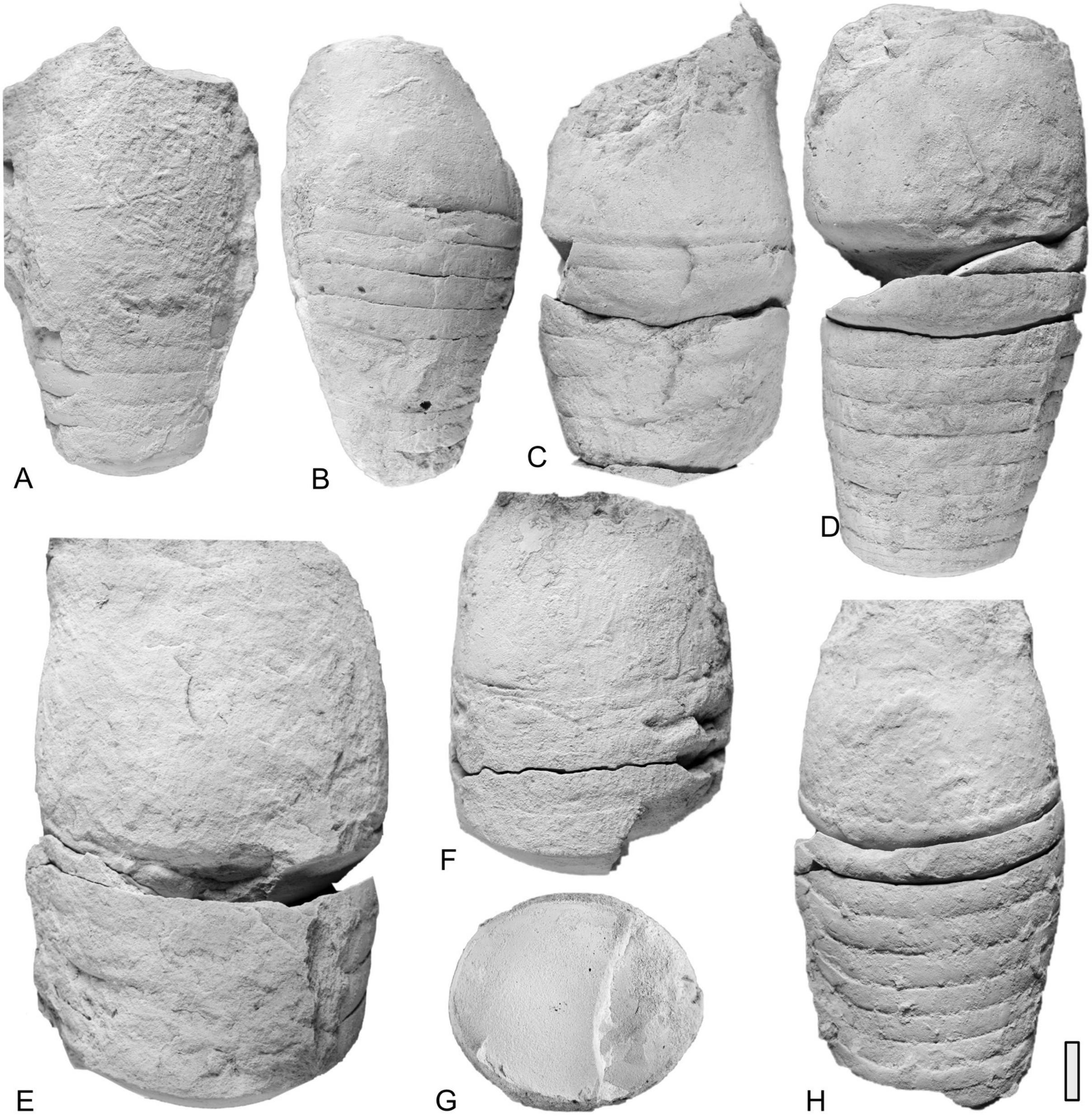


Fig. 24. *Danoceras* Troedsson, 1926 from the Vormsi–Pirgu regional stages, Estonia. **A**. *Danoceras oviforme* sp. nov., holotype GIT 878-108, from Moe trench, Vormsi Regional Stage, lateral view. **B**. *Danoceras breve* Strand, 1934, holotype GIT 426-988, from Haapsalu holm, Haapsalu, Pirgu Regional Stage, lateral view. **C**. *Danoceras oviforme* sp. nov., specimen GIT 80-510, from Piirsalu quarry, Pirgu Regional Stage, lateral view prosiphuncular side toward right. **D**. *Danoceras piersalense* (Teichert, 1930) comb. nov., specimen GIT 840-271, from Hosholm shore (tower), Vormsi Island, lateral view. **E**. *Danoceras vohilaidense* sp. nov., holotype GIT 878-273, from Vohilaid shore (E), Vohilaid Island, Pirgu Regional Stage, lateral view, prosiphuncular side left. **F–H**. *Danoceras piersalense* specimen GIT 840-93, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage. **F**. Lateral view. **G**. Adapical view, prosiphuncular side to the right. **H.** Specimen TUG 1745-302, from Pirgu River outcrop, Pirgu Regional Stage, lateral view. Scale bar = 10 mm, same scale in all figures.

Paratypes

ESTONIA • 1 spec.; Vormsi Island, Hosholm shore; Adila Formation, Pirgu Regional Stage; TUG 1745-276 • 1 spec.; Piirsalu quarry; Adila Formation, Pirgu Regional Stage; TUG 80-510 • 1 spec.; Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-70.

Description

The holotype (Fig. 24A) is a fragment of a phragmocone and a mature body chamber with parts of the outer shell preserved. The outer shell is apparently smooth at the position of the body chamber. The conch height at the base of the body chamber is 36 mm and the conch width 30 mm (CHI = 1.2). The conch cross section is oval, narrower at the ventral side. The phragmocone grows at a length of 33 mm from a conch height of 24 mm to 36 mm (angle of expansion = 21°) and the septa are 4.5 mm distant where the conch height is 35 mm (RCL = 0.13). The sutures are nearly directly transverse, forming only a very shallow lateral lobe. The septal foramen is 2 mm in diameter and positioned 2 mm from the conch margin where the conch height is 24 mm (RSH = 0.08, RSP = 0.09).

More complete mature body chambers are preserved in specimens GIT 878-70, TUG 80-510, TUG 1745-276 where a body chamber length of 32 mm is reached (0.9 of the corresponding conch height at the base of the body chamber). The conch height and width of the mature body chamber decreases toward the peristome with a convex outlines in lateral view. Probably a slight widening occurs at the adoral most part, resulting in an amphora-like apertural shape.

The conch dimensions vary very little among the four specimens: TUG 80-510 having the largest conch height with 37 mm and no smaller mature conch heights than 36 mm.

Comparison

This species is most similar to *Danoceras fusiforme* Balashov 1959, from the Rakvere Regional Stage of Estonia, which, however, has an even smaller mature size (maximum mature conch width = 19 mm). *Diestoceras acuminatum* Strand, 1934, which has a similar conch height at the base of the mature body chamber, can easily be distinguished from the new species in having an angle of expansion of the phragmocone of 28° (Strand 1934: 86).

Danoceras piersalense (Teichert, 1930) comb. nov.
Figs 16C–D, F, 24D, F–H, 25C, 26

Dowlingoceras (?) *piersalense* Teichert, 1930: 284, pl. 6 figs 17–18.

Dowlingoceras (?) *piersalense* – Strand 1934: 79. — Miller & Youngquist 1947: 415. — Balashov 1953a: 208. — Frye 1987: 95–96.

Emended diagnosis

Danoceras with compressed oval conch-cross section (CHI = 1.2–1.3); mature body chamber with maximum conch height near its base with height of ca 40–45 mm and height to length ratio of ca 0.8–0.9; conch surface with distinct constriction near peristome and amphora-like apertural opening.

Material examined

ESTONIA • 1 spec.; Vormsi Island, Hosholm shore; Adila Formation, Pirgu Regional Stage; GIT 840-93 • 16 specs; Vormsi Island, Hosholm shore (tower locality); Adila Formation, Pirgu Regional Stage; GIT 426-988, GIT 840-261, GIT 840-270, GIT 840-258a, GIT 840-272, GIT 878-263 to GIT 878-268, GIT 878-270 to GIT 878-272, GIT 878-276, GIT 878-279 • 1 spec.; same locality as for preceding; TUG 1745-48 • 2 specs; Pirgu River outcrops; Adila Formation, Pirgu Regional Stage; TUG 1745-296, TUG

1745-302 • 1 spec.; Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage; GIT 878-267.

Type locality and horizon

Piirsalu, Lääne County, in western Estonia; Moe Formation, Pirgu Regional Stage.

Description

None of the specimens assigned to this species is complete, all of them preserve parts of the mature or near mature body chamber and parts of the phragmocone. Specimen GIT 840-271 is a fragment of a mature specimen preserving the most important characters of this species. At the base of the body chamber, the conch height is 46 mm, the width cannot be is estimated as ca 36 mm. A length of 35 mm of the body chamber is preserved, where is has a convex outline and decreases to a conch height of 43 mm at its adoral end. The conch cross section is preserved near the adoral end of the phragmocone; it has a height of 42 mm and a width of ca 31 mm (CHI = 1.35) and an oval shape with a narrower margin at the ventral side. In a length of 39 mm, the phragmocone diameter increases from 31 mm to 41 mm (angle of expansion = 16°). The sutures form a shallow lateral sinus on the dorsal side. At a conch height of 40 mm, they are 6 mm apart (RCL = 0.1). On the surface of the internal mold of the phragmocone, faint longitudinal, ca 1 mm wide striae are visible. The siphuncular segments are subtrapezoidal (Fig. 16F). They have their greatest height near the adapical surface of the septa where they are broadly adnate. At a conch height of 37 mm, the septal distance is 4.2 mm, the greates height of the siphuncle 3.8 mm, and the septal foramen ca 2 mm. The septal necks are suborthochoanitic.

Amongst those specimens with complete mature body chamber preserved, their size, relative lengths, and cross section is slightly variable: in GIT 878-263 the conch height at the body chamber base is

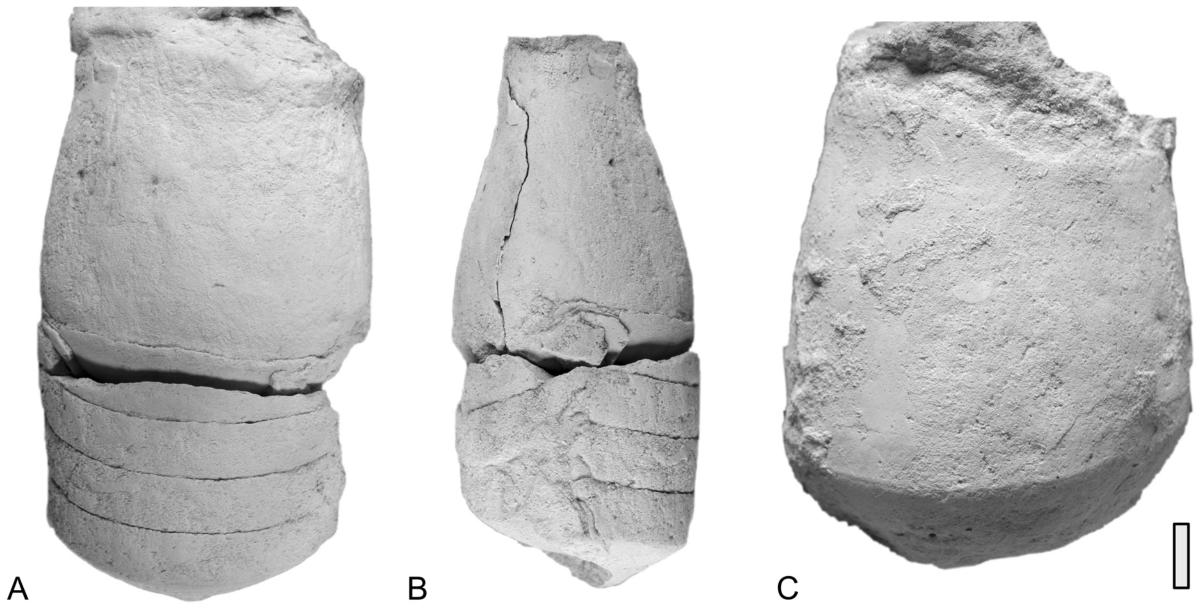


Fig. 25. Diestoceratids from the Pirgu Regional Stage, Estonia. **A–B**. *Dowlingoceras tornense* sp. nov., paratype GIT 840-273, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage. **A**. Lateral view, prosiphuncular side left. **B**. View of the prosiphuncular side. **C**. *Danoceras piersalense* (Teichert, 1930) comb. nov., specimen GIT 878-263, from Hosholm shore (tower), Vormsi Island. Scale bar = 10 mm, same scale in all figures.

44 mm, 38 mm at the peristome. The length of the body chamber is 44 mm (relative body chamber length = 1) and ca 10 mm from the peristome an inconspicuous constriction occurs (Fig. 25C). In TUG 1745-48, the conch height at the body chamber base is 44 mm, 37 mm at the peristome. The length of the body chamber is 30 mm (relative body chamber length = 0.68), and ca 10 mm from the peristome an inconspicuous constriction is present.

The mean relative body chamber length of all measured specimen is 0.79 (n= 18). The mean CHI at the base of the body chamber is 1.3 (n = 18) and the mean conch height at the base of the body chamber is 43 mm (n = 21, max. = 47 mm, min. = 40 mm). The frequency distribution of the mature conch sizes is bimodal: of the 21 specimens with mature body chamber preserved six specimens have a conch height of 40 mm at its body chamber base and four specimens have a conch height of 45 mm (Fig. 26A).

The conch cross section is oval, generally narrower on the ventral side, where it is almost angular in some specimens (e.g., TUG 1745-302, GIT 878-264; Fig. 24G). In specimen TUG 1745-302 the complete body chamber has a length of ca 35 mm, decreases in dorsoventral diameter from the base to the peristome and until ca 20 mm, where a shallow, inconspicuous constriction is present, beyond which, the body chamber diameter increases to ca 33 mm.

The sutures form wide, shallow lateral lobes, almost perpendicular to the growth axis, and a relatively deep saddle on the dorsum. The septa are spaced with a mean RCL of 0.12 (n = 56, max. = 0.13, min. = 0.09). In some specimens, narrow longitudinal furrows are visible on the surface of the internal mold of the phragmocone (e.g., TUG 1745-302, Fig. 24H). The conch surface is poorly preserved in all specimens and was apparently smooth on the mature body chamber and adjacent parts of the phragmocone.

The characters of the siphuncle are well-preserved in TUG 80-510 (Fig. 16C); at a conch height of 28 mm the septal foramen is circular with a diameter of ca 2.4 mm (RSH = 0.09). The septal necks are very short suborthochoanitic, and the connecting rings are expanded, forming subtrapezoidal segments with slightly convex outline in longitudinal view. The maximum diameter of the siphuncle is more than 3 mm. Near the adapical surface of the septum, the connecting ring is widest, forming a wide adnate area.

The siphuncle is also preserved in GIT 1745-296 at a position where the conch height is 34 mm and septa are 3.8 mm apart (RCL = 0.11). There, the septal foramen is 1.9 mm wide and 2.4 mm high (RSH = 0.07). The septal necks, which are poorly preserved, appear to be suborthochoanitic to cyrtochoanitic

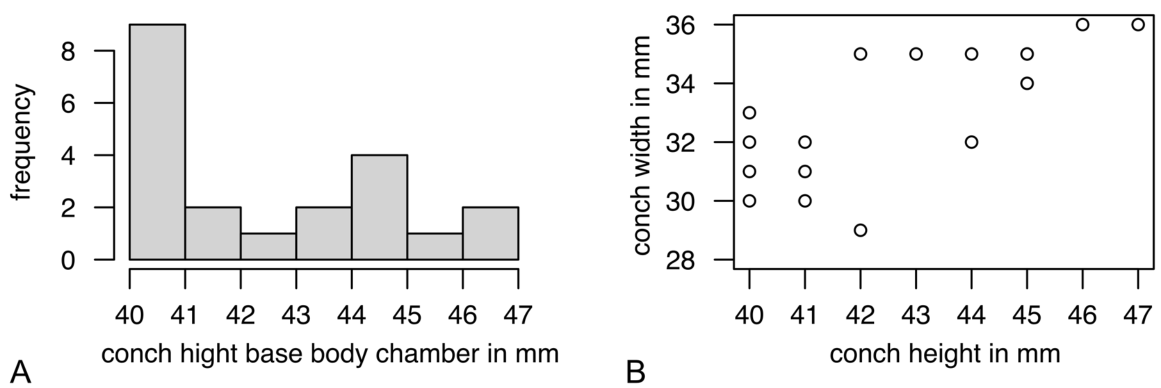


Fig. 26. Diagrams of the variation mature conch size in *Danoceras piersalense* (Teichert, 1930) comb. nov. **A**. Histogram of the frequency of conch heights at the base of the mature body chamber (note the bimodal distribution). **B**. Conch height and conch width at the base of the body chamber of mature specimens.

(Fig. 16D). The connecting ring forms subtrapezoidal siphuncular segments, which are widest and have a wide adnation area on the adapical surface of the septa (ca 3.8 mm).

Remarks

Teichert's original diagnosis is emended here based upon the description and figures of Teichert (1930) and additional information from the specimens described here regarding the CHI, and the location and shape of the siphuncle. Most of the Estonian specimens are slightly deformed. The mean CHI therefore slightly overestimates the compression of the conch cross section. The type specimen, described by Teichert (1930) has a conch height at the base of the body chamber of 47 mm, and a conch width of 35 mm, and hence is larger than most of the specimens described herein, but falls within their range of variation. A bimodal frequency distribution of the mature conch size occurs in the material (Fig. 26A; supplementary data 4), but this does not allow for an unambiguous distinction of two species, because all morphological features measured form a continuum of variation.

Danoceras piersalense is identical in its mature size, rate of compression, and angle of phragmocone expansion to *D. scandinavicum* Strand, 1934. The latter species has been distinguished from *D. piersalense* by its more convex adoral part of the phragmocone, which is also more sharply "marked out from the upper part of the conch" (Strand 1934: 84). These subtle differences are difficult to detect in the often fragmentary material from Estonia, and little is known about the variability of this character among species assigned to *D. scandinavicum* and *D. piersalense*. It is therefore highly likely, that *D. scandinavicum* represents a subjective junior synonym of *D. piersalense* or that both species are present in the Estonian material but remain undetected therein. Additional, and better-preserved material is needed to solve the problem. The species is assigned to *Danoceras*, herein, because of the *Danoceras*-like shape of siphuncle.

Comparison

This is a relatively large species of *Danoceras*, which can be distinguished from other late Katian species of the genus mainly by its size (conch height at the base of the mature body chamber 40–45 mm). The mature body chamber height of *Danoceras breve* Strand, 1934 (42 mm) is within the range of the specimens assigned to *D. piersalense*, herein, but differs in having a phragmocone with a higher angle of expansion (25°).

Dowlingoceras kallholnense Frye, 1987 and *Danoceras scandinavicum* Strand, 1934 have a mature body chamber of similar conch height at its base (40 mm, 39–42 mm, respectively) but their conch cross section is less compressed (CHI = 1.1–1.2), and the latter additionally is sharply curved on its ventral side. The mature body chamber height of *Danoceras broeggeri* Strand, 1934 is 56 mm.

Danoceras vohilaidense sp. nov.
urn:lsid:zoobank.org:act:7564A1C1-841D-4E29-A39F-73A476806D3D
Fig. 24E

Diagnosis

Danoceras with compressed oval conch-cross section (CHI = 1.6) with narrow, almost angular, dorsal, and ventral margins; mature body chamber with maximum conch height near its base with height of ca 53 mm and height length ratio of ca 1.3; conch surface, with distinct constriction near peristome and amphora-like apertural opening.

Etymology

Refers to the type locality.

Type material

Holotype

ESTONIA • Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage; GIT 878-273.

Paratypes

ESTONIA • 2 specs; same data as for holotype; GIT 878-274, GIT 878-278.

Description

In all three specimens the outer shell is not preserved. In the holotype and in GIT 878-274, the conch height is 52–53 mm at the base of the body chamber, and at the peristome 48 mm, the conch width is 34 mm at the base of the body chamber (CHI = 1.56), and the length of the body chamber 40 mm. A slight taphonomic compression can be assumed, the conch cross section is oval with narrow, almost angular, dorsal, and ventral margins. In the holotype, the phragmocone has a height of 51–47 mm at a length of 28 mm (angle of expansion = 8°). The sutures form very shallow lateral lobes, and the septal foramen is close to the conch margin with a width of 3.5 mm.

Remarks

The two mature body chambers (holotype and in specimen GIT 878-274) are almost identical in size and shape, identifying them as belonging to the same species. They are larger than those known from other Estonian *Danoceras*, and approximately similar to that of *D. broeggeri* Strand, 1934 from the Upper *Isotelus* Limestone of Norway. The latter differs in size and CHI (mature body chamber height 56 mm, CHI 1.3–1.4).

Danoceras sp. A
Fig. 27D

Material examined

ESTONIA • Vormsi Island, Hosholm shore (tower locality); Adila Formation, Pirgu Regional Stage; GIT 878-269.

Description

The specimen comprises parts of a nearly complete mature body chamber and four chambers of the phragmocone, lacking the outer shell. At the base of the body chamber, the conch height and width are 34 mm and 29 mm respectively (CHI = 1.12). The conch cross section is oval, compressed with narrow dorsal and ventral margins, the ventral (prosiphuncular) margin is narrower. The body chamber is 28 mm long, very slightly exogastrically curved. At its base, a narrow band of oncomyarian, buttressed muscle scars occur. A wide, inconspicuous constriction occurs ca 5 mm adapically from the peristome. The peristome is incompletely preserved, and the hyponomic sinus is not seen. At the peristome, the conch height is 32 mm. The sutures form shallow lateral lobes. The adoralmost two sutures are crowded. Adapically, the sutures are 5 mm apart, where the conch height is 33 mm. The siphuncle is preserved near the conch margin. The septal foramen is ca 2 mm wide and the siphuncular segments apparently are relatively narrow, *Danoceras*-like.

Remarks

This single specimen differs from all known species of *Danoceras* in its small mature size in combination with a relatively long and tubular body chamber. However, based on this single, fragmentary preserved specimen the erection of a new species is not possible.

Genus ***Diestoceras*** Foerste, 1924

Type species

Gomphoceras indianense Miller & Faber, 1894, Versailles, Indiana, USA, upper part of Hudson River group, Late Ordovician; by original designation.

Diagnosis

Short diestoceratids with straight or slightly curved shell, and circular conch cross section; conch reaches largest diameter at adoral end of mature phragmocone, contracting to aperture; peristome straight, transverse, with shallow hyponomic sinus; siphuncle positioned near conch margin, cyrtochoanitic; segments subquadrate in longitudinal section; thin annulosiphonate deposits with distinctive irregular linear processes, which extend adapically and adorally without fusing from segment to segment. (Compiled from Sweet 1964b.)

Diestoceras stensioei (Troedsson, 1926)
Fig. 27L, N

Cyrtogomphoceras stensioei Troedsson, 1926: 108–109, pl. 63 fig. 5, pl. 64 figs 1–2.
Diestoceras stoermeri Strand, 1934: 85 (partim).

Cyrtogomphoceras stensioei – Foerste 1929: 231.
Diestoceras stensioei – Teichert 1930: 294, 296. — Miller & Carrier 1942: 538. — Flower 1946: 398. — Balashov 1953a: 208. — Stumbur 1956: 176. — Flower in Flower & Teichert 1957: 65. — Zhuravlyeva 1962: pl. 26 fig. 6. — Bolton 1977: 36.

Diagnosis

Diestoceras with slightly curved shell and compressed conch cross section; mature body chamber highest near its base with height of ca 80 mm, width of ca 65 mm and length of ca 30–50 mm; sutures straight, more narrowly spaced at venter. (Compiled from Troedsson 1926: 108–109.)

Material examined

ESTONIA • 5 specs; Vormsi Island, Hosholm shore (tower locality); Adila Formation, Pirgu Regional Stage; GIT 840-264, GIT 840-249-1, GIT 878-254, GIT 878-258, GIT 878-165 • 1 spec.; Piirsalu quarry; Moe Formation, Pirgu Regional Stage; GIT 426-987 • 4 specs; Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage; GIT 878-253, GIT 878-255, GIT 878-259, GIT 878-262.

Type locality and horizon

Rannaküla old quarry, near Haapsalu, western Estonia; Adila Formation, Pirgu Regional Stage.

Description

The most complete specimen is GIT 840-264 (Fig. 15N), which preserves parts of the mature body chamber and of the phragmocone. The complete cross section is not preserved but the conch height can be measured throughout the preserved parts of the conch. The maximum conch height of 74 mm is located at the base of the body chamber. Toward the peristome the conch height decreases to 58 mm at the peristome. The peristome is simple with a very shallow (ca 5 mm) hyponomic sinus. The outline of the mature body chamber in lateral view is convex. The cross section apparently circular or slightly compressed. At the base of the body chamber traces of a thin band of oncomyarian muscle scars are preserved; the band is ca 5 mm wide. The phragmocone has a convex outline in lateral view and decreases in diameter from 74 mm to 56 mm in 31 mm (angle of expansion = 32°). The septa are shallowly curved, 6 mm apart where the conch height is 68 mm (RCL = 0.09). No traces of the septal foramen or siphuncle are preserved.

The phragmocone is also well-preserved in GIT 878-259. It has a circular cross section and increases in diameter from 36 mm to 48 mm in a distance of 11 mm (angle of expansion = 43°). GIT 878-253, GIT 878-259, and GIT 878-262 preserve the circular conch cross section.

Remarks

This is a large *Diestoceras*. Other species known from Norway and Sweden reach mature diameters of ca 55 mm or less (Strand 1934; Frye 1987). *Diestoceras breviconum* (Portlock, 1843) reaches a smaller adult size (<35 mm), and has a wider angle of expansion (38°).

In his description of *Diestoceras stoermeri* Strand, 1934, the author describes a specimen with a mature body chamber diameter of 75 mm as paratype (Strand 1934: 85). The holotype of this species has a conch diameter of only 50 mm at the base of the mature body chamber. The complete original diagnosis given for *D. stoermeri* is very brief and without explicitly mentioning the adult size: "Short rounded *Diestoceras* with circular cross section and low camerae" (Strand 1934: 85). Hence, based on the size of the holotype *D. stoermeri* has an adult diameter of ca 50 mm. Consequently, the paratype must be assigned to another, larger, species, which is most probably *D. stensioei*. Therefore, it can be assumed that this species occurs in the uppermost Katian strata ("Gastropod Limestone") of Norway.

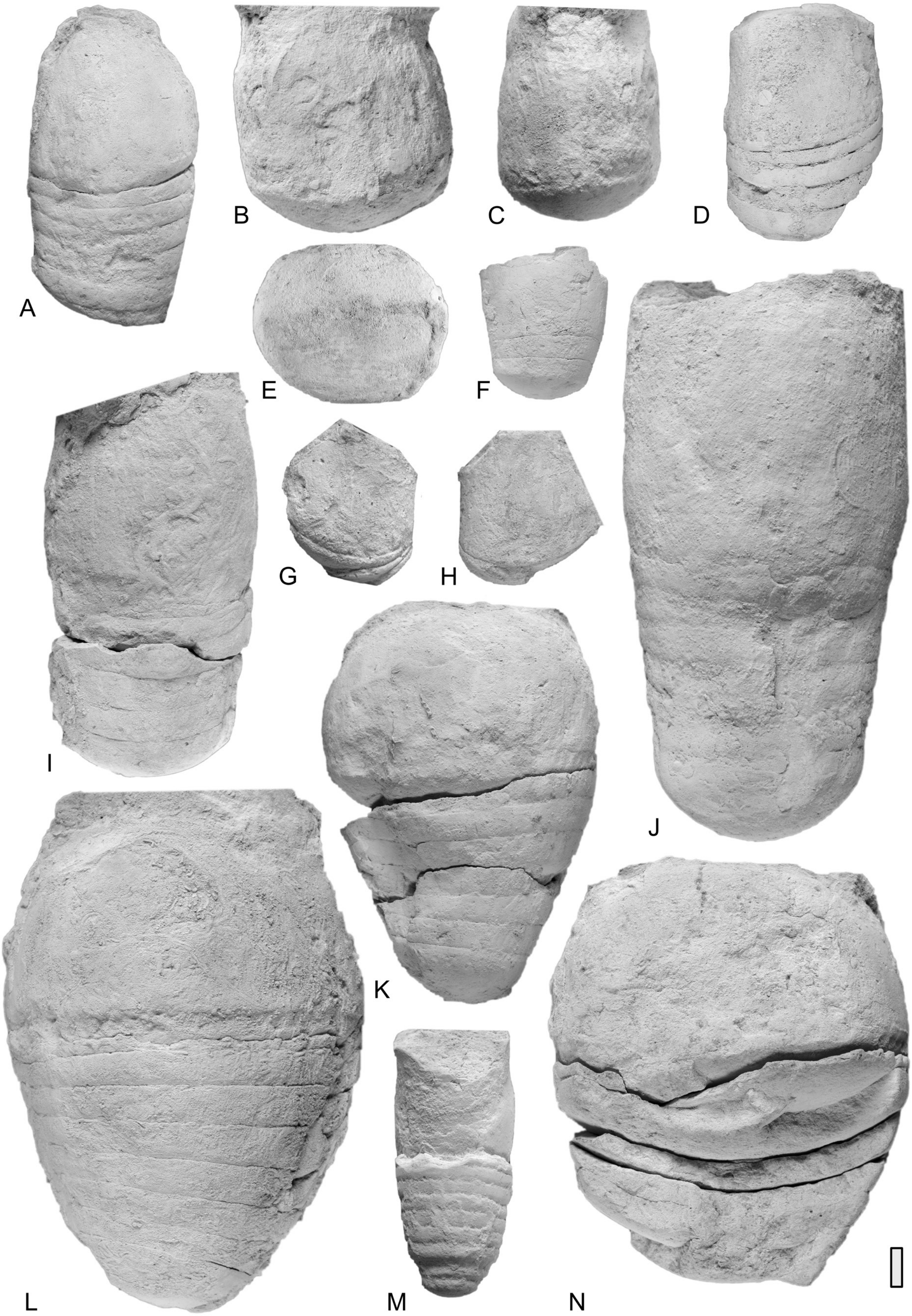
The holotype of *C. stensioei* differs slightly from the specimens described herein. The height of the mature body chamber of the holotype is 79 mm (compared with 74 mm in specimen GIT 840-264) and it has a compressed conch cross section (CHI = 1.22). However, Troedsson (1926) describes only the mature body chamber and not the conch cross section of the phragmocone and its intraspecific variability. Moreover, depending on the orientation of the specimens in the sediment and on the specific sediment stratum, various degrees of taphonomic compaction occur among the specimens. The deviations of the material described herein from the holotype are therefore interpreted as within the range of the intraspecific variability or as a result of taphonomic processes.

Diestoceras sp. A
Fig. 27K

Material examined

ESTONIA • Vormsi Island, Hosholm shore (tower locality); Adila Formation, Pirgu Regional Stage; GIT 878-252.

Fig. 27 (next page). Breviconic cephalopods from the Vormsi–Pirgu regional stages, Estonia. **A**. *Dowlingoceras kallholnense* Frye, 1987, specimen GIT 878-247, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage, lateral view. **B–C**, **E**. *Dowlingoceras* sp., specimen GIT 878-249, from Vohilaid shore (E), Vohilaid Island, Pirgu Regional Stage. **B**. Lateral view. **C**. View of antisiphuncular side. **D**. *Danoceras* sp. A., specimen GIT 878-269, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage, lateral view. **E**. Adoral view. **F**. *Rizosceras teres* sp. nov., holotype TUG 1745-188, from Saaremõisa (Lyckholm), Vormsi Regional Stage, lateral view. **G–H**. *Kallholnoceras* sp. **G**. GIT 878-323, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage, lateral view. **H**. Specimen GIT 878-233, from Vohilaid shore (E), Vohilaid Island, Pirgu Regional Stage, lateral view. **I**. *Dowlingoceras tornense* sp. nov., holotype GIT 840-254, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage, lateral view. **J**. *Dowlingoceras* sp. B, specimen GIT 47-866, from Vohilaid shore (E), Vohilaid Island, Pirgu Regional Stage, lateral view. **K**. *Diestoceras* sp., specimen GIT 878-252, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage, lateral view. **L**. *Diestoceras stensioei* (Troedsson, 1926), specimen GIT 426-987, from Piirsalu quarry, Pirgu Regional Stage. **M**. Diestoceratidae gen. et sp. indet., specimen TUG 1745-192, from Salu, Pirgu Regional Stage, view from antisiphuncular (?) side. **N**. *Diestoceras stensioei* (Troedsson, 1926), specimen GIT 840-264, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage, lateral view. Scale bar = 10 mm, same scale in all figures.


A
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Description

The specimen preserves parts of the mature body chamber and the phragmocone. Two thirds of the shell (in longitudinal direction) are preserved, so that the conch cross section cannot be determined with certainty; but was apparently circular. The body chamber is 45 mm long. The conch height at the base of the body chamber is 64 mm, ca 10 mm adorally the conch height reaches its maximum at 67 mm and at the peristome the height is ca 57 mm. In longitudinal direction, the outline of the body chamber is convex, and the peristome is simple and directly transverse. The hyponomic sinus is not preserved. At the base of the body chamber, a ca 0.4 mm wide band of oncomyarian muscle scars is preserved. The phragmocone is slightly curved, its height increases from 30 mm to 62 mm at a length of 38 mm (angle of expansion = 46°). At a conch height of 62 mm, the sutures are 7 mm apart (RCL = 0.11). The sutures are straight and directly transverse. Traces of the septal foramen and siphuncle are not preserved.

Remarks

The short, rounded conch, simple mature peristome, and apparently circular conch cross section identify this specimen as a species of *Diestoceras*. The size of the mature body chamber differs from known species of the genus described from Baltoscandia. However, because of the fragmentary preservation of this single specimen a species level determination is not possible.

Genus ***Dowlingoceras*** Foerste, 1928d

Type species

Poterioceras gracile Whiteaves, 1892, Black Island, Swampy Harbour, Lake Winnipeg, Manitoba, Canada, Red River Formation, Katian; by original designation.

Diagnosis

Slender diestoceratids with straight or slightly curved shell, and elliptically compressed to oval conch cross section; mature body chamber with widest height and width near its base, with simple constriction close to mature aperture, with apertural widening and shallow hyponomic sinus; siphuncle positioned near conch margin, with, compared to other diestoceratids, narrow septal foramen and only slightly expanding segments. (Compiled from Teichert 1930, and Sweet 1964b.)

Comparison

Danoceras and *Dowlingoceras* differ mainly in the shape of the siphuncular segments (i.e., subtrapezoidal versus fusiform, respectively, Strand 1934: 80). In the Estonian material, a difference in the shape the mature body becomes also apparent: in *Dowlingoceras*, it is relatively long (ratio height / length ca one or more) and simple convex, while *Danoceras* has an adorally constricted, amphora-like body chamber.

Dowlingoceras kallholnense Frye, 1987
Figs 16E, 27A

Dowlingoceras kallholnense Frye, 1987: 95–96, figs 6a–b, 7.

Dowlingoceras kallholnense – Kröger 2013: tab.2.

Diagnosis

Dowlingoceras with a slightly compressed cross section (CHI = 1.1); oval cross section, venter narrower than dorsum; mature body chamber is more gibbous than those of the other species of the genus, ca 40 mm high at its base, and with marked constriction near the peristome. (Compiled from Frye 1987.)

Material examined

ESTONIA • Vormsi Island, Hosholm shore; Adila Formation, Pirgu Regional Stage; GIT 878-247.

Type locality and horizon

Kallholn, Dalarna, Sweden; Boda Formation, latest Katian.

Description

Specimen GIT 878-247 preserves parts of the mature body chamber and the phragmocone with a conch height and width of 39 mm and 32 mm, respectively (CHI = 1.2) The conch cross section is oval with a narrower curvature on the ventral compared to the dorsal side. The conch height increases from 36–37 mm at a length of 17 mm (angle of expansion 8°). The body chamber is only partly preserved, had a length of more than 38 mm and decreases in conch height from its base with a convex outline in lateral view toward ca 35 mm in height. The sutures form a wide lateral lobe and are ca 6 mm apart where the conch height is 39 mm (RCL = 0.15). The siphuncular segments are elongated (7 mm long, 4 mm high, SCR = 0.57) fusiform, wider adorally and adnate to the adoral septal surfaces. The septal necks are poorly preserved, apparently cyrtochoanitic.

Remarks

The Swedish types of *D. kallholnense* have conch dimensions (maximum height of mature body chamber = 40 mm; CHI = 1.1, and a low angle of expansion in the adoral parts of the phragmocone) (Frye 1987) which are nearly identical to the specimen described herein. The differences in the connecting ring shape (presence of an adnate area in specimen GIT 878-247 are interpreted as taphonomic or the effects of orientation of the cut. (See also Turek & Aubrechtová 2024, and Pohle *et al*. 2024, on this topic.) The view is oblique to the dorso-ventral body axis, in Frye (1987: fig. 7), it is apparently perpendicular to that axis in specimen GIT 878-247 (Fig. 16E).

Dowlingoceras tornense sp. nov.
urn:lsid:zoobank.org:act:9E94767A-9B7E-440B-84D7-12F695042F30
Figs 25A–B, 27I

Diagnosis

Dowlingoceras with compressed elliptical conch-cross section (CHI = 1.3); mature body chamber with maximum conch height of ca 45 mm near its base and height to length ratio of ca 1, with a nearly straight, simple peristome and apparently lacking or only with a very shallow hyponomic sinus; angle of expansion of the phragmocone ca 12°.

Etymology

The Estonian "*torni*", 'tower', refers to the type locality.

Type material

Holotype
ESTONIA • Vormsi Island, Hosholm shore (tower locality); Adila Formation, Pirgu Regional Stage; GIT 840-254.

Paratype
ESTONIA • same data as for holotype; GIT 840-273.

Description

The holotype preserves parts the phragmocone and the mature body chamber. Where preserved (near the peristome), the conch surface is apparently smooth. The conch height and width at the base of the mature body chamber are 45 mm and 34 mm, respectively (CHI = 1.3). There, the shape of conch cross section is apparently elliptically to oval compressed. The ventral side is slightly more narrowly curved. In lateral view, the conch is straight. The body chamber is 46 mm long with a nearly straight, simple peristome and apparently without a hyponomic sinus. The lateral outline of the body chamber is slightly convex, reaching the greatest conch height 47 mm at ca mid-length location of the body chamber.

The phragmocone increases in height from 38 mm to 45 mm at a length of 32 mm (angle of expansion = 12°). The sutures form a shallow lobe at the lateral sides of the phragmocone, a sharp saddle on the ventral side and a rounded saddle on the dorsal side; they are 8 mm apart where the conch height is 42 mm (RCL = 0.19). The septal foramen is nearly marginal with a diameter of 5 mm where the conch height is 43 mm (RSH = 0.12). A natural cut of the siphuncle shows a fusiform, elongated, *Dowlingoceras*-like siphuncular segments (length 6 mm, height 3.8 mm, SCR = 0.63).

Comparison

The conch shape, including the shape of the mature body chamber is similar to that of *D. kallholnense* Frye, 1987. However, the mature body chamber of *D. tornense* sp. nov. is greater in height, width, and length than that of *D. kallholnense* (40 mm, 36 mm, 40 mm, respectively, in *D. kallholnense*) and the conch cross section is more compressed (CHI = 1.1 in *D. kallholnense*).

Dowlingoceras sp. A
Fig. 27B–C, E

Material examined

ESTONIA • Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage, GIT 878-249.

Description

The specimen is an internal mold of a mature body chamber with a conch height and width at its base of 44 mm and 38 mm, respectively (CHI = 1.2). At the peristome, the height and width are 40 mm and 32 mm, respectively. The body chamber is 36 mm long and in lateral view has slightly convex margins. The conch cross section is elliptical. At a distance of ca 10 mm from the peristome, a ca 10 mm wide and 1.5 mm deep constriction forms an amphora-like aperture. The peristome is directly transverse with a wide, inconspicuous hyponomic sinus on the prosiphuncular side. Traces of a septal foramen close to the conch margin are preserved.

Remarks

The specimen is assigned to *Dowlingoceras* based on shape of the mature body chamber. Its size and rounded elliptical cross section can be compared with *D. torni*, while the gibbous shape and terminal constriction can be compared with *D. kallholnense*. Based on this single incomplete specimen, erection of a new species is impossible.

Dowlingoceras sp. B
Fig. 27J

Material examined

ESTONIA • Paope quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 47-866.

Description

The specimen is a straight, slightly deformed (compressed) fragment of ca eight chambers of the phragmocone and a nearly complete mature body chamber. At the base of the body chamber, the conch diameter is 47 mm, the diameter slightly increases adorally over a distance of ca 20 mm to 60 mm, then continuously decreases to a diameter of 58 mm near the aperture. A shallow and wide constriction is present ca 20 mm from the peristome. The peristome is only partially preserved. The body chamber is ca 60 mm long.

The phragmocone increases in diameter from 42 mm to 57 mm at a length of 52 mm (angle of expansion 16°). The sutures are straight and directly transverse while traces of the siphuncle are present near the conch margin, which are too poorly preserved measure. The remaining traces suggest that the siphuncle was fusiform.

Remarks

The poor preservation of this specimen does not allow further determination. The conch shape combined with the subfusiform siphuncle identify the specimen as a *Dowlingoceras*.

Diestoceratidae gen. et sp. indet.
Fig. 27M

Material examined

ESTONIA • Salu; Pirgu Regional Stage; TUG 1745-192.

Description

The specimen is a fragment of a nearly straight mold of a mature body chamber and nine chambers of the phragmocone which is partially deformed. Parts of the shell are eroded. The conch surface is not preserved. The fragmentary preservation does not permit measurement of the original conch cross section. The maximum conch diameter (28 mm) is located at the base of the body chamber. The body chamber is ca 28 mm long with slightly convex conch margins, it contracts adorally to a diameter of ca 27 mm where a shallow, inconspicuous constriction is located ca 5 mm distant from the peristome. The phragmocone diameter increases from 23 mm to 27 mm at a length of 16 mm (angle of expansion = 18°). The sutures are directly transverse and 3.5 mm apart where the conch diameter is 27 mm (RCL = 0.13). On the surface of the phragmocone, faint longitudinal lirae may be seen.

Remarks

The conch shape, shape of the mature body chamber as well as spacing and pattern of sutures of this specimen are suggestive of a small diestoceratid. The small mature size and the relatively long body chamber are not known from any species of *Danoceras*, *Dowlingoceras* or *Diestoceras* described in the literature. However, as crucial features for determination, including the siphuncle position and shape, are not preserved, while the conch cross section cannot be fully be reconstructed, a genus and species level determination of this specimen is impossible.

Family Graciloceratidae Flower in Flower & Kummel, 1950

Genus ***Hiiumoceras*** gen. nov.
urn:lsid:zoobank.org:act:18791ECD-C1D4-4806-9566-DC4C4B724F5A

Type species

Hiiumoceras hiiuense gen. et sp. nov. Hiiumaa Island, Estonia; Pirgu Regional Stage.

Diagnosis

Small, strongly curved, exogastric cyrtocones with short body chamber; circular conch cross section; siphuncle at some distance from conch margin (subventral); ornamented with fine, directly transverse striae.

Etymology

Refers to Hiiumaa Island, the region of the type species of this genus.

Comparison

The genus is very similar to *Ringoceras* Strand, 1934, from the Bønsnes Formation, late Katian, Ringerike, Norway, from which it differs in having a circular conch cross section and in lacking the longitudinal ornamentation.

Hiiumoceras hiiuense gen. et sp. nov.
urn:lsid:zoobank.org:act:CBB9CFFF-F108-4D62-8667-64A3318EE96D
Figs 28A–D, 29A

Diagnosis

Same as for genus, by monotypy.

Etymology

Refers to the Hiiumaa, Estonia, the region, where this species is known from.

Type material

Holotype

ESTONIA • Hiiumaa Island, Paope quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 1745-11.

Paratype

ESTONIA • 1 spec.; Hiiumaa Island, Paluküla quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-421.

Description

The holotype is an exogastrically curved fragment of parts of a body chamber, and two chambers of the phragmocone. The conch cross section is circular with a diameter increasing from 16 mm to 22 mm and an angle of expansion of 16°. The outer shell is not preserved but on the surface of the inner mold, traces of directly transverse, shallow striae are visible. The sutures are 3 mm apart (RCL = 0.19), straight and directly transverse. A septal foramen with a diameter of 1 mm is preserved 2 mm from the conch margin, where the conch diameter is 16 mm (RSH = 0.06, RSP = 0.13). The septal necks are suborthochoanitic. The connecting rings are relatively thick and form nearly tubular segments; slightly expanded into the chambers (Fig. 29A). No endosiphuncular deposits are observed.

Specimen GIT 426-421 (Fig. 28A–D) is a mold of a complete body chamber with a circular conch-cross section increasing from 17 mm to 22 mm at a length of 20 mm (angle of expansion 18°). In lateral view, the dorsal margins and ventral margins of the body chamber are concavely and convexly curved, respectively. The conch expands gradually. On the surface of the specimen, shallow, directly transverse striae are visible (ca one per millimeter). The trace of a septal foramen is preserved at the base of the body chamber. It has a height of 2 mm and is 3 mm distant from the conch margin (RSH =0.11, RSP = 0.2).

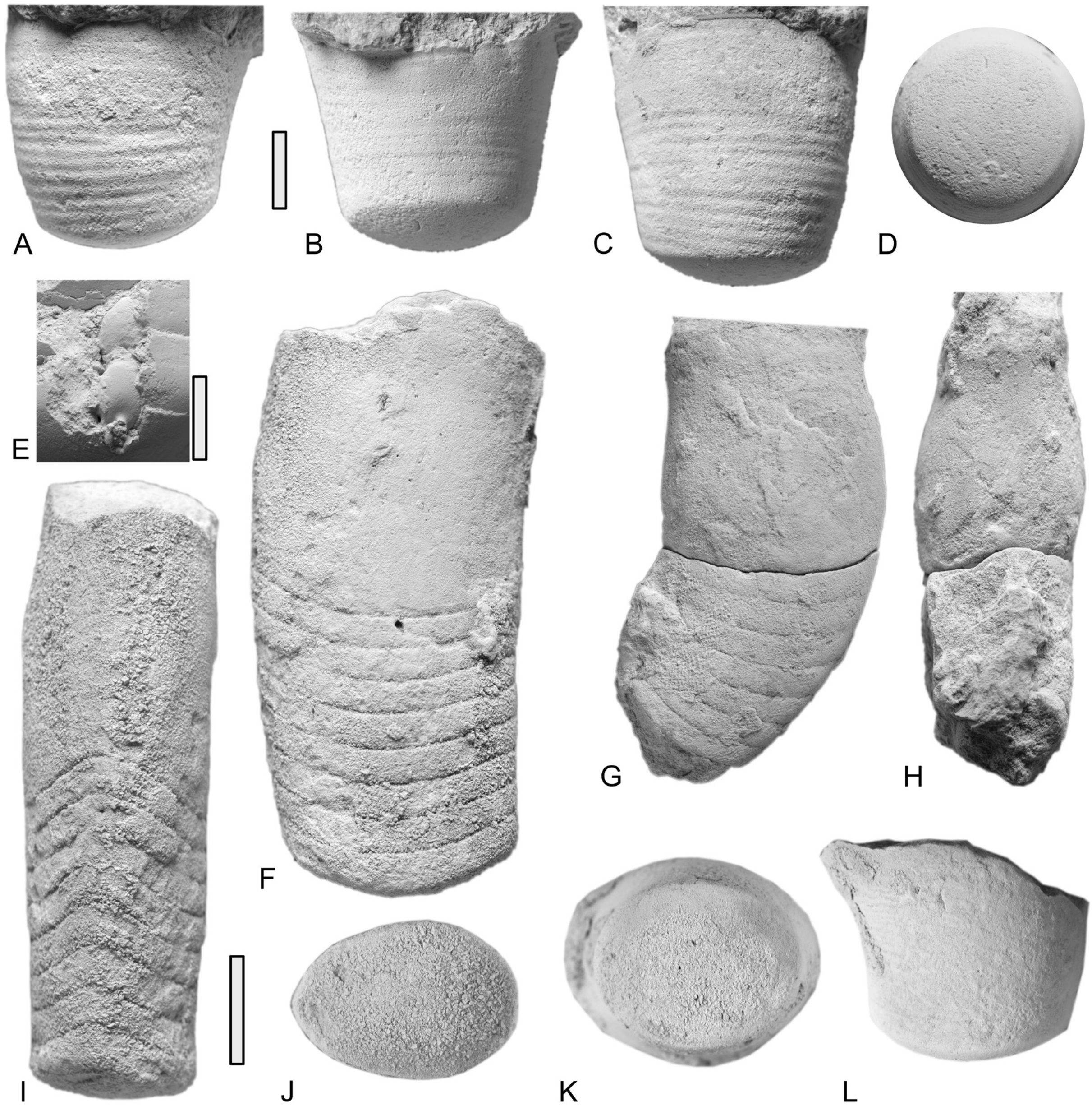


Fig. 28. Graciloceratidae Flower, 1950 and Oncoceratidae Hyatt, 1884 of the Vormsi–Pirgu regional stages, Estonia. **A–D**. *Hiiumoceras hiiuense* gen et sp. nov., paratype GIT 426-421, from Paluküla, Hiimuaa Island, Vormsi Regional Stage. **A**. Lateral view. **B**. View of antisiphuncular side. **C**. View of prosiphuncular side. **D**. Adapical view. **E**. *Rizosceras teres* sp. nov., holotype TUG 1745-188, from Saaremõisa (Lyckholm), Vormsi Regional Stage, view of prosiphuncular side with details of siphuncle visible. **F**, **I–J**. *Beloitoceras* (?) sp., specimen GIT 426-1081, from Pirgu river outcrops, Raplamaa, Pirgu Regional Stage. **F**. Lateral view. **G–H**. *Beloitoceras uuemoisense* sp. nov., holotype GIT 1745-290, from Uuemõisa, Läänemaa, Pirgu Regional Stage. **G**. Lateral view. **H**. View of antisiphuncular side. **I**. View of prosiphuncular side. **J**. Adapical view. **K–L**. Multiceratoidea gen. et sp. indet. C, specimen GIT 878-234, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage. **K**. Adapical view. **L**. Lateral view. Scale bar = 10 mm in all figures except E, same scale in A–D, and in F–K. Scale bar in E = 5 mm.

Comparison

This species differs from the otherwise similar *Ringoceras praecurvum* Strand, 1934 in size, conch cross section and ornamentation. The Norwegian species is smaller (with an adult size of less than 20 mm), is additionally ornamented with longitudinal lirae, and has a compressed conch cross section.

Genus ***Piersaloceras*** Teichert, 1930

Type species

Piersaloceras gageli Teichert, 1930, from Piirsalu, Estonia; Moe Formation, Pirgu Regional Stage, late Katian; by original designation.

Diagnosis

Exogastric, gradually enlarging cyrtocones with nearly circular conch cross section and low angle of expansion; ornamented with low longitudinal ribs and distinct transverse frills; siphuncle nearly subcentrally positioned, cylindrical siphuncle. (Adopted from Teichert 1930.)

Piersaloceras (?) sp.
Figs 30C, 31A

Material examined

ESTONIA • Sutlema old quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 1827-163.

Description

The specimen is a fragment of a curved body chamber, preserved in its total length but lateral parts of the body chamber are missing (Fig. 30C). The outer shell is well-preserved, it is ornamented with narrowly spaced (ca 15–20 per 10 mm) imbricated frills (Fig. 31A), which are directly transverse, and parallel to the peristome. No hyponomic sinus occurs. In lateral view, both margins are curved. The curvature of the concave margin is wider than that of the convex margin, which results in a gibbous outline of the body chamber. The greatest conch height of 50 mm is located at ca mid-length of the body chamber. At its base, the height is 48 mm and at the aperture 43 mm. The suture, reconstructed from the base of

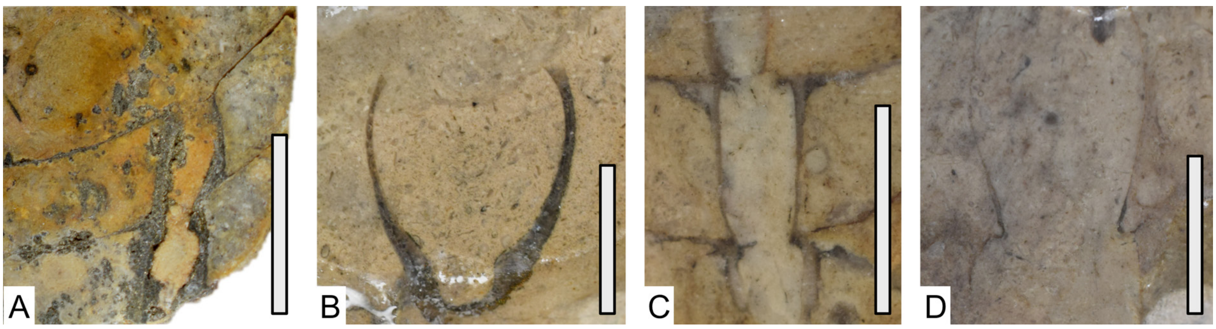


Fig. 29. Median sections of phragmocones of Gracilоceratidae Flower, 1950 and Oncoceratidae Hyatt, 1884 of the Vormsi–Pirgu regional stages, Estonia. **A**. *Hiiumoceras hiiuense* gen et sp. nov., holotype TUG 1745-11, from Paope quarry, Hiiumaa Island, Vormsi Regional Stage. **B**. *Rizosceras teres* sp. nov., paratype TUG 80-508, from Saxby shore, Vormsi Island, Vormsi Regional Stage. **C**. *Beloitoceras siljanense* Frye, 1987, specimen TUG 939-56, from Haapsalu holm, Pirgu Regional Stage. **D**. *Dalecarlioceras constrictum* Frye, 1987, specimen GIT 878-248, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage. Scale bars = 5 mm.

the body chamber, forms a narrow lateral lobe. No traces of the siphuncle and of the septal foramen are preserved.

Remarks

The characteristically frilled ornamentation of this fragment is most similar to that of *P. gageli* Teichert, 1930, which, in turn, is known only from a single, immature specimen. It differs from the type specimen (and, to date, only known specimen of this genus) in lacking the longitudinal furrows on the impression of the mold, which could be an effect of the typical oncoceratid longitudinal ridges, and which is present in more apical conch parts of many oncocerids (see discussion in Frye 1987: 92). Because details of the siphuncle and parts of the phragmocone are unknown from the specimen described above, a definite determination is not possible. The general shape of the body chamber is similar to that of *Redpathoceras saxbyense* sp. nov., and to Uranoceratidae, such as *Deckeroceras* Foerste, 1935b. The mature body chamber of the former is however longer (68 mm) and at its base less high (45 mm). More complete, better-preserved material is needed to evaluate the relationship of this specimen to *Redpathoceras*, or whether *Piersaloceras* might belong to the Uranoceratidae or Probillingsitidae Flower, 1941.

Notably, some oncoceratids, such as *Beloitoceras* or *Neumatoceras* also have similarly shaped body chambers, but are more strongly compressed and have a hyponomic sinus. This could link oncoceratids and uranoceratids, as suggested by the phylogeny in Pohle *et al*. (2022).

Family Karoceratidae Teichert, 1939

Genus ***Kallholnoceras*** Frye, 1987

Type species

Kallholnoceras cornutum Frye, 1987, Kallholn quarry, Kallholn, Dalarna, Sweden, Boda Formation, late Katian; by original designation.

Diagnosis

Exogastric, strongly curved cyrtocones with compressed conch cross section and gibbous mature body chamber; siphuncle close to conch margin, without endosiphuncular deposits with gradually enlarging; septal necks suborthochoanitic; siphuncle slightly expanded within chambers, without endosiphuncular deposits. (Compiled from Frye 1987.)

Kallholnoceras sp.
Fig. 27G–H

Material examined

ESTONIA • 1 spec.; Haapsalu holm; Adila Formation, Pirgu Regional Stage; TUG 1745-4 • 1 spec.; Vormsi Island, Hosholm shore (tower locality); Adila Formation, Pirgu Regional Stage; GIT 878-323 • 1 spec.; Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage; GIT 878-233.

Description

Specimen GIT 878-233 (Fig. 27H) is a fragment of a mature body chamber with a height and width of 33 mm and 20 mm, respectively (CHI = 1.65). The preserved length of the body chamber is 28 mm. The body chamber is slightly exogastrically curved and slightly gibbous. An inconspicuous constriction occurs near the adoral margin of the preserved part where the conch height is ca 30 mm.

The second specimen (GIT 878-323) preserves parts of a mature body chamber and three chambers of the phragmocone (Fig. 27G). The conch height at the base of the body chamber was estimated ca 33 mm. The body chamber is similar in shape and preserved height to that of specimen GIT 878-233.

The preserved part of the phragmocone indicates a relatively strong exogastric conch curvature. The third specimen (TUG 1745-4) is a strongly curved fragment of a phragmocone of seven chambers with a maximum conch height of 26 mm.

Remarks

The two specimens belong to a strongly curved, compressed oncocerid species with a gibbous body chamber. Their general conch shape is similar to that of *Kallholnoceras*. All three specimens are larger than the type species of this monotypic genus, which has a mature conch of 20 mm. Because of the fragmentary character of the material, a species level determination, and the erection of a new species is not currently possible.

Family Oncoceratidae Hyatt, 1884

Genus ***Beloitoceras*** Foerste, 1924

Type species

Oncoceras pandion Hall, 1861, from Beloit, Wisconsin, USA, Black River Formation; by original designation.

Diagnosis

Strongly curved, relatively slender brevicones with ovate, compressed cross section; conch smooth or with fine transverse ornament; maximum conch diameter situated within adapical half to third of body chamber; antisiphuncular outline of conch concave over entire length in dorsoventral section,

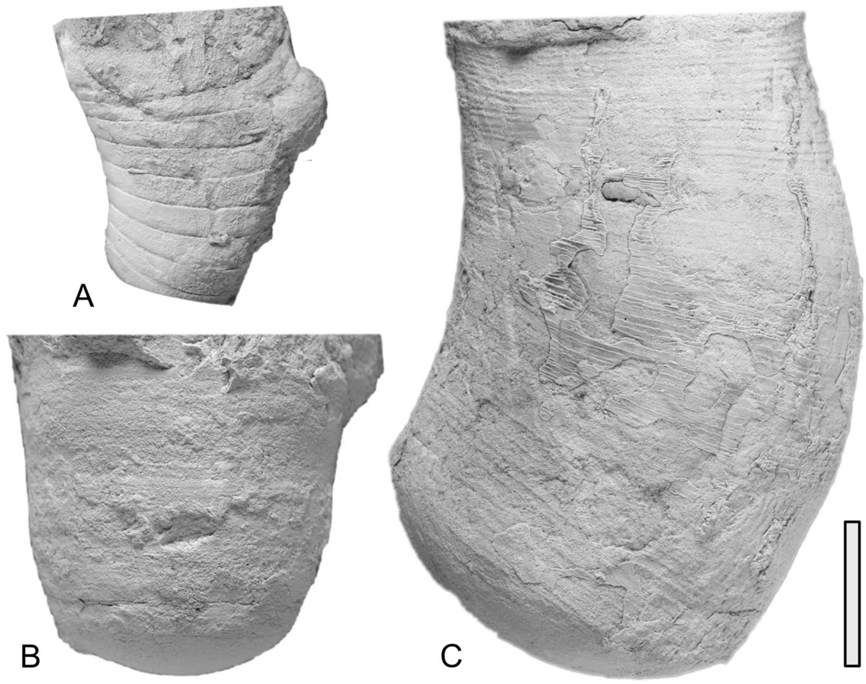


Fig. 30. Graciloceratidae Flower, 1950 and Oncoceratidae Hyatt, 1884 of the Vormsi–Pirgu regional stages, Estonia. **A**. *Beloitoceras siljanense* Frye, 1987, specimen TUG 939-56 from Haapsalu holm, Pirgu Regional Stage, lateral view. **B**. *Rizosceras teres* sp. nov., paratype GIT 426-550, from Kõrgessaare quarry, Vormsi Regional Stage, lateral view. **C**. *Piersaloceras* (?) sp., specimen TUG 1827-163, from Sutlema old quarry, Vormsi Regional Stage, lateral view. Scale bar = 20 mm, same scale in all figures.

prosiphuncular outline broadly convex; five to eight chambers per distance similar to corresponding conch cross section; body chamber short with well-developed hyponomic sinus at convex side; siphuncle

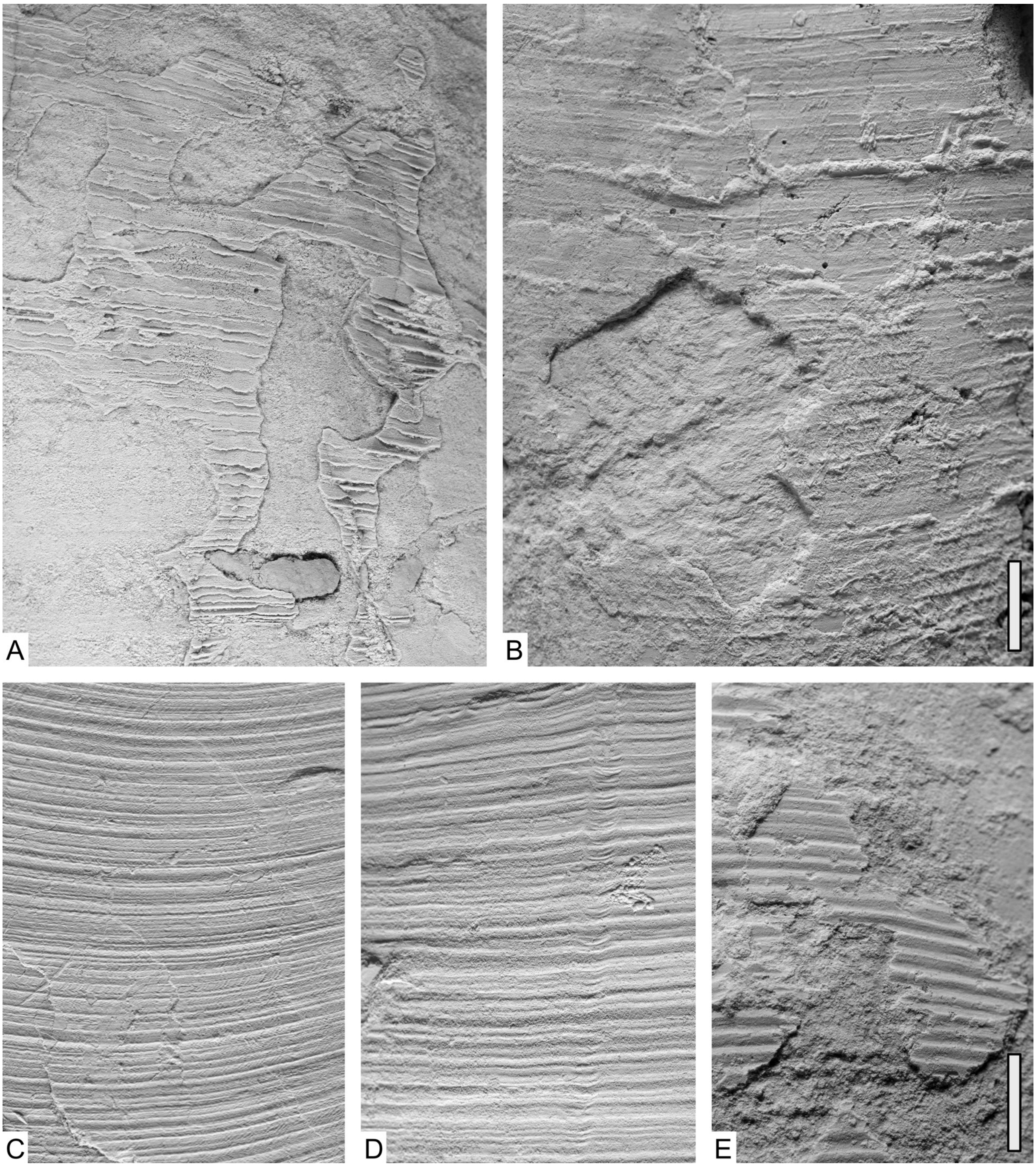


Fig. 31. Details of shell ornamentation of cephalopods of the Vormsi–Pirgu regional stages, Estonia. **A**. *Piersaloceras* (?) sp., specimen TUG 1827-163, from Sutlema old quarry, Vormsi Regional Stage. **B**. *Kiaeroceras urgense* sp. nov. holotype TUG 103-75, from Urge quarry, Vormsi Regional Stage. **C–D**. *Strandoceras sphynx* (Schmidt, 1858). **C**. Specimen TAM G432:68, from Niibi hillock, Pirgu Regional Stage. **D**. Specimen TUG 1672-29, from Saxby village, Pirgu Regional Stage. **E**. *Strandoceras sulevipoegi* sp. nov., paratype TUG 899-55, from Saxby shore, Vormsi Regional Stage. Scale bar = 5 mm in all figures, same scale in A–B, and in C–E.

slender, situated close to convex margin of conch curvature, with subtubular segments; septal necks short suborthochoanitic to cyrtochoanitic; connecting rings thin. (Compiled from Sweet 1964b, and Frey 1995.)

Beloitoceras siljanense Frye, 1987
Figs 29C, 30A

Beloitoceras siljanense Frye, 1987: 86–88, figs 3e–f, 4, 6c.

Beloitoceras siljanense – Kröger 2013: 20, figs 9c–d, 11, tab. 2. — Pohle *et al*. 2022: fig. 2.

Diagnosis

Beloitoceras with compressed cross section; in longitudinal section, antisiphuncular conch margin nearly straight approaching mature peristome; angle of expansion of phragmocone typically more than 17°; mature conch with maximum height and width at peristome. (Adopted from Frye 1987.)

Material examined

ESTONIA • 1 spec.; Haapsalu holm; Adila Formation, Pirgu Regional Stage; TUG 939-56.

Type locality and horizon

Kallholn, Dalarna, Sweden; Boda Limestone, late Katian.

Description

The specimen is a fragment of a phragmocone with a conch height that increases from 20 mm to 29 mm and respective conch width increasing from 13 mm to 21 mm (angle of expansion = 18°). The conch cross section is oval compressed with narrower prosiphuncular side (CHI: 1.4–1.5). The conch surface is not preserved. The sutures form shallow lateral lobes and rounded saddles on the venter and dorsum. Mid-laterally, the sutures are 3.3 mm apart where the conch height is 24 mm (RCL = 0.14). The septal necks are cyrtochoanitic. The siphuncle is relatively narrow, and slightly expanded within the chambers (Fig. 29C)

Remarks

This specimen can be identified as *B. siljanense* because of the characteristic straightened dorsal conch margin as well as of the relatively large angle of expansion.

Beloitoceras sinuososeptatum (Roemer, 1861)
Fig. 32A–B

Orthoceras sinuoso-septatum Roemer, 1861: pl. 6 fig. 3a–c.
Beloitoceras heterocurvatum Strand, 1934: 76, pl. 10 figs 8–9 (partim).

Richardsonoceras sinuososeptatum – Dzik 1984: 58, 188, text-fig. 16a–b, pl. 8 fig. 1a–d.
Beloitoceras heterocurvatum – Frye 1987: 84, fig. 3a–d. — Kröger *et al.* 2011: 38, fig. 5a–b.
Beloitoceras sinuososeptatum – Kröger 2013: 17–20, figs 9a–b, 11.

Diagnosis

Beloitoceras with compressed cross section and keeled conch margins on concave and convex side of conch curvature throughout entire length; in longitudinal section, antisiphuncular conch margin concave; angle of expansion of phragmocone ca 16–17°; length of body chamber somewhat less than maximum conch height; conch surface ornamented with irregularly spaced, rounded striae, which form a shallow sinus on the prosiphuncular side and a deep V-shaped sinus on the antisiphuncular side; about six chambers similar to the height of the conch cross section (RCL = 0.17); sutures with deep lateral lobes; siphuncle situated near ventral margin, segments ca twice as long as high (SCR = 0.5), with slightly convex vertical outline. (From Kröger 2013.)

Material examined

ESTONIA • 4 specs; Vormsi Island, Hosholm shore; Adila Formation, Pirgu Regional Stage; GIT 426-110, GIT 840-248, GIT 840-92, GIT 840-251 • 3 specs; same data as for preceding; TUG 1743-76, TUG 1745-10, TUG 939-59 • 10 specs; Vormsi Island, Hosholm shore (tower locality); Adila Formation, Pirgu Regional Stage; GIT 426-2, GIT 840-256, GIT 840-267, GIT 840-268, GIT 878-237 to GIT 878-239, GIT 878-241 to GIT 878-243 • 2 specs; Sutlepa quarry; Adila Formation, Pirgu Regional Stage; TAM G5:9, TAM G149:127 • 8 specs; Vardi manor (Schwarzen); Adila Formation, Pirgu Regional Stage; TAM G5:1 to TAM G5:8 • 7 specs; Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage; GIT 878-144 to GIT 878-146, GIT 878-151, GIT 878-152, GIT 878-240, GIT 878-244 • 1 spec.; same data as for preceding; TUG 1723-26.

Type locality and horizon

Zawidowice by Oleśnica, Poland; erratic boulder, Vormsi–Pirgu regional stages ("Lyckholm Stufe" of Teichert 1930).

Remarks

The species has been revised and described in detail by Kröger (2013). The Estonian material adds to the knowledge of the variability of this species. Combined with the total dataset of 32 measurements, derived

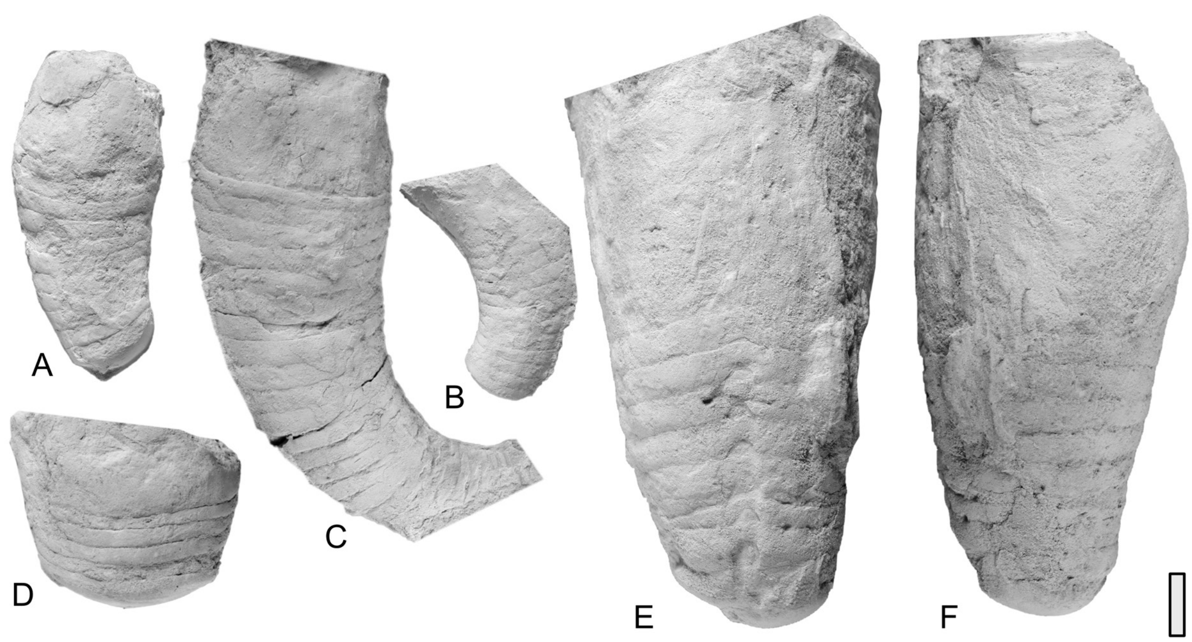


Fig. 32. Oncoceratidae Hyatt, 1884 of the Vormsi–Pirgu regional stages, Estonia. **A–B**. *Beloitoceras sinuososeptatum* (Roemer, 1861). **A**. Specimen TUG 939-56, from Haapsalu holm, Pirgu Regional Stage, lateral view. **B**. Specimen TUG 1723-26, from Vohilaid shore (E), Vohilaid Island, Pirgu Regional Stage, lateral view. **C**. *Beloitoceras* cf. *sinuososeptatum* (Roemer, 1861), specimen GIT 878-231, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage. **D**. *Cyrtorizoceras* sp. A., specimen GIT 878-260, from Vohilaid shore (E), Vohilaid Island, Pirgu Regional Stage, lateral view. **E–F**. *Cyrtorizoceras hariense* sp. nov., holotype GIT 878-71, from Saxby shore (N), Vormsi Island, Estonia, Vormsi Regional Stage. **E**. View of prosiphuncular side. **F**. Lateral view. Scale bar = 20 mm, same scale in all figures.

from the types from erratic boulders in Poland (Dzik 1984), the specimens known from Norway (Strand 1934), and Sweden (Kröger 2013), a decreasing angle of expansion is now evident for this species with ca 15°–20° in early growth stages and angles lower than 10° in nearly mature phragmocones (Fig. 33A). Conversely, the CHI increases during ontogeny (note, however, the possible taphonomic compression of some of the Estonian and Norwegian specimens; Fig. 33B). As with the Swedish material, the variability of the curvature of the conch varies quite strongly among specimens but distinct groups of weakly and strongly curved conchs could not be identified (compare, e.g., specimens TUG 939-59 and TUG 1723-26, Fig. 32A–B). The largest known specimen has a height at the base of the mature body chamber of 44 mm (TUG 939-59, Fig. 32A).

Beloitoceras cf. ***sinuoseptatum*** (Roemer, 1861)
Figs 16G, 32C, 33

Material examined

ESTONIA • 2 specs; Vormsi Island, Hosholm shore; Adila Formation, Pirgu Regional Stage; GIT 878-231, GIT 426-2.

Description

The nearly complete specimen GIT 878-231 (Fig. 32C) is relatively strongly curved during early growth stages (corresponding to conch heights < ca 40 mm) and reaches a maximum conch height of 53 mm at the base of the mature body chamber. There, the conch width is ca 37 mm (CHI = 1.43), and the conch cross section is oval in shape with narrow dorsal and ventral margins. The body chamber is 35 mm long and at the aperture 48 mm high. In lateral view, the dorsal and ventral margin of the body chamber is slightly convex. The peristome appears to be straight and simple. The phragmocone height increases from 40 mm to 53 mm at a length of 55 mm (angle of expansion = 13°). Between conch heights of 21–40 mm the conch expands at an angle of 19°. The sutures form shallow lateral lobes.

In specimen GIT 426-2, which is a short fragment of a phragmocone with five chambers, the details of the siphuncle are well-preserved (Fig. 16G). The siphuncular segments are trapezoidal, with adnate areas at the adapical surfaces of the septa. The septal necks are cyrtochoanitic.

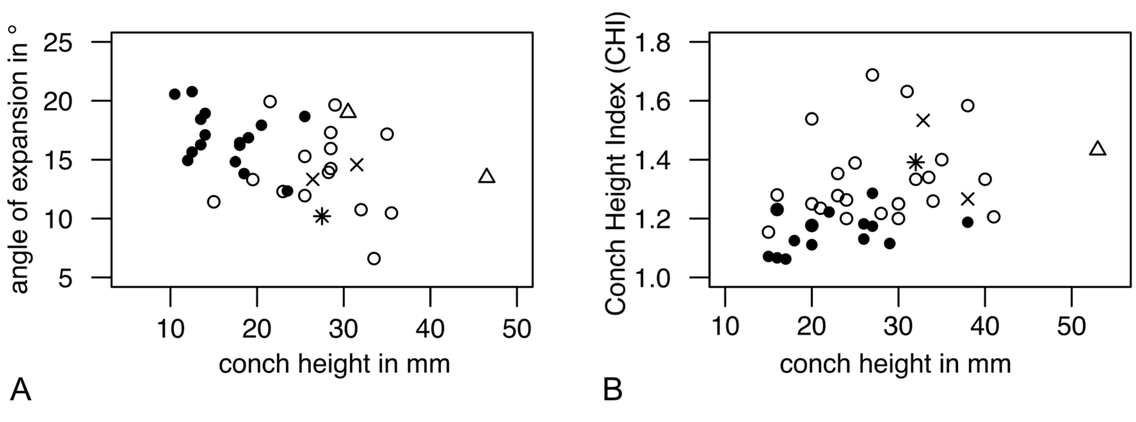


Fig. 33. Diagrams of morphological variability of specimens of *Beloitoceras sinuososeptatum* (Roemer, 1861). **A**. Angle of expansion. **B**. Conch width index (CHI). Explanation of symbols: White circles = *B. sinuososeptatum* Estonian specimens, Vormsi–Pirgu regional stages (herein); black circles = *B. sinuososeptatum* Boda Limestone, Sweden (Kröger 2013); star = type *B. sinuososeptatum* in Dzik (1984); cross = types *B. sinuososeptatum* in Strand (1934); triangle = *B.* cf. *sinuososeptatum* (herein). See text for discussion.

Remarks

The two specimens are slightly more curved and larger than the fragments assigned to *B. sinuoseptatum* but otherwise indistinguishable from the types and the material herein assigned to *B. sinuoseptatum* sensu stricto, in which a maximum conch height of ca 44 mm occurs (see above).

Beloitoceras uuemoisense sp. nov.
urn:lsid:zoobank.org:act:F793DBD7-51A6-4A8B-8939-F9372673A510
Fig. 28G–H

Diagnosis

Beloitoceras with a maximum conch height of ca 18 mm near mid-length of mature body chamber; compressed conch cross section with CHI of ca 1.35; angle of expansion of the phragmocone ca 20°, in lateral view ventral conch margin convex and dorsal conch margin concave throughout entire length; body chamber with constriction near mature peristome.

Etymology

Referring to the type locality.

Type material

Holotype
ESTONIA • Läänemaa, Uuemõisa; Adila Formation, Pirgu Regional Stage; TUG 1745-290.

Description

The holotype is a nearly complete conch of a small mature curved brevicone (Fig. 28G–H). Its greatest conch height of 17.5 mm occurs slightly adoral of the base of its body chamber, where the conch width is 13 mm (CHI = 1.35). At the base of the body chamber, the conch height is 17 mm and the corresponding width 12 mm (CHI = 1.42). The conch cross section is elliptical with nearly equally narrowly rounded dorsal and ventral margins. The body chamber is nearly straight, in lateral view its prosiphuncular margin is more curved (convex) than the antisiphuncular margin (concave). The conch height decreases toward the aperture with a marked constriction ca 2 mm from the peristome forming an amphora like apertural opening. The peristome appears to be straight transverse. The phragmocone is curved and increases in height from 11 mm to 17 mm at a length of 16 mm (angle of expansion = 21°). The sutures form wide lateral lobes, they are ca 2 mm apart where the conch height is 17 mm (RCL = 0.12). Details of the siphuncle are not known.

Comparison

This is a small species of *Beloitoceras*, superficially similar to species of *Oncoceras*. It differs from species of *Oncoceras* in having a gibbous mature body chamber and in lacking the convex portion of the conch margin at the antisiphuncular conch margin. The genus *Beloitoceras* is species rich, palaeogeographically widespread and stratigraphically relatively long ranging. Flower (1946) distinguished several groups within the genus. *Beloitoceras uuemoisense* sp. nov. can be placed in Flower's (1946) group III of *B. pandion* Flower, 1946, which comprises faintly gibbous species with a concave conch margin at the antisiphuncular side. Within this group, *B. uuemoisense* is unique because of its small adult size of less than 20 mm.

Beloitoceras (?) sp.
Fig. 28F, I–J

Material examined

ESTONIA • 1 spec.; Raplamaa, Pirgu River outcrops; Adila Formation, Pirgu Regional Stage, GIT 426-1081.

Description

The specimen is a fragment of a nearly complete body chamber and part of a phragmocone. The conch is slightly exogastrically curved. The height and width of the 23 mm long phragmocone are 20–23 mm and 13.5–15 mm, respectively (angle of expansion = 8°; CHI = 1.4–1.5). The septa form wide lateral lobes and pointed angular saddles on the prosiphuncular side. The siphuncle is nearly marginal, empty and the septal foramen has a diameter of 1 mm at the apical end of the specimen (RSH = 0.05). The body chamber is slightly gibbous, reaching its greatest height of 24 mm at ca mid-length of the preserved part. Its preserved length is ca 25 mm.

Remarks

The relatively long and slender (but still gibbous) body chamber distinguishes this specimen from known species of *Beloitoceras*. Its uniqueness would justify the erection of a new species and genus. Alternatively, the specimen is related to *Richardsonoceroides* Kröger, Zhang & Isakar, 2009, or *Richardsonoceras priscum* (Eichwald, 1860) (see below). However, knowledge about the shape of the complete mature body chamber and information on the siphuncle is needed for a definitive determination. The specimen therefore is left in open nomenclature.

Genus ***Cyrtorizoceras*** Hyatt, 1900

Type species

Cyrtoceras minneapolis Clarke, 1897, from Minneapolis, Minnesota, USA, Platteville Formation, Black River Group, Sandbian; by original designation.

Diagnosis

Compressed cyrtocones; dorsal and ventral profiles diverging constantly adorally; sides converging slightly over mature body chamber; aperture with deep hyponomic sinus; nearly smooth or ornamented with transverse costae; siphuncle subventral, slender; segments slightly expanded, probably empty. (Adopted from Sweet 1964b.)

Cyrtorizoceras hariense sp. nov.

urn:lsid:zoobank.org:act:08D1598D-B9FB-4C73-B47A-C2C7371DE0A7

Fig. 32E–F

Diagnosis

Large *Cyrtorizoceras* with nearly circular conch cross section, reaching a mature size of more than 60 mm; phragmocone expands at an angle of 18°–20°; conch only weakly curved; conch surface nearly smooth.

Etymology

Refers to Hari Strait, which is the sea strait west of Saxby shore, the type locality.

Type material

Holotype

ESTONIA • Vormsi Island, Saxby shore (N); Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-71.

Description

The holotype is a curved fragment of a phragmocone and a nearly complete body chamber. The conch surface is nearly smooth, ornamented with relatively coarse growth lines near the aperture. At the base of the body chamber, the conch cross section is circular or nearly so with a height of 48 mm. At the peristome, the width is 62 mm. The body chamber is 55 mm long, with a slightly curved growth axis, and in lateral view its dorsal and ventral margins have a concave and a convex curvature, respectively. The diameter of the body chamber increases continuously from its base toward the peristome. The phragmocone is 45 mm long and increases in diameter from 34 mm to 48 mm (angle of expansion = 18°). The sutures are directly transverse and 6 mm apart where the conch height is 45 mm (RCL = 0.13). The siphuncle is marginal or nearly so and expands into the chambers with a diameter of ca 5 mm where the chamber length is ca 6 mm (SCR = 0.83).

Remarks

This species of *Cyrtorizoceras* is unique in having large mature size in combination with a nearly circular conch cross section.

Cyrtorizoceras sp. A
Fig. 32D

Material examined

ESTONIA • 1 spec.; Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage; GIT 878-260.

Description

The specimen is a fragment of an exogastrically curved mature body chamber and five chambers of the phragmocone. At the base of the body chamber, the conch height and width are 58 mm and ca 45 mm, respectively (CHI = 1.29), and the conch cross section is ovate, oval compressed with the prosiphuncular margin slightly narrower than the antisiphuncular margin. The preserved part of the body chamber is 22 mm in height. In lateral view, only the antisiphuncular side of the body chamber is sufficiently preserved to describe its shape; it is slightly concave throughout the preserved length. The prosiphuncular side is convex and more strongly curved than the antisiphuncular side. The phragmocone height expands with an angle of 26° through an increase in conch height of 48–58 mm. The sutures form a shallow lateral lobe and are slightly more adaperturally located on the antisiphuncular side of the conch. The adoral-most sutures are crowded and 4 mm distant. At a conch height of 53 mm the sutures are 5 mm apart (RCL = 0.09). The siphuncle is almost marginally positioned with segments that are expanded within the chambers.

Remarks

Like *C. hariense* sp. nov., *C.* sp. A is a large *Cyrtorizoceras*. It differs from *C. hariense* in being more compressed, in having a larger angle of expansion (angle of expansion = ca 20° in *C. hariense*) and a shorter mature body chamber. No similar species is known. Species of *Diestoceras*, which have similar high angles of expansion and short body chambers, may be distinguished by the contraction of the mature body chambers.

Genus ***Dalecarlioceras*** Frye, 1987

Type species

Dalecarlioceras bodense Frye, 1987, Kallholn, Dalarna, Sweden, Boda Limestone, latest Katian; by original designation

Diagnosis

Moderately to rapidly enlarging, cyrtoconic, exogastric brevicones with compressed conch cross section; mature body chamber gibbous with maximum gibbosity at mid-length, becoming compressed orad;

dorsal conch profile straight to faintly concave, ventral conch profile moderately convex; aperture may be constricted with prominent hyponomic sinus; siphuncle situated close to venter, small in diameter, with tubular to fusiform segments, no endsiphuncular deposits known. (Adopted from Frye 1987.)

Dalecarlioceras bodense Frye, 1987
Fig. 34D–F

Dalecarlioceras bodense Frye, 1987: 90–92, fig. 5a–b.

Diagnosis

Rapidly enlarging, large *Dalecarlioceras* with compressed conch cross section; mature body chamber gibbous with maximum width and height at mid-length of ca 65–70 mm, aperture compressed, unconstricted with well-defined hyponomic sinus; mature body chamber in lateral view with straight dorsal profile and convex ventral side throughout its length; siphuncle small and situated close to the venter. (Adopted from Frye 1987.)

Material examined

ESTONIA • 1 spec.; Paluküla quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-1099 • 1 spec.; Saaremõisa (Lyckholm); Kõrgessaare Formation, Vormsi Regional Stage; TUG 1745-213.

Type locality and horizon

Kallholn, Dalarna, Sweden; Boda Limestone, latest Katian.

Description

The better-preserved of the two specimens is TUG 1745-213 (Fig. 34A–B); it is a mold of a complete mature body chamber and one chamber of the phragmocone. The specimen is slightly deformed. At the base of the body chamber, the conch height and width are 58 mm and 57 mm, respectively (CHI = 1.02). The cross section is nearly circular, with a slightly narrower margin on the prosiphuncular side. The length of the body chamber is 56 mm. In lateral view, the body chamber is nearly straight with convex margins on the pro- and antisiphuncular sides. Deformation during diagenesis has caused the antisiphuncular margin to be more curved than the prosiphuncular side. The greatest height is reached at ca mid-length of the body chamber with 66 mm. The peristome is slightly constricted with a height of 65 mm. The peristome is too poorly preserved to recognize the hyponomic sinus if present. At the base of the body chamber, traces of a thin, ca 5 mm wide, oncomyarian band of muscle-scars is preserved. The preserved chamber of the phragmocone is 5 mm long. The sutures are straight and directly transverse. The septal foramen is ca 1 mm distant from the conch margin and 6 mm in diameter (RSH = 0.09, RSP = 0.02).

The second specimen is a poorly preserved portion of a body chamber and one chamber of the phragmocone with a conch height of 60 mm at the base of the body chamber and a maximum height of 63 mm at the mid-length of the body chamber. The preserved length of the body chamber is 47 mm. The conch cross section of the specimen was apparently sub-circular.

Remarks

The two specimens described above can be assigned to *D. bodense* based on the similarities of the conch shape and dimensions with the types of this species.

Dalecarlioceras constrictum Frye, 1987
Figs 29D, 34A–B

Dalecarlioceras constrictum Frye, 1987: 92–93, fig. 3g–h.

Dalecarlioceras constrictum – Kröger 2013: 24, fig. 7a, tab.2.

Diagnosis

Moderately expanding *Dalecarlioceras* with curved, relatively short conch and compressed conch cross section; mature body chamber gibbous with maximum conch height of ca 44 mm, not greatly inflated; mature aperture constricted apicad of peristome, aperture height is one-fourth of body chamber length; peristome with well-developed hyponomic sinus. (Adopted from Frye 1987.)

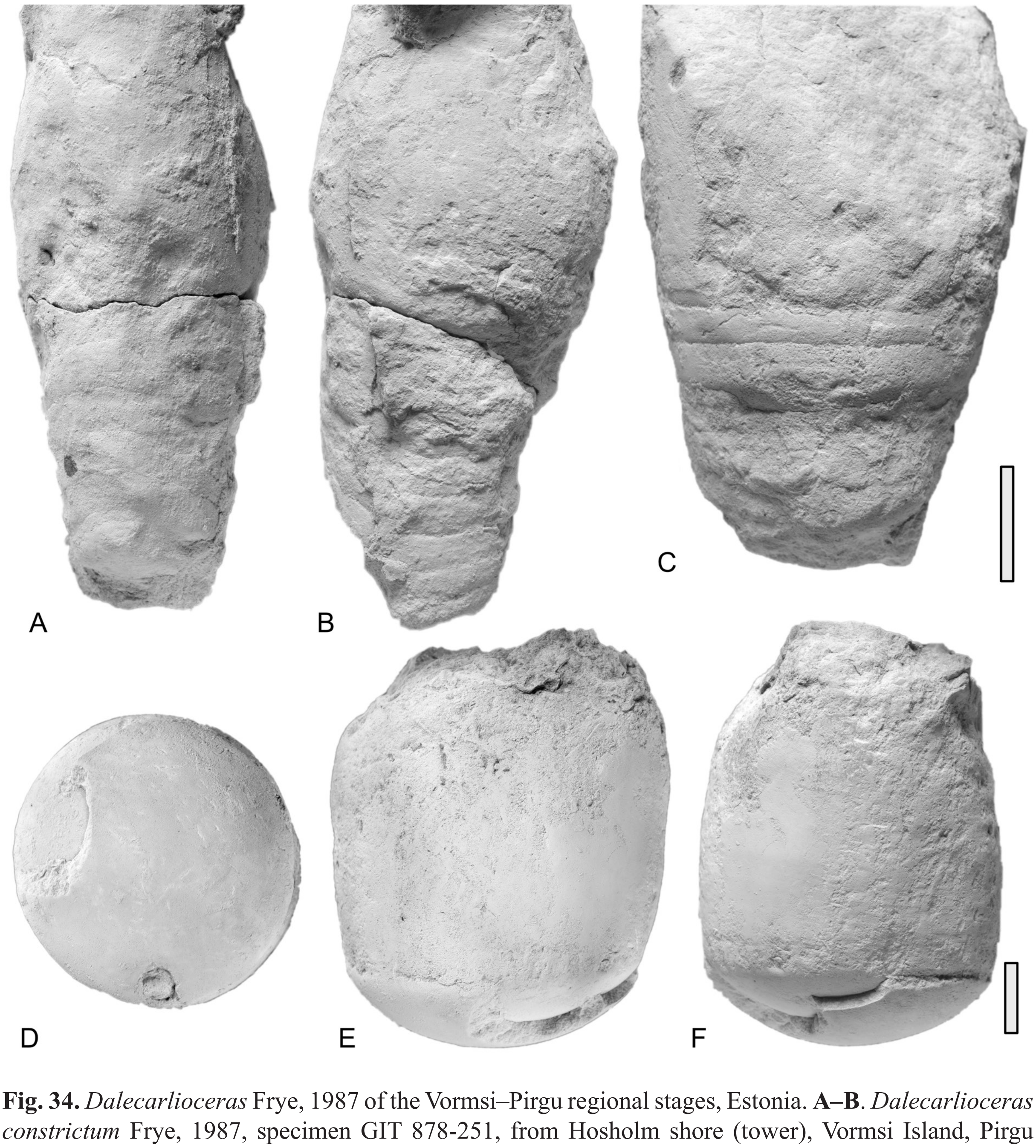


Fig. 34. *Dalecarlioceras* Frye, 1987 of the Vormsi–Pirgu regional stages, Estonia. **A–B**. *Dalecarlioceras constrictum* Frye, 1987, specimen GIT 878-251, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage. **A**. View of the prosiphuncular side. **B**. Lateral view. **C**. *Dalecarlioceras* sp., specimen GIT 878-250, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage, lateral view. **D–F**. *Dalecarlioceras bodense* Frye, 1987, specimen TUG 1745-213, from Saaremõisa (Lyckholm), Vormsi Regional Stage. **D**. Adapical view. **E**. Lateral view. **F**. View of the antisiphuncular side. Scale bar = 20 mm in all figures, same scale in A–C, and in D–F.

Material examined

ESTONIA • 2 specs; Vormsi Island, Hosholm shore (tower); Adila Formation, Pirgu Regional Stage; GIT 878-248, GIT 878-251.

Type locality and horizon

Kallholn, Dalarna, Sweden; Boda Limestone, latest Katian.

Description

Specimen GIT 878-248 is a fragment of a mature body chamber and three chambers of the phragmocone. The conch surface is poorly preserved. Near the peristome, it is almost smooth with fine, irregularly spaced growth lines. At the base of the body chamber, the conch height and widths are 41 mm and 35 mm, respectively (CHI = 1.1). The body chamber is gibbous, 35 mm long, and in lateral view has convex outlines with the greatest conch height of 44 mm 20 mm adoral of the base of the body chamber. The phragmocone increases in height from 40 mm to 34 mm at a length of 18 mm (angle of expansion = 19°). The sutures form shallow lateral lobes and are 6 mm apart where the conch height is 38 mm (RCL = 0.16). The siphuncle is nearly marginal, has fusiform segments and is without endosiphuncular deposits. The septal necks are suborthochoanitic to cyrtochoanitic (Fig. 29D).

In GIT 878-251, a nearly complete mature body chamber and seven chambers of the phragmocone are preserved (Fig. 34A–B). At its base the body chamber is 37 mm high, and 34 mm wide (CHI = 1.1), has a broad elliptical conch cross section, and a gibbous form in lateral view. The greatest height is reached ca 20 mm adorad from its base (ca 44 mm), its total length is 43 mm. The mature peristome has a ca 7 mm deep, wide hyponomic sinus developed on the prosiphuncular side. The height of the phragmocone increases from 27 mm to 37 mm at a length of 31 mm (angle of expansion 18°). The siphuncle is located near the conch margin, its segments are fusiform (siphuncular height = 3.2 mm, segment length = 5.5 mm).

Remarks

The species was described in detail by Frye (1987). The Estonian specimens are very similar to the Swedish types.

Dalecarlioceras sp.
Fig. 34C

Material examined

ESTONIA • Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage; GIT 878-250.

Description

GIT 878-250 is a fragment of a phragmocone with part of the body chamber, in which details of the siphuncle are well-preserved. The conch increases in height from 35 mm to 49 mm over 31 mm (angle of expansion 25°). At a height of 38 mm, its width is 30 mm (CHI = 1.27), and the conch cross section is ovate with a slightly narrower margin on the prosiphuncular side. The preserved part of the body chamber is 40 mm long. In lateral view, the conch is nearly straight with a convex margin on the prosiphuncular side and a straight margin at the antisiphuncular side, which is slightly convex near the adoral end of the body chamber. The sutures are straight and directly transverse, 6 mm apart where the conch height is 49 mm (RCL = 0.12). The siphuncle is close to the conch margin, ca 3 mm in diameter where the conch height is 35 mm (RSH = 0.09). The siphuncular segments are expanded within the chambers, with their greatest width near the adoral end of the segments.

Remarks

The near mature size of this specimen is indicated by the convex shape of its antisiphuncular body chamber margin. The fragmentary preservation of the specimen does not permit species level determination.

Genus ***Richardsonoceras*** Foerste, 1933

Type species

Cyrtoceras simplex Billings, 1857, from Nepean township, Ottawa, Ontario, Canada, Leray Formation, Sandbian; by original designation.

Diagnosis

Gradually enlarging strongly curved shells; cross section compressed with elliptical to oval cross section, convex side of conch curvature more narrowly rounded; adult body chamber slightly contracted adorally; sutures with shallow lateral lobe, slightly oblique sloping slightly adapically on the antisiphuncular side; siphuncle small, close to margin on convex side of conch curvature; segments slightly expanded. (Adopted from Kröger *et al*. 2009b: 286.)

Richardsonoceras priscum (Eichwald, 1860) comb. nov.
Fig. 35C–D

Cyrtoceras priscum Eichwald, 1860: 1285, pl. 47 fig. 10a–c.
Beloitoceras (?) *estonicum* Teichert, 1930: 292, pl. 6 figs 11–12.
Richardsonoceras nikiforovae Balashov, 1962b: 114–115, 128, pl. 46 fig. 5a–b.

Richardsonoceras nikiforovae – Zhuravlyeva 1962: pl. 23 fig. 4.
"*Richardsonoceras*" *nikiforovae* – Dzik 1984: 63, 67, text-fig. 18.34.
Oonoceras priscum – Dzik & Kiselev 1995: 66, fig. 2 (non fig. 1f–g, fig. 3c–d).

Emended diagnosis

Richardsonoceras with a relatively weak conch curvature, with an angle of expansion of ca 8°; oval compressed conch cross section with CHI of 1.2–1.6 which increases with conch height; mature conch height ca 18 mm.

Material examined

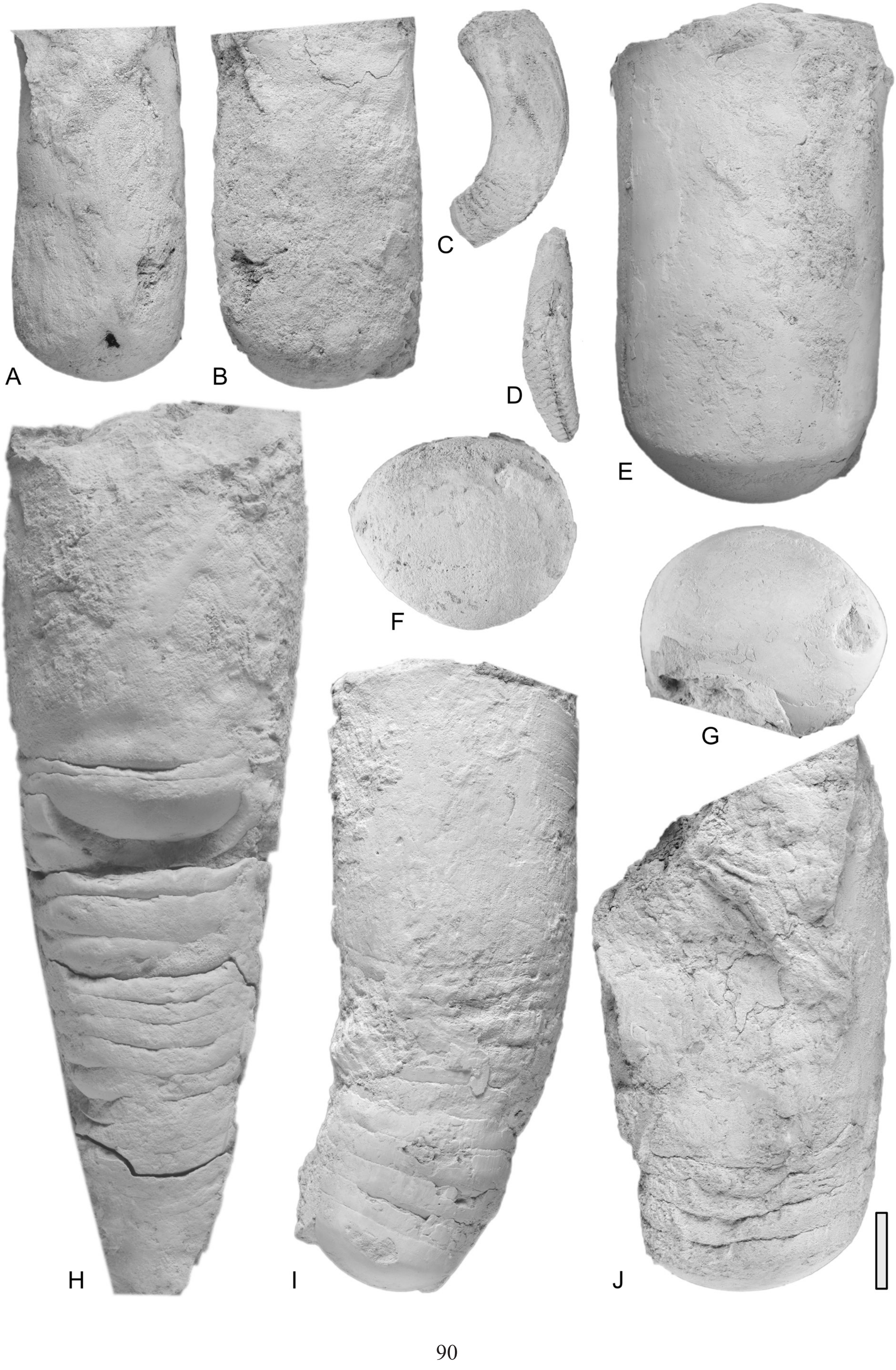
ESTONIA • 13 specs; Hiiumaa Island, Kõrgessaare quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-129, GIT 878-130, GIT 426-387, GIT 426-388, GIT 426-390, GIT 426-397 to GIT 426-399, GIT 426-428, GIT 426-554, GIT 426-607 to GIT 426-609.

Type locality and horizon

Kõrgessaare quarry, Hiiumaa island, Estonia; Kõrgessaare Formation, Vormsi Regional Stage (Lyckholm Stage of Teichert 1930).

Description

The most complete specimen (GIT 426-608, Fig. 35C) is a deformed (compressed), curved fragment of a mature body chamber, and possessing at least ten chambers of the phragmocone. The phragmocone increases in height from 11.5 mm to18 mm (angle of expansion of 8°). The conch height at the base of the body chamber is 14 mm and its preserved length ca 35 mm. The peristome is not preserved. In lateral view, the dorsal and ventral conch margins are concave and convex, respectively, throughout the entire length of the body chamber. The adoralmost part of the body chamber appears to be less curved


A
B
C
D
E
F
G
H
I
J

than the rest of the specimen. The sutures form wide lateral lobes and distinct and sharp saddles on the prosiphuncular side. They are 2 mm apart where the conch height is 12 mm (RCL = 0.17). The two adoralmost septa are crowded. Traces of a narrow siphuncle (0.7 mm in width) are preserved near the conch margin. The siphuncular segments expand slightly into the chambers.

The oval compressed conch cross section is well-preserved in specimen GIT 426-399, with a CHI of 1.3 at a conch height of 13 mm. There, the conch margin on the prosiphuncular side is narrower rounded than on the antisiphuncular side.

The CHI increases during ontogeny from ca 1.2 at a conch height of 10 mm (specimen GIT 878-129) to 1.5 at conch a height of 18 mm (specimen GIT 426-608). The mean angle of expansion is 10° (range: 6°–15°, n = 5). The high variability results from deformation during the diagenesis of the specimens. The mean RCL is 0.13 (range: 0.1–0.15, n = 6).

Remarks

The material described herein provides for the first time a comprehensive overview of this species, which has a complicated history. The original description of *Cyrtoceras priscum* Eichwald, 1860 is based on a specimen from near Kõrgessaare, Hiiumaa Island (Eichwald 1860: 1285). An original from the Eichwald collection was figured in Dzik & Kiselev (1995: fig. 2) and designated as the lectotype of "*Oonoceras priscum* (Eichwald, 1861)" (sic). Earlier, Teichert (1930) had designated a small fragment, also from Kõrgessaare, Hiiumaa Island, as type of his new species *Beloitoceras* (?) *estonicum* Teichert, 1930 noting its similarity to *C. priscum* (Teichert 1930: 271). However, based on the single, fragmentary type of *B*. (?) *estonicum* and the single fragment available from the Eichwald collection in St Petersburg, he could only speculate regarding a possible synonymy of the two species. The additional material described above comes exclusively from the Kõrgessaare Formation, Vormsi Stage of Kõrgessaare, the type locality of *C. priscum* and *B*. (?) *estonicum*. The new material shows that *B*. (?) *estonicum* must be considered a junior synonym of C. *priscum*, and that this species is best placed within *Richardsonoceras*. The placement with *Richardsonoceras* is preferred over *Beloitoceras* because of the slender, non-gibbous or only very weakly gibbous mature body chamber of this species.

It is now clear that this species is identical in size and shape to *R. nikiforovae* Balashov, 1962b; described from the Dolborian Regional Stage, Katian, of the Siberian platform and which should be considered as a subjective junior synonym of *C. priscum*.

The complication arises from a misinterpretation of the stratigraphical horizon from which Eichwald's type originated by Dzik & Kiselev (1995: 66). They literally translated Eichwald's "calcaire à Orthocératites" as the "*Orthoceras* limestone" of later authors, which is late Darriwilian in age. However, Eichwald (1860) generally termed Ordovician limestone strata as "calcaire à Orthocératites", as is evident from

Fig. 35 (preceding page). Oncoceratidae Hyatt, 1884 and Cyrtogomphoceratidae Flower, 1940 of the Vormsi–Pirgu regional stages, Estonia. **A–B**. *Kiaeroceras* sp. B, specimen GIT 878-161, from Saxby shore, Vormsi Island, Vormsi Regional Stage. **A**. View of the prosiphuncular side. **B**. Lateral view. **C–D**. *Richardsonoceras priscum* (Eichwald, 1860) comb. nov. from Kõrgessaare quarry, Hiiuma Island, Vormsi Regional Stage. **C**. Specimen GIT 426-608, lateral view. **D**. Specimen GIT 426-607, view of the prosiphuncular side. **E, G**. *Kiaeroceras* sp. C, specimen GIT 225-997, from Niibi hillock, Pirgu Regional Stage. **E**. Lateral view. **G**. Adapical view. **F, H**. *Kiaeroceras* (?) *ormsoense* sp. nov., holotype GIT 878-63, from Saxby shore (N), Vormsi Island, Vormsi Regional Stage. **F**. Adapical view. **H**. Lateral view. **I**. *Kiaeroceras urgense* sp. nov., holotype TUG 103-75, from Urge quarry, Vormsi Regional Stage. **J**. *Kiaeroceras* (?) cf. *ormsoense*, specimen TUG 1680-20, from Saxby shore (N), Vormsi Island, Vormsi Regional Stage. Scale bar = 20 mm, same scale in all figures.

his descriptions of other specimens collected from Late Ordovician strata. There is no evidence that the Kõrgessaare specimens are from glacial boulders of Darrwilian age, and the specimens described above are clearly from a Kõrgessaare Formation lithology.

This stratigraphic misinterpretation probably led Dzik & Kiselev (1995) to synonymize a specimen figured in Dzik (1984: text-fig. 15a, pl. 9 fig. 1), which significantly differs from *C. priscum* in having a lower angle of expansion, a wider chamber spacing and a nearly circular conch cross section and thus represents a different species. Hence, *C. priscum* is a genuine late Katian *Richardsonoceras*, presently known only from Kõrgessaare, Hiiumaa Island.

Comparison

Several specimens are deformed and / or are only fragmentarily preserved, making a definite determination of the conch curvature difficult. However, three comparatively well-preserved specimens (GIT 426-607, -608, GIT 878-129) reveal the relatively low degree of curvature of the conch compared with other species of *Richardsonoceras*. The species of *Richardsonoceras* described from the Black River Group (Foerste 1932, 1933) have a stronger conch curvature. All, except *R. simplex* (Billings, 1857), also have a larger mature conch height (> 20 mm). The mature size of *R. bellatulum* Sweet & Miller, 1957 from the Cape Phillips Formation, Cornwallis islands, Canada, is similar than that of *R. estonicum*, but the Cape Phillips species is also more strongly curved (see also Balashov 1962b: 115).

Genus ***Rizosceras*** Hyatt, 1884

Type species

Orthoceras indocile Barrande, 1866 from Kocorc, Bohemia, Czech Republic, Middle Silurian; by original designation.

Diagnosis

Compressed, rapidly enlarging, straight to faintly curved brevicones with hyponomic sinus and distinct, faintly rugose transverse surficial ornament; siphuncle ventrally positioned near conch margin; septal necks cyrtochoanitic; siphuncular segments cardioid in dorsoventral section. (Adopted from Sweet 1964b.)

Rizosceras teres sp. nov.
urn:lsid:zoobank.org:act:8A906D01-DEF8-402F-9CF3-7CCE72E51F9B
Figs 27F, 28E, 29B

Diagnosis

Rizosceras with nearly smooth conch surface, ornamented only with fine, irregularly spaced growth lines or lirae; mature conch height ca 45 mm; phragmocone expands with an angle of ca 20°; conch cross section slightly elliptically compressed; siphuncle close to conch margin, with expanded segments, which are wider at their adoral ends.

Etymology

Refers to the Latin '*teres*' ('fine', 'well-rounded') because of its relatively smooth conch surface.

Type material

Holotype

ESTONIA • Saaremõisa (Lyckholm); Kõrgessaare Formation, Vormsi Regional Stage; TUG 1745-188.

Paratypes

ESTONIA • 2 specs; Kõrgessaare quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-550, GIT 426-1141 • 1 spec.; Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; TUG 80-508.

Description

The holotype, TUG 1745-188 (Figs 27F, 28E), is a slightly deformed (compressed) fragment of a phragmocone and a body chamber. The conch surface was apparently smooth. The conch height increases at a length of 25 mm from of 22 mm to 30 mm (angle of expansion = 18°). The sutures are straight and directly transverse, 5 mm apart where the conch height is 25 mm (RCL = 0.2). The siphuncle is close to the conch margin at a conch height of ca 22 mm. There, the septal foramen is almost marginally positioned and has a width of 2 mm. The siphuncular segments are fusiform, expanded into the chambers, wider near the adoral septal surface.

Specimen GIT 426-550 (Fig. 30B) is a fragment of a body chamber and one chamber of the phragmocone, it has a length of 28 mm and an apical angle of 20°. The conch surface is nearly smooth, ornamented with fine, irregularly spaced growth lines or lirae. At its apical end, the conch height and width are 32 mm and 27 mm, respectively (CHI = 1.18). Its maximum conch height is ca 43 mm at the peristome. The peristome is simple, directly transverse; no traces of a hyponomic sinus are visible at the venter, which is relatively poorly preserved. In lateral view, the body chamber is nearly conical, straight, with a very slight convexity at the dorsal and ventral sides. The relatively narrow spacing of the two preserved septa indicates that this is a body chamber of a mature specimen. The sutures are 4 mm apart where the conch height is 32 mm (RCL = 0.13) and are straight and directly transverse. The septal foramen is located near the conch margin but too poorly preserved to be measured.

In specimen TUG 80-508, the septal foramen is ca 3 mm in diameter and the siphuncle expands toward 6 mm into the chambers where the septa are 7 mm apart and the conch height is ca 30 mm (RSH = 0.1, SCR = 0.9).

Remarks

This new species is placed in *Rizosceras* based on similarity of the general conch shape, the shape of the siphuncular segments, and the position of the siphuncle in the type-species of this genus. Its relatively smooth surface could be used as an argument to erect a new genus, similar to *Rizosceras*, but with a smooth conch surface. *Rizosceras* is a very species rich and long ranging genus (see e.g., Barskov 1972) probably containing unrelated species with similar conch shapes and ornamentation. A revision, therefore, would be desirable but is out of scope of this work. Moreover, the erection of a new genus, based on relatively poorly preserved fragments of *Rizosceras teres* sp. nov. seems unwise until better material is available and a detailed comparison with the type species of the genus is possible.

Comparison

This is a *Rizosceras* with a relatively smooth surface, low angle of expansion and a relatively strongly curved apical conch part. The shape of the mature body chamber almost resembles the Silurian *Metarizoceras* Foerste, 1930b.

Family Uranoceratidae Hyatt , 1900

Genus ***Deckeroceras*** Foerste, 1935a

Type species

Deckeroceras adaense Foerste, 1935a, from Ada, Pontotoc County, Oklahoma, USA, lower Fernvale Formation, late Katian; by original designation.

Diagnosis

Strongly exogastrically curved conch with nearly circular cross section, becoming depressed at the aperture of the mature body chamber; broad and shallow hyponomic sinus; siphuncle positioned near venter but not marginal; siphuncular segments nearly tubular, slightly contracted near septal foramens. (Adopted from Foerste 1935a: 93.)

Remarks

The sutures of this genus have been described as having a ventral sutural lobe in a previous genus diagnosis (Flower 1943a: 262; Sweet 1964a: K382). This is erroneous. In the original diagnosis, a ventral sutural lobe is not mentioned (Foerste 1935a: 92) and in the description of the type of the genus, the sutures are described as follows: "The sutures of the septa curve only slightly downward laterally, both the dorsal and ventral margins reaching about the same level transversely" (Foerste 1935a: 93). "Downward" here probably refers as directed toward the apex, and thus, Foerste (1935a) described a shallow lateral lobe instead of a ventral lobe in *Deckeroceras*. The phrase "curve downward" in (Foerste 1935a: 93) could also refer to the distal ends of the lateral suture. This issue can only be definitely resolved by revisiting the type material, which is beyond the scope of this work. *Deckeroceras* has been placed within the Apsidoceratidae by Flower (1943a) and Sweet (1964a: K382) without explicit justification. A classification of this genus is equally possible within the Uranoceratidae (based on the family diagnosis given in Sweet 1964a: K374). Here, *Deckeroceras* is provisionally placed within the Uranoceratidae, to emphasize the similarity of this genus with *Warburgoceras* Kröger, 2013 and its relation to the early evolution of the Ascocerida (see discussion in Kröger 2013: 83, 100).

Deckeroceras balticum sp. nov.
urn:lsid:zoobank.org:act:05BFB795-1743-407B-8866-5030650628D2
Fig. 36A

Winnipegoceras sp. – Teichert 1930: 294, pl. 8 fig. 23.

Diagnosis

Deckeroceras with mature conch height of ca 65 mm, nearly circular to slightly compressed conch cross section at mature body chamber; mature body chamber strongly curved and contracted.

Etymology

Refers to type region.

Type material

Holotype

ESTONIA • Vohilaid Island, Vohilaid shore (E): Adila Formation, Pirgu Regional Stage; GIT 878-227.

Description

The specimen is a fragment of a mature body chamber and five chambers of the phragmocone. The outer shell of the specimen is not preserved. At the base of the body chamber, the conch is ca 65 mm high. At the apical end of the specimen, 32 mm from the base of the body chamber, the conch height is 49 mm, and the conch cross section was nearly circular or slightly compressed. The angle of expansion of the phragmocone is ca 28°. The sutures are directly transverse and 8 mm apart where the conch height is 49 mm (RCL = 0.15). The siphuncle and the septal foramen are either not preserved or not visible. The body chamber is strongly curved and ca 65 mm long. In lateral view the convex side of the conch is much more strongly curved than the concave side, resulting in a relatively narrow mature aperture (height ca 40 mm).

Remarks

A specimen from Piirsalu, Estonia, figured and described in Teichert (1930), is identical in size and shape, and can be assigned to the same species, based on the knowledge of this more complete specimen, described herein.

Comparison

The two other species of this genus (*D. adaense*, *D. clermontense* Foerste 1935b, known from the type-region and from the Elgin Member of the Maquoketa Shale, Iowa, USA) have smaller adult sizes

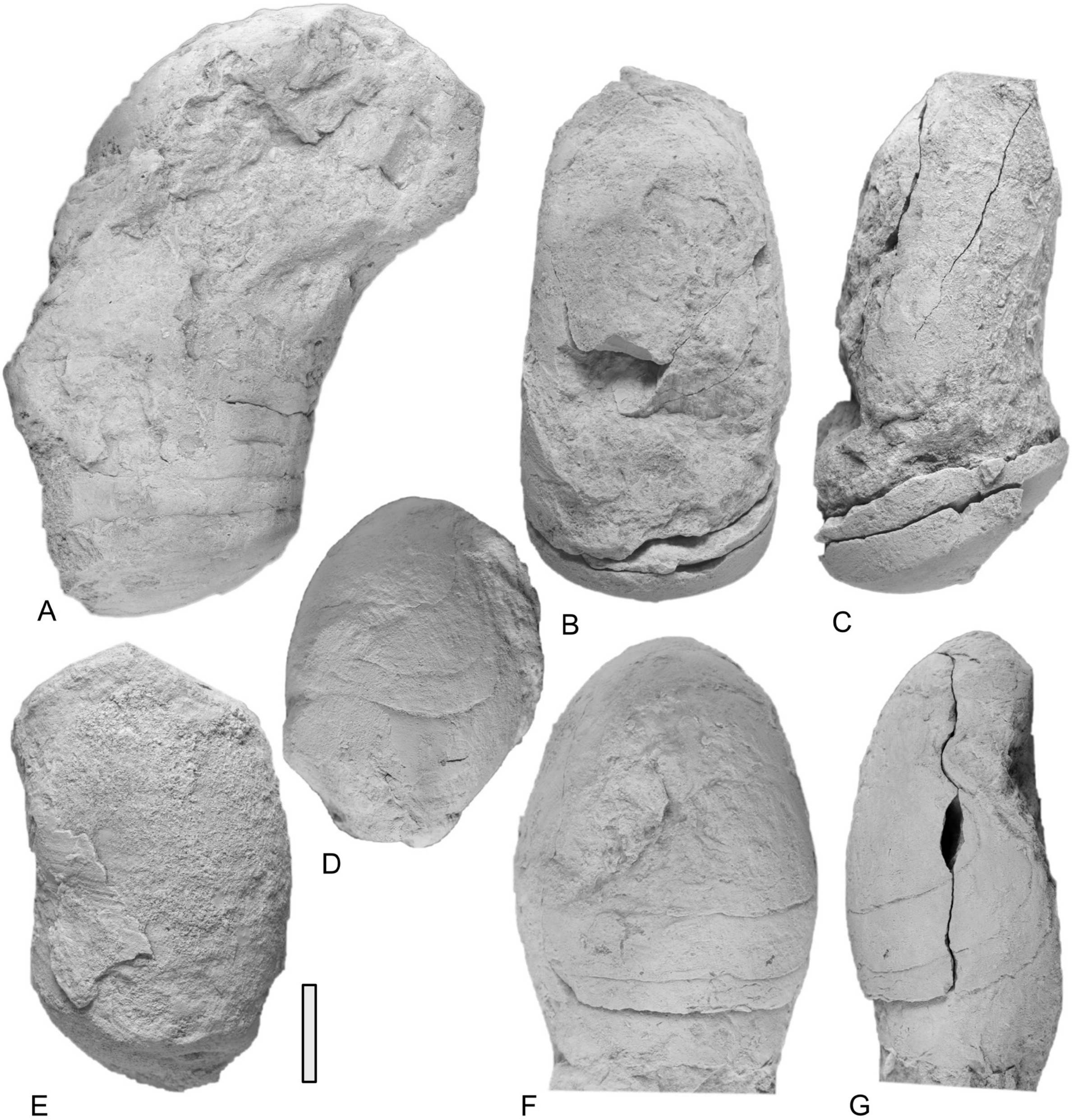


Fig. 36. Ascoceratidae Barrande, 1867 and Uranoceratidae Hyatt, 1900 of the Vormsi–Pirgu regional stages, Estonia. **A**. *Deckeroceras balticum* sp. nov., holotype GIT 878-227, from Vohilaid shore (E), Vohilaid Island, Pirgu Regional Stage, lateral view. **B–C**. *Redpathoceras saxbyense* sp. nov., holotype GIT 426-346, Saxby shore (N), Vormsi Island, Vormsi Regional Stage. **B**. View of the prosiphuncular side. **C**. Lateral view. **D**. *Schuchertoceras deformis* (Eichwald, 1860), specimen GIT 878-191, from Vohilaid shore (E), Vohilaid Island, Pirgu Regional Stage, oblique lateral view. **E**. *Redpathoceras saxbyense* sp. nov., paratype GIT 76-97, from Moe stratotype outcrop, Pirgu Regional Stage. **F–G**. *Schuchertoceras deformis* (Eichwald, 1860), specimen TUG 2-734, Uuemõisa, Läänemaa, Pirgu Regional Stage. **F**. View of the antisiphuncular side. **G**. Lateral view. Scale bar = 20 mm, same scale in all figures.

(maximum conch heights 40–50 mm), and in *D. clermontense* Foerste, 1935a the mature body chamber is less strongly curved.

Order Ascocerida Kuhn, 1949
Family Ascoceratidae Barrande, 1867

Genus ***Schuchertoceras*** Miller, 1932

Type species

Ascoceras anticostiensis Billings, 1866, Junction cliff, Anticosti Island, Canada, probably from Ellis Bay Formation, Hirnantian, Late Ordovician; by original designation.

Diagnosis

Ascoceratid cephalopods with basal non-ascoceroid septum between septum of truncation and the first ascoceroid septum in mature conch. (Adopted from Frye 1982.)

Schuchertoceras deformis (Eichwald, 1860) comb. nov.
Fig. 36D, F–G

Ascoceras deforme Eichwald, 1860: 1192, pl. 42 fig. 18.

Billingsites deformis – Foerste 1929: 157, pl. 20 fig. 3. — Strand 1934: 54–55, pl. 4 fig. 7. — Frye 1982: 1278.

non *Billingsites deformis* – Sweet & Miller 1957: 43, pl. 4 figs 1–2.

Diagnosis

Schuchertoceras with three ascoceroid septa which are detached from each other throughout their entire length; with elliptically depressed conch cross section and nearly straight growth axis in ascoceroid growth stages.

Material examined

ESTONIA • 1 spec.; Haapsalu holm; Adila Formation, Pirgu Regional Stage; TUG 46-138 • 1 spec.; Läänemaa, Uuemõisa; Adila Formation, Pirgu Regional Stage; TUG 2-734 • 1 spec.; Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage; GIT 878-191.

Type locality and horizon

Kõrgessaare quarry, Hiiumaa Island; Kõrgessaare Formation, Vormsi Regional Stage.

Description

TUG 2-734 is the most complete specimen (Fig. 37F–G), which preserves an almost complete ascoceroid portion of the conch including the basal septum, three ascoceroid septa and the nearly complete mature peristome. The width of the specimen is 36 mm at the basal septum, 47 mm at approximate, mid-length where it reaches its maximum width, and 35 mm at the aperture. The conch cross section is elliptically depressed (CHI: 0.75–0.85), but not completely preserved in portions between ca 20 mm from the aperture and 10 mm from the apical end. At the aperture, the height is 28 mm; at the basal septum the height can be reconstructed as ca 27 mm and its maximum height can be reconstructed as ca 40 mm. In lateral view, the conch is nearly straight and egg-shaped with a rounded but narrow apical tip and a constricted adoral part with a simple straight peristome. The ventral (prosiphuncular) margin of the peristome is poorly preserved, and the presence of a shallow shallow hyponomic sinus cannot be excluded. The maximum height is reached at ca 25 mm from the aperture. The basal suture is directly transverse at ca 17 mm from the apical end of the specimen. On the dorsum, the respective distances of the ascoceroid sutures from the peristome are 8 mm, 14 mm, and 23 mm. In lateral view, they form a pointed lateral lobe at ca 10 mm from the basal septum and a wide lateral sinus.

The ventral part and the interior of the basal septum are well-preserved in TUG 46-138. The ventral part is shallowly convex in lateral view and in cross section. The basal septum is located at a conch width of 38 mm and the septal foramen is in a nearly marginal position (ca 2 mm from ventral margin) with a diameter of ca 4 mm (RSH = 0.1, RSP = 0.06).

The third specimen (GIT 878-191) is a poorly preserved, deformed fragment of an ascoceroid conch with the three ascoceroid sutures and a straight peristome preserved (Fig. 36D).

Remarks

These specimens can be referred to *Ascoceras deforme* Eichwald, 1860 based on the three ascoceroid septa, which are clearly visible in Eichwald's (1860: pl. 49 fig. 18) figures. There, the basal septum is not figured or is not preserved, which is the reason why this species was classified within *Billingsites* Hyatt, 1884 in Foerste (1929) and Strand (1934). Strand's (1934) identification of the genus was questioned by Frye (1982: 1278) but the poorly preserved material to hand at the time did not permit a solution to the problem. The faint suture of the basal septum can easily be overlooked. In the material described above it is best visible in specimen TUG 46-138.

Comparison

Schuchertoceras deformis differs from the two species of *Schuchertoceras* known from the Boda Limestone of Dalarna, Sweden in having three instead of two (in *S. bodense* Frye, 1982) or one (in *S. troedssoni* (Foerste, 1929)) ascoceroid septa, and in its more slender conch. It differs from North American species of *Schuchertoceras* in having ascoceroid sutures which are detached from each other throughout their entire length (compare Frye 1982: fig. 3a–j).

The specimen described under *Billingsites deformis* (Eichwald, 1860)? by Sweet & Miller (1957) does not belong to this species because it has less than three ascoceroid septa and probably no basal septum. Additionally, the shape of the ascoceroid septum, visible in Sweet & Miller (1957: pl. 4 figs 1–2) differs considerably from that of the Estonian specimens in that it is less strongly curved.

Family Probillingsitidae Flower, 1941

Genus ***Redpathoceras*** Flower, 1963

Type species

Redpathoceras clarki Flower, 1963, northeast of Joliette, Quebec, Canada; Leray Limestone, early to middle Katian, Ordovician; by original designation.

Diagnosis

Gyrocones with circular to depressed mature conch cross section; mature body chamber inflated with greatest diameter at approximate mid-length; broad shallow hyponomic sinus; septum of truncation deeply rounded; sutures of septa in mature specimen slightly oblique, sloping in adoral direction on concave side of conch curvature; siphuncle eccentric, close to conch margin at convex side of conch curvature. (Adopted from Flower 1963.)

Redpathoceras saxbyense sp. nov.

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Figs 36B–C, E, 37E

Diagnosis

Redpathoceras with weakly annulated mature body chamber, which is ornamented with irregularly spaced, transverse lirae or frills; exogastrically curved mature body chamber with nearly circular conch cross section at base and depressed at aperture, ca 45 mm high and 70 mm long.

Etymology

Refers to the type locality.

Type material

Holotype

ESTONIA • Vormsi Island, Saxby shore (N); Kõrgessaare FormationVormsi Regional Stage; GIT 426-346.

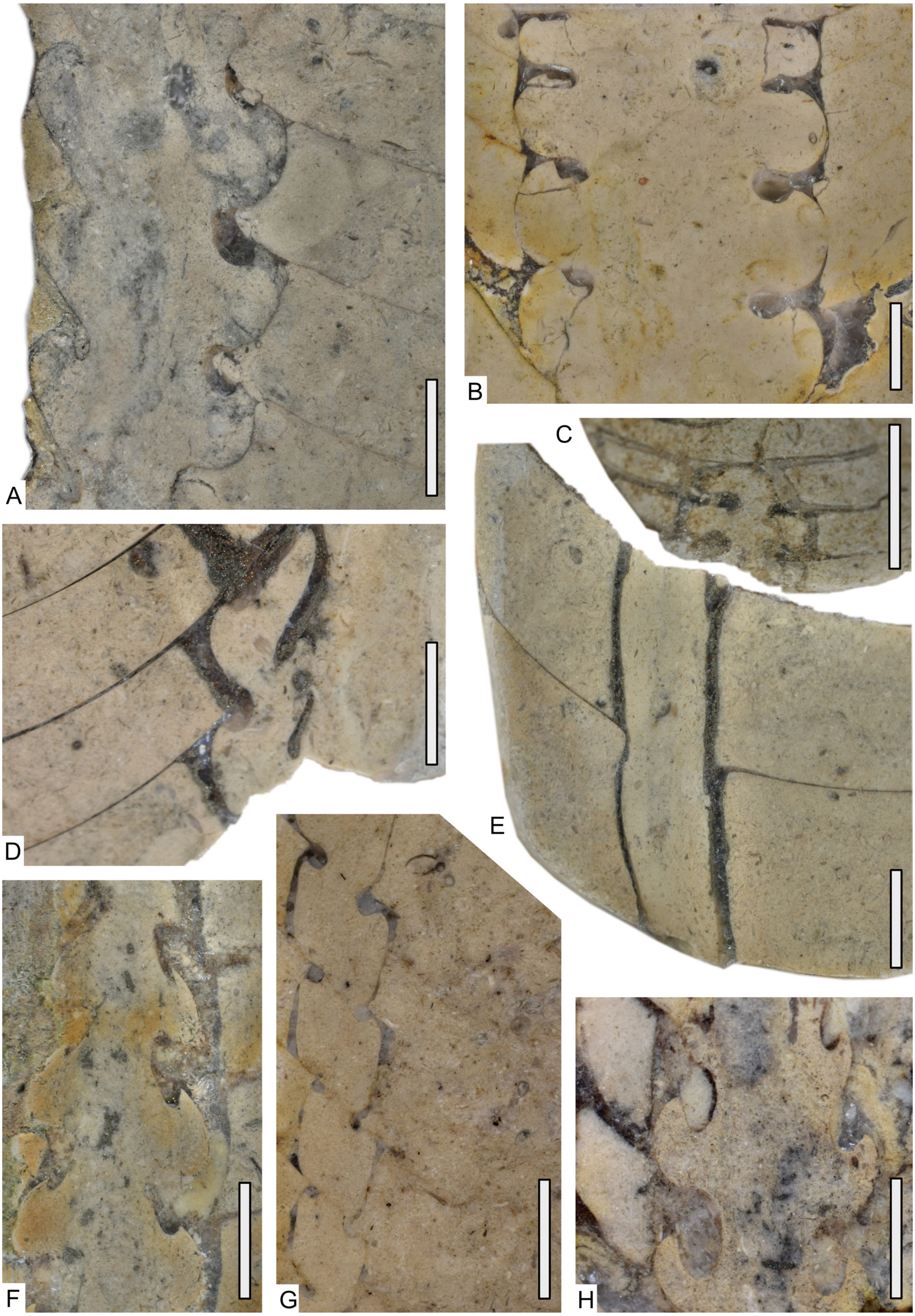
Paratypes

ESTONIA • 2 specs; same data as for holotype; GIT 878-84, GIT 878-156 • 1 spec.; Moe stratotype outcrop; Moe Formation, Pirgu Regional Stage; TUG 76-97 • 1 spec.; Salu; Pirgu Regional Stage; TUG 1745-316 • 1 spec.; Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage; GIT 878-236.

Description

GIT 426-346 (Fig. 36B–C) is a fragment of a mature body chamber and two chambers of the phragmocone. The outer shell is poorly preserved and apparently smooth or with fine irregular rounded lirae. The conch cross section at the base of the body chamber is nearly circular (conch height = 45 mm, conch width = 43 mm). The body chamber is 68 mm long and exogastrically curved. In lateral view, the antisiphuncular margin of the body chamber has a convex, and the prosiphuncular side a concave outline with an increasingly narrow conch cross section toward the aperture. The outline undulates slightly, resulting from a weak irregular annulation. Approximately two annulations occur on the body chamber. They are oblique, slightly shifted orad at the antisiphuncular side. At the aperture, the conch cross section is depressed with a height of 35 mm and a width of ca 25 mm, respectively. The sutures are directly transverse and 6 mm apart where the conch height is 45 mm (RCL = 0.13). There, the septal foramen has a diameter of 4.5 mm and is 5 mm distant from the conch margin.

Fig. 37 (next page). Median sections of phragmocones of Multiceratoidea Mutvei, 2013 of the Vormsi–Pirgu regional stages, Estonia. **A**. *Kiaeroceras* sp. E, specimen GIT 878-21 from Saxby shore (N), Vormsi Island, Vormsi Regional Stage. **B**. *Cyrtogomphoceras troedssoni* Teichert, 1930, specimen TUG 939-60, from Kõrgessare, Hiiumaa Island, Vormsi Regional Stage (section is approximate median only). **C**. *Hosholmoceras ovalis* gen. et sp. nov., holotype GIT 840-252, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage (section is approximate median only). **D**. *Kiaeroceras* (?) *ormsoense* sp. nov., holotype GIT 878-63, from Saxby shore (N), Vormsi Island, Vormsi Regional Stage. **E**. *Redpathoceras saxbyense* sp. nov., specimen GIT 878-156, from Saxby shore (N), Vormsi Island, Vormsi Regional Stage. **F**. *Kiaeroceras kaebliki* sp. nov., paratype GIT 426-1123, from Saxby shore, Vormsi Island, Vormsi Regional Stage. **G**. *Lyckholmoceras norvegiae* Strand, 1934, specimen GIT 878-187, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage. **H**. *Kiaeroceras kaebliki* sp. nov., holotype GIT 878-31, Saxby shore (N), Vormsi Island, Vormsi Regional Stage. Scale bars = 5 mm in all figures.


A
B
C
D
E
F
G
H

GIT 878-156 is a weakly exogastrically curved fragment of a phragmocone and part of a body chamber showing the details of the siphuncle and septal necks (Fig. 37E). The phragmocone height increases from 34 mm to 41 mm at a length of 27 mm (angle of expansion = 15°). The conch cross section is slightly compressed (CHI = 1.07). The septa form directly transverse sutures, 7 mm apart where the conch height is 37 mm (RCL = 0.19). The septal foramen is ca 4.5 mm in diameter and ca 5 mm distant from the conch margin (RSH = 0.12, RSP = 0.16). The siphuncular segments are nearly tubular and the septal necks are loxochoanitic dorsally and suborthochoanitic ventrally.

In TUG 76-97 (Fig. 36E), and TUG 1745-316 the conch surface of the mature body chamber is well-preserved. In the three specimens, the shell is slightly irregularly annulated, similar to GIT 426-346. Additionally, the conch surface is ornamented with irregularly spaced rounded lirae (ca one to two per millimeter) which are slightly shifted orad on the dorsum.

Comparison

This species of *Redpathoceras* differs from other species of the genus in having a weakly annulated and transversally frilled mature body chamber. A specimen, assigned by Evans (1993) to *Charactoceras*? *cinerum* (Blake, 1882), probably represents another similarly ornamented species of *Redpathoceras*, which has, however, a larger adult size (mature body chamber 60 mm wide and 200 mm long).

The possibility exists that the specimens described herein are related to *Piersaloceras gageli* Teichert, 1930, which is known only from a single immature fragment, or to another, yet to be discovered species of *Piersaloceras*. This is suggested based on the similar ornamentation and similar position of the siphuncle. If this is the case, *Piersaloceras* could be interpreted as an uranoceratid or probillingsitid. The strongly curved, isolated, body chamber described herein under *Piersaloceras* (?) sp. (Fig. 30C), would support such a hypothesis. Because of the fragmentary character of the known specimens, however, this relation must remain speculative, for now.

Order Discosorida Flower in Flower & Kummel, 1950

Family **Cyrtogomphoceratidae** Flower, 1940

Remarks

The genera (especially the new genera) placed within the Cyrtogomphoceratida vary widely in features, such as chamber spacing, siphuncular shape, and in conch shape. Here, following Teichert (1964b) I placed all endogastrically curved brevicones with expanded siphuncular segments into this family. A family revision and probably the erection of a new family for *Hosholmoceras* gen. nov. are required, but a revision of the Cyrtogomphoceratidae is beyond the scope of this work.

Genus ***Cyrtogomphoceras*** Foerste, 1924

Type species

Oncoceras magnum Whiteaves, 1890, East Selkirk, Selkirk Member, Red River Formation, late Katian, Ordovician, by original designation

Diagnosis

Compressed endogastric cyrtocones with fusiform outline in lateral view; rapidly expanding in adoral part of mature phragmocone and / or basal part of mature body chamber; mature body chamber gibbous, conically contracted; aperture with hyponomic sinus; sutures with shallow lateral lobes, sloping increasingly toward the antisiphuncular side of the conch in later growth stages; siphuncle large, not strictly marginal, with short cyrtoconic septal necks, thick connecting rings, and endosiphuncular bullettes, cameral deposits absent. (Adopted from Teichert 1964b.)

Cyrtogomphoceras troedssoni Teichert, 1930
Figs 37B, 38C–D

Cyrtogomphoceras (?) *troedssoni* Teichert, 1930: 296–297, pl. 8 figs 32–33.

Faberoceras troedssoni – Flower 1946: 452.
Cyrtogomphoceras (?) *troedssoni* – Balashov 1953a: 208.
Faberoceras ? *troedssoni* – Flower in Flower & Teichert 1957: 66, 91, text-fig. 27.

Diagnosis

Small *Cyrtogomphoceras* with conch height of mature body chamber ca 40 mm, slightly compressed conch cross section (CHI ca 1.1) and irregularly, transversally constricted and undulating conch surface; sutures straight, directly transverse; siphuncle marginally located with very widely expanded segments; septal necks cyrtochoanitic, recumbent; small to moderate endosiphuncular bulletes.

Material examined

ESTONIA • 1 spec.; Hiiumaa Island, Kõrgessaare quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-392-1 • 1 spec.; same data as for preceding; TUG 939-60.

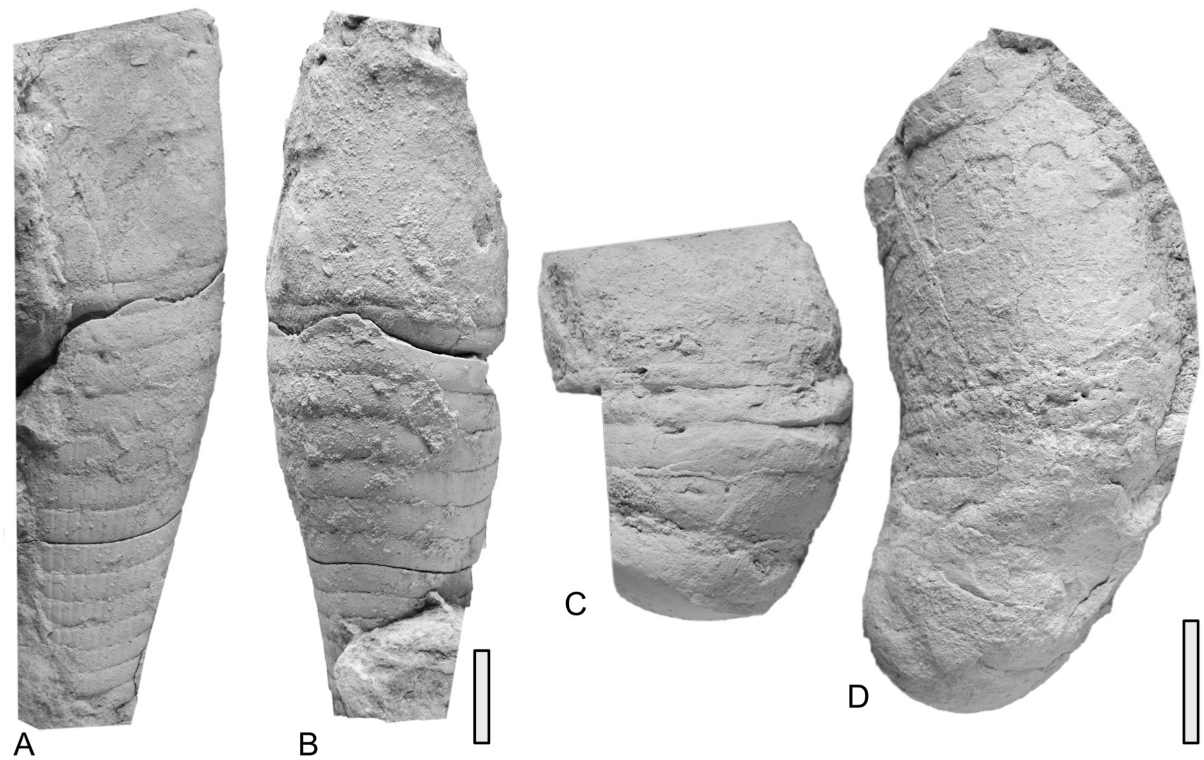


Fig. 38. Cyrtogomphoceratidae Flower, 1940 of the Vormsi–Pirgu regional stages, Estonia. **A–B**. *Lyckholmoceras norvegiae* Strand, 1934, specimen GIT 878-226, from Hosholm shore (tower), Pirgu Regional Stage. **A**. Lateral view. **B**. View of antisiphuncular side. **C–D**. *Cyrtogomphoceras troedssoni* Teichert, 1930, from Kõrgessaare quarry, Hiiumaa Island, Estonia, Vormsi Regional Stage. **C**. Specimen TUG 939-60, lateral view. Note the cutout of the prosiphuncular side. **D**. Specimen GIT 426-392-1, lateral view. Scale bars = 20 mm in all figures, same scale in A–B, and in C–D.

Description

GIT 426-392-1 (Fig. 38D) is a fragment of an endogastrically curved phragmocone and mature body chamber, with the outer shell partly preserved. The conch surface is hidden under an overgrowth of epibionts, but a fine transverse striation is visible on the inner mold of parts of the body chamber. At the base of the mature body chamber, the conch height and width are 40 mm and 35 mm, respectively (CHI = 1.14). The conch cross section has an oval shape with a narrower prosiphuncular side. The body chamber is at least 43 mm long and slightly curved with a convex antisiphuncular margin and a concave prosiphuncular margin. At its adoral end, the height of the body chamber is 38 mm. The peristome is either not preserved, or only very fragmentarily preserved. In lateral view, the entire specimen (body chamber and phragmocone) appears slightly irregularly undulated with shallow constrictions at irregular distances. The phragmocone has a height of 30–40 mm at a length of 36 mm (angle of expansion = 15°). The sutures are straight and directly transverse and 7 mm apart where the conch height is 35 mm (RCL = 0.2). The siphuncle is marginal and very wide, it is too poorly preserved to measure the septal foramen. The segments have a height of 9 mm where the chamber length is 6 mm, and the conch height is 32 mm (SCR = 1.5).

The second specimen TUG 939-60 is a short fragment of the phragmocone and body chamber, showing the typical irregular undulation of the shell (Fig. 38C). At a conch height of 40 mm, the conch width its 35 mm, similar to GIT 426-392-1. The sutures are straight and directly transverse. The siphuncle and septal necks are well-preserved in this specimen (Fig. 37B). The siphuncle is very wide; the septal foramen has a height of 9 mm and the siphuncular segments expand toward 15 mm where the chamber length is 5 mm, the conch height is 40 mm (RSH = 0.23, RSS = 1.67, SCR = 3). The connecting ring is thin, the septal necks are cyrtochoanitic recumbent and small endosiphuncular bullettes are present.

Remarks

This species is unique to *Cyrtogomphoceras* with regard to its relatively small size (the type species *C. magnum* Whiteaves, 1890 has a conch length of ca 270 mm) and its slightly irregularly undulated shell. *C.* cf. *thompsoni* Miller & Furnish, 1937, from the late Katian of Norway (Sweet 1959) is more curved, slightly larger (ca 70 mm maximum conch height) and the adoral-most sutures are more oblique than in *C. troedssoni* Teichert, 1930.

Genus ***Hosholmoceras*** gen. nov.
urn:lsid:zoobank.org:act:67E22CEA-BE72-42D4-9847-5F0A216039FC

Type species

Hosholmoceras ovalis gen. et sp. nov. from Hosholm shore, Vormsi Island, Estonia, Adila Formation, Pirgu Regional Stage.

Diagnosis

Endogastrically curved brevicones with very short chambers (RCL ca 0.05–0.07); conch cross section compressed or subtriangular; in lateral view mature conch slightly gibbous with largest conch heights near the base of the mature phragmocone; mature body chamber short, simple conical; sutures with shallow lateral lobes; siphuncle marginal, small; siphuncular segments rounded, expanded; septal necks cyrtochoanitic; endosiphuncular bulettes occur.

Etymology

Hosholm is the type locality of this genus.

Comparison

This genus is superficially similar to *Hemibeloitoceras* Balashov, 1962b, in having very short chambers (RCL ca 0.08) and a relatively thin, marginal siphuncle with simple expanded siphuncular segments. However, the conch of *Hemibeloitoceras* is exogastrically curved, expands gradually and is slenderer (angle of expansion ca 8°) while the sutures are directly transverse without a lateral lobe. Another curved breviconic form with very short chambers is *Antiphragmoceras* Foerste, 1925. This also differs from *Hosholmoceras* gen. nov. in having an exogastrically curved conch.

Hosholmoceras ovalis gen. et sp. nov.
urn:lsid:zoobank.org:act:221233FB-02D1-4F7C-A010-B574D890913D
Figs 37C, 39E–G

Diagnosis

Elliptically to oval compressed *Hosholmoceras* gen. nov., with CHI of ca 1.3–1.5, with angle of expansion of up to ca 26°, maximum mature conch size of ca 50 mm, mature body chamber length of ca 30 mm; ornamented with fine, narrowly spaced transverse lirae.

Etymology

The name refers to Hosholm, Vormsi Island, the type locality.

Type material

Holotype

ESTONIA • Vormsi Island, Hosholm shore (tower locality); Adila Formation, Pirgu Regional Stage; GIT 840-252.

Paratypes

ESTONIA • 3 specs; same data as for holotype; GIT 878-171 to GIT 878-173 • 11 specs; Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage; GIT 878-170, GIT 878-174 to GIT 878-177, GIT 878-179 to GIT 878-184.

Description

The holotype is an endogastrically curved, compressed fragment of a phragmocone and body chamber (Fig. 39G). The conch is slightly deformed (compressed). Parts of the outer shell are preserved on the antisiphuncular margin near the adoral end of the specimen. There, it is ornamented with fine transverse lirae of which ca 8 occur per 5 mm where the conch height is 53 mm. In lateral view, the pro-, and antisiphuncular conch margins, respectively, are convex and concave throughout their entire length. The concave side is nearly straight adorally, so that in lateral view the entire specimen has a bulbous shape. The greatest width is near the adoral end of the phragmocone. The greatest rate of expansion occurs in adapical parts of the phragmocone, where it increases in height from 28 mm to 42 mm over a distance of ca 30 mm (angle of expansion = 26°). The length of the preserved part of the body chamber is 20 mm. The conch cross section is rounded elliptical to oval with a slightly narrower margin at the antisphuncular side. At the base of the body chamber the height and width are 52 mm and 34 mm, respectively (CHI = 1.53). At the apical end of the specimen, the height and width are 28 mm and 21 mm, respectively (CHI = 1.33). The sutures are narrowly spaced, ca 2–3 mm apart throughout the entire length of the phragmocone (RCL ca 0.05–0.07). The sutures form wide lateral lobes. Details of the siphuncle and septal necks are preserved at the apical end of the specimen (Fig. 37C). The septal foramen is nearly marginal (ca 1 mm from the conch margin), very small (ca 1 mm in diameter, RSH = 0.04) and the septal necks are cyrtochoanitic. The siphuncular segments are rounded, expanded within the chambers with a width of 4 mm where the chamber length is ca 1.8 mm (SCR = 2.2). Thin bullettes are present.

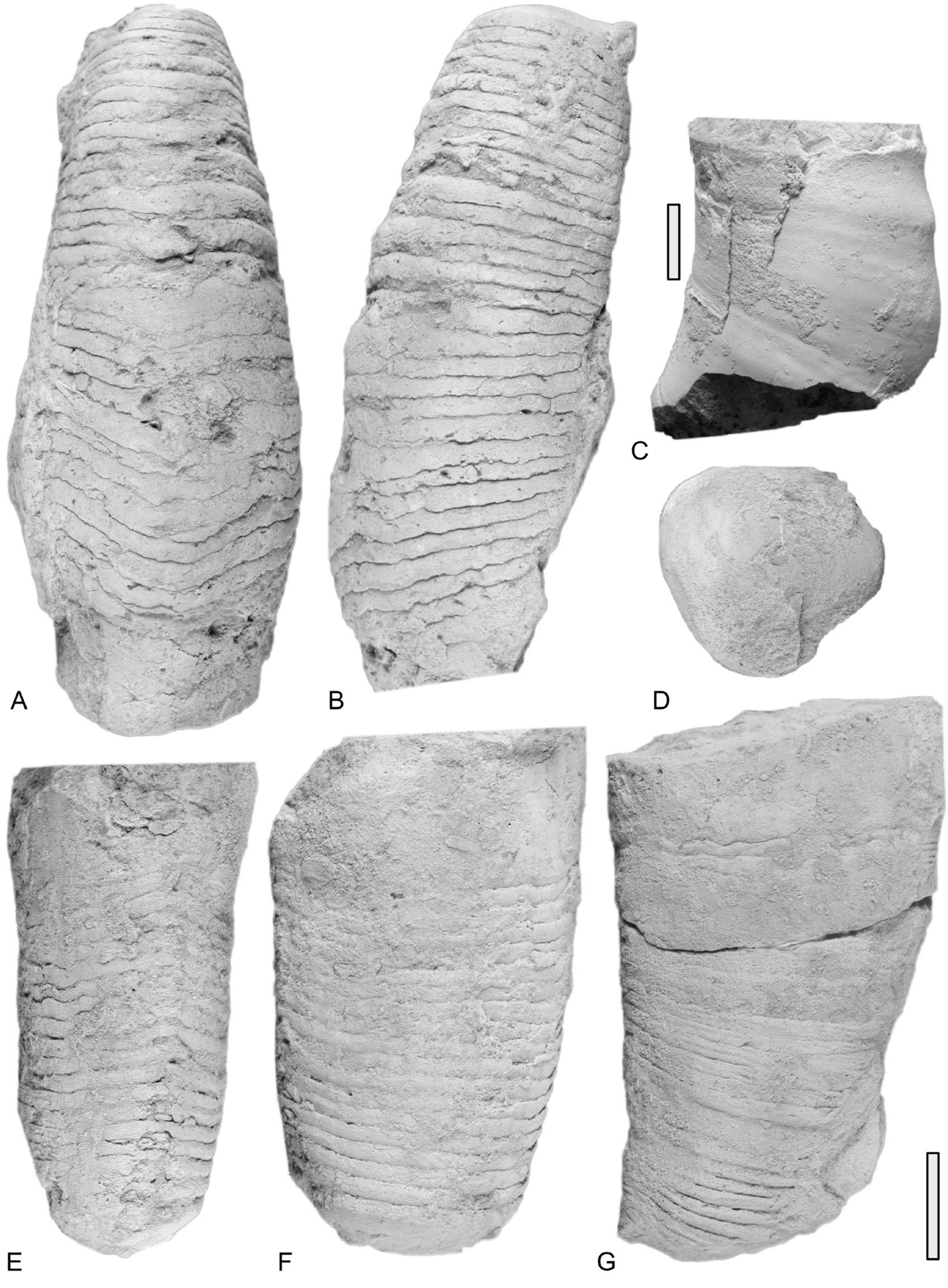


Fig. 39. *Hosholmoceras* gen. nov., and an indeterminate fragment of a multiceratid of the Pirgu Regional Stage, Estonia. **A–B, D**. *Hosholmoceras triangulatum* sp. nov., holotype TUG 119-2, from Hosholm shore (tower), Vormsi Island. **A**. View of the antisiphuncular side. **B**. Lateral view. **C**. Multiceratoidea gen. et sp. indet. B, specimen TUG 1743-37, from Saxby shore, Vormsi Island, Vormsi Regional Stage, lateral view. **D**. Adapical view. **E–G**. *Hosholmoceras ovalis* gen et sp. nov., specimen GIT 840-252 (holotype), from Hosholm shore (tower), Vormsi Island. **E–F**. Specimen GIT 878-170. **E**. View of the prosiphuncular side. **F**. Lateral view. **G**. Specimen GIT 840-252 (holotype), lateral view.

Three other specimens in the collection (GIT 878-170, GIT 878-181, GIT 878-183) have a maximum conch height of ca 50–52 mm, suggesting that this is the mature size of this species. A nearly complete body chamber is preserved in specimen GIT 878-170 (Fig. 39E–F), it is simple conical, 23 mm long, and has a straight peristome at the antisiphuncular side of the conch.

Remarks

See Remarks on *Hosholmoceras triangulatum* gen. et sp. nov. (below).

Hosholmoceras triangulatum gen. et sp. nov.

urn:lsid:zoobank.org:act:CF3EC75F-3CF1-464E-A7B4-2AFC3874F932

Fig. 39A–B, D

Diagnosis

Slender *Hosholmoceras* gen. nov. (angle of expansion ca 15°), with rounded triangular conch cross section, with CHI ca 1, maximum mature conch size of ca 50 mm, and mature body chamber length of ca 30 mm; ornamented with fine, narrowly spaced transverse lirae.

Type material

Holotype

ESTONIA • Vormsi Island, Hosholm shore; Adila Formation, Pirgu Regional Stage; TUG 119-2.

Paratypes

ESTONIA • 2 specs; same data as for holotype; GIT 878-168, GIT 878-169 • 1 spec.; Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage; GIT 878-178.

Description

The holotype is a fragment of the phragmocone and the mature body chamber. The conch surface is not preserved (Fig. 39A–B, D). The conch is endogastrically curved (siphuncle at the concave side of the conch curvature). The complete conch cross section is preserved only in the apical portion of the specimen. There, it is rounded triangular with three sides of equal width and a narrowly rounded venter. The siphuncle is not visible or not preserved but apparently lies in the mid-position on the flat dorsum. At the apical end, the conch height and width are ca 27 mm and 26 mm, respectively. The greatest width of the specimen is reached ca 80 mm in the adoral direction from apical end of the specimen with 45 mm (angle of expansion = 14°). Beyond this point, the conch width decreases and at the base of the body chamber is ca 42 mm. The greatest conch width is located ca 20 mm adorally from the base of the body chamber. The preserved part of the body chamber is ca 25 mm long. The sutures forms shallow lateral lobes; they are narrowly spaced, ca 15–20 occur in a distance equal to the corresponding conch height (RCL ca 0.05–0.07).

Specimen GIT 878-169 is a small fragment of a phragmocone with ca four chambers preserved, it shows the rounded triangular conch cross section where the conch height and width are 32 mm and 37 mm, respectively (CHI = 0.86). The third specimen is a poorly preserved fragment of a phragmocone with a triangular conch cross section with a conch width of 27 mm.

Remarks

The siphuncle is only poorly preserved in the four specimens available. The poor preservation of the siphuncle is also a feature that can be seen in *H. ovalis* sp. nov. Amongst the 14 specimens of *H. ovalis* available for study only two preserved traces of the thin marginal siphuncle. *Hosholmoceras triangulatum* sp. nov. is similar to the type species of *Hosholmoceras* in having extremely narrowly spaced chambers and a bulbous phragmocone but differs in having a triangular conch cross section.

Genus ***Kiaeroceras*** Strand, 1934

Type species

Kiaeroceras frognoyense Strand, 1934, from Frognoyøa island, Ringerike, Norway, "*Trinucleus* limestone, (4cβ)" (Strand 1934: 98), Sørbakken Formation, Late Katian; by original designation.

Diagnosis

Orthocones with ovate conch cross section, narrower ventral conch margin; mature body chamber slightly bulbous, with shallow constriction near aperture; aperture with deep and broad hyponomic sinus; sutures with lateral lobes and pronounced ventral saddle; siphuncle close to ventral conch margin, with broadly expanded siphuncular segments, with prominent bullettes. (Adopted from Strand 1934.)

Remarks

The diagnosis of the genus given in Kröger (2013) is imprecise, it is corrected herein and features now the important characters described in Strand (1934). Moreover, the relatively rich Estonian material described herein reveals a few features, not known from type material of the type species. These include the shape and dimensions of the more apical phragmocone parts, variability in conch cross section shape as well as the extent and development of endosiphuncular deposits. Consequently, species are included here, which have conch cross sections with a CHI of nearly 1, although possessing the characteristically narrow margin on the prosiphuncular side. Additionally, the hyponomic sinus which is deep in the type species, does not seem to be deep in all species. Finally, the more complete specimens of this genus reveal that the curvature is endogastric and that the suture develops a lateral lobe during the latest growth stages (compare, e.g., Fig. 34H, and Strand 1934: pl. 9 fig. 4 and pl. 12 fig. 2). The genus is interpreted here sensu lato, to include these deviations from the original diagnosis.

The genus was placed within the Cyrtogomphoceratidae by Teichert (1964b) and has been compared to *Protophragmoceras* by Strand (1934). This was based on the presence of heavy endosiphuncular bullettes in the type-material. The new material, described herein, shows that in specimens assigned to *Kiaeroceras* transitions exist from typical discosorid-like bullettes toward valcouroceratid-like actinosiphonate deposits (see below in description of *K. kaebliki* sp. nov.).

Moreover, Strand (1934) described *Mixosiphonoceras norvegicum* Strand, 1934 from late Katian strata in Norway. The type species of *Mixosiphonoceras* is mid Silurian in age and the genus is placed within the Brevicoceratidae, which are known otherwise only from the mid Silurian to Devonian. Therefore, it is likely that the Norwegian species represents another *Kiaeroceras*.

The presence of actinosiphonate deposits in endogastrically curved *Kiaeroceras*, in orthocones (*Mixosiphonoceras norvegicum* Strand, 1934), and in exogastrically curved valcouroceratids suggests either multiple independent origins of this type of endosiphuncular deposit or a close relationship between these taxa. A detailed phylogenetic, or cladistic analysis of the oncocerid-discoserid groups, which could help to solve this open question (suggested also by Pohle *et al.* 2022) is beyond the scope of this work.

Below, four species of *Kiaeroceras* are described in open nomenclature. These are known almost exclusively from their mature body chambers. Their differing sizes and shapes are unique, and they differ from species described in the literature and herein. However, the relatively low number of known specimens of *Kiaeroceras* does not permit evaluation of the intraspecific and interspecific variability in, e.g., mature body chamber size, and CHI. The possibility therefore exists, that some of these species, represent intraspecific variability.

Kiaeroceras kaebliki sp. nov.
urn:lsid:zoobank.org:act:50E19EA5-FCD5-4F44-8B9A-2A14C1789E05
Figs 37F, H, 40C, G

Diagnosis

Kiaeroceras with a CHI of 1.2, with an adult body chamber height of less than 40 mm; mature body chamber slightly longer than high (RBL ca 1.1).

Etymology

From the small bird Käblik (Estonian), referring to the small size of this species.

Type material

Holotype
ESTONIA • Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-31.

Paratypes
ESTONIA • 2 specs; same data as for holotype; GIT 426-1123, GIT 878-158 • 1 spec.; Sutlema quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-163

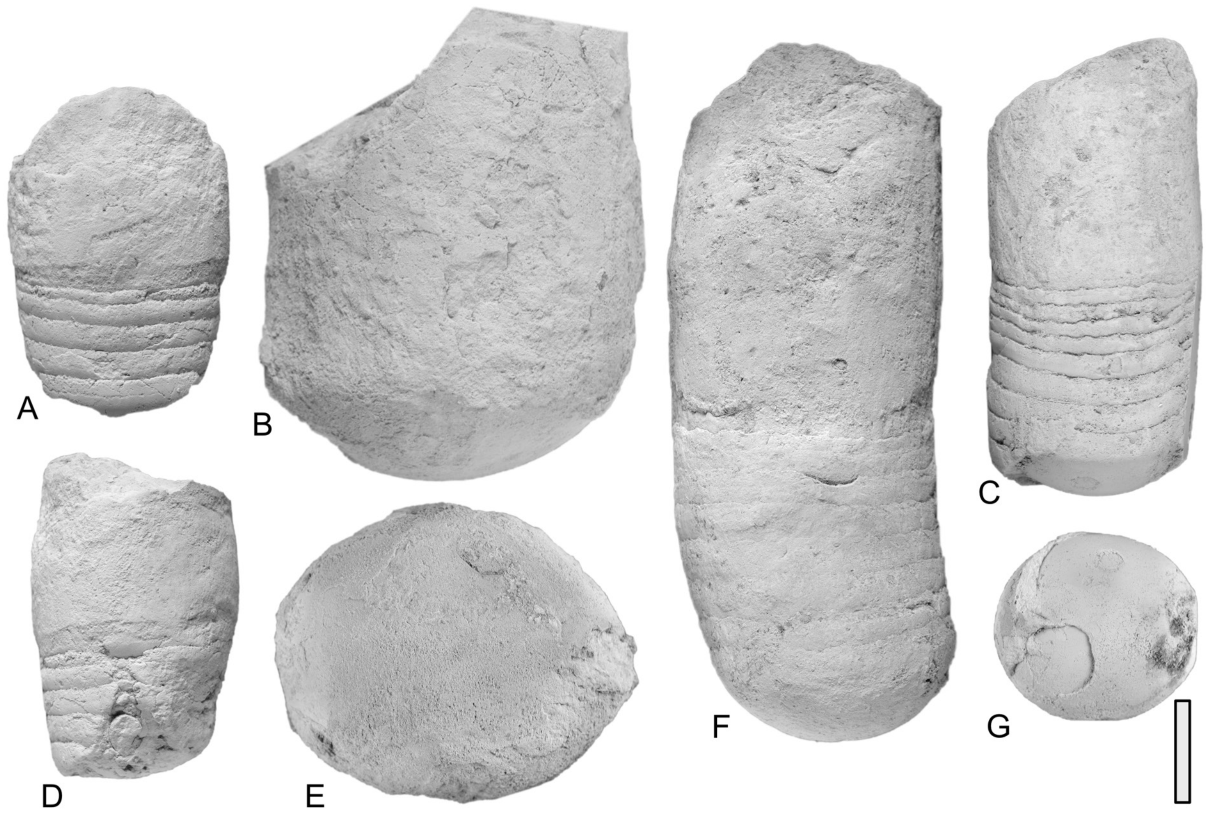


Fig. 40. *Kiaeroceras* Strand, 1934 of the Vormsi Regional Stage, Estonia. **A, D**. *Kiaeroceras* sp. A, specimen TUG 895-69, from Kõrgessare, Hiiumaa Island, lateral view. **B, E**. *Kiaeroceras* sp. D, specimen TUG 1745-201, from Kärdla quarry, lateral view. **C, G**. *Kiaeroceras kaebliki* sp. nov., paratype GIT 426-1123, from Saxby shore. **D**. View of the prosiphuncular side. **E**. Adapical view. **F**. *Kiaeroceras* sp. E, specimen GIT 878-21 from Saxby shore (N), Vormsi Island. **G**. Adapical view. Scale bar = 20 mm, same scale in all figures.

Description

Specimen GIT 878-31 is an orthoconic fragment of a mature body chamber and parts of the phragmocone. At the base of the body chamber, the conch height is 37 mm and the width 32 mm (CHI = 1.2). The outer shell is not preserved but the conch surface was apparently smooth. The conch cross section is oval, the conch margin on the prosiphuncular side is more narrowly curved. The body chamber is 40 mm long and has a simple, straight peristome with an inconspicuous, wide hyponomic sinus, ca 3 mm deep, at the antisiphuncular side. The conch height is 34 mm at the peristome. In lateral view, the body chamber is slightly convex, its greatest width occurs at the adapical third of the length with a conch height of 38 mm. The phragmocone height increases from 35 mm to 37 mm at a length of 17 mm (angle of expansion = 7°). The sutures form wide, shallow lobes laterally and have a distance of 5 mm where the conch height is 37 mm (RCL = 0.14). The siphuncle (Fig. 37H) is nearly marginal with a septal foramen 4 mm in diameter, where the conch height is 37 mm (RSH = 0.11).

Specimen GIT 878-1123 is a fragment of a mature body chamber and eight chambers of the phragmocone (Fig. 40C, G). In this specimen, the ontogenetic change of the suture shape is well seen. At a conch height of ca 37 mm, the sutures are nearly straight and 5 mm distant (RCL = 0.14) and ca 20 mm further adorally the sutures form shallow lateral lobes, and are only 2–3 mm apart. The preserved part of the phragmocone is nearly tubular and straight. The siphuncular segments are expanded within the chambers and wide. Endosiphuncular bullettes deposits occur which protract in apical direction from the septal necks (Fig. 37F).

Comparison

This species of *Kiaeroceras* differs from all other species of the genus in having a small adult size of less than 40 mm conch height at the base of the mature body chamber.

Kiaeroceras (?) ***ormsoense*** sp. nov.

urn:lsid:zoobank.org:act:DF10785E-0267-4AD5-B8E6-90B2BBD9EA1F

Figs 35F, H, 37D

Diagnosis

Kiaeroceras with CHI of ca one, and an adult body chamber with a height of ca 50 mm, which is nearly as long as high.

Type material

Holotype

ESTONIA • Vormsi Island, Saxby shore (N); Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-63.

Description

The holotype is a fragment of the phragmocone and a mature body chamber (Fig. 35F, H). Parts of the outer shell are preserved, which show that the shell was apparently smooth or was ornamented with fine irregularly spaced growth lines. At the base of the body chamber, the conch height is 52 mm and the CHI nearly 1. In cross section, the margin on the prosiphuncular side is narrower than the opposite margin. The body chamber is 52 mm long and at the aperture 54 mm in diameter. The peristome is only partially preserved and where visible is simple and directly transverse. In lateral view, the body chamber is straight with straight or very slightly convex dorsal and ventral conch margins. The phragmocone is slightly curved endogastrically. The sutures are directly transverse and straight. The adoral-most sutures are crowded, indicate maturity of the specimen. At a conch height of 42 mm, the phragmocone is 39 mm wide (CHI = 1.07), and 30 mm further adorally, the height is 31 mm (angle of expansion = 21°). The septa are 4 mm apart where the conch height is 40 mm (RCL = 0.1). The siphuncle is strongly expanded within the chamber in lateral view, wider near the adapical surface of the septa with a maximum height of 8 mm where the septal foramen is 6 mm the chamber length is 4 mm, and the conch height is 40 mm (RSH = 0.15, RSS = 1.33, SCR = 2). There, the distance of the septal foramen from the conch margin is 2 mm. The connecting ring is thick and thick endosiphuncular bulletes occur. The septal necks are cyrtochoanitic (Fig. 37D).

Remarks

This specimen is placed with question mark into *Kiaeroceras* because it differs from other members of the genus in having a circular conch cross section, a wider angle of expansion, resulting also in a slightly bulged mature body chamber, and it is slightly endogastrically curved. Its gross morphology is intermediary between typical members of *Diestoceras* and *Kiaeroceras*. It differs from the former in having a slender shell and a relatively elongate body chamber. The erection of a new genus for this species must wait until more material is known, especially from the apical parts of *Kiaeroceras*, which is mostly known from isolated mature body chambers. Herein, this species is placed within *Kiaeroceras* because it fits the existing (relatively broadly defined) diagnosis of this genus (see above).

The siphuncular structure, and in particular the actinosiphonate deposits of *Diestoceras* are poorly known. Flower & Teichert (1957: 42) discuss the possibility that the actinosiphonate deposits seen in some species of the genus are modified bullettes, which would mean that it should be transferred to the Discosorida. This species, being intermediate between *Kiaeroceras* and *Diestoceras* could support this hypothesis.

Comparison

The species is unique to the genus in having a CHI of nearly one and a slightly inflated mature body chamber.

Kiaeroceras (?) cf. ***ormsoense***

Fig. 35J

Material examined

ESTONIA • 1 spec.; Vormsi Island, Saxby shore (N); Kõrgessaare Formation, Vormsi Regional Stage; TUG 1680-20.

Description

Specimen TUG 1680-20 is a slightly endogastrically curved fragment of a mature body chamber and four chambers of the phragmocone. The conch surface is apparently smooth. At the base of the body chamber the conch height is 47 mm. The body chamber is 52 mm long, with parts of the peristome preserved. In lateral view, the dorsal and ventral margins of the body chamber are straight. The preserved part of the phragmocone is 20 mm long and increases in height from 43 mm to 47 mm (angle of expansion = 11°). At its adapical end, the conch width is 40 mm (CHI = 1.08). There, the conch cross section is elliptically rounded. The sutures are directly transverse and 6 mm apart where the conch height is 45 mm (RCL = 0.13)

Remarks

The specimen is similar in conch shape, suture spacing, suture shape and siphuncular shape and position to *K.* (?) *ormsoense* sp. nov. but differs from this species in angle of expansion and mature size. More material is needed to evaluate the interspecific variability in mature size among specimens of *K.* (?) *ormsoense* in order to establish a new species for the two specimens described above.

Kiaeroceras urgense sp. nov.
urn:lsid:zoobank.org:act:4B0FA1B5-E540-4E9C-B93B-AEC7648EF1A2
Figs 31B, 35I

Diagnosis

Kiaeroceras with CHI of ca 1.1, a relatively long mature body chamber (RBL ca 1.7) and a mature conch height of ca 50 mm.

Etymology

Referring to the type locality.

Type material

Holotype

ESTONIA • Urge quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 103-75.

Paratypes

ESTONIA • 2 specs; Hiimuaa Island, Paluküla quarry; Moe Formation, Pirgu Regional Stage; TAM G136:33, TAM G432:727 • 1 spec.; same data as for preceding; TUG 47-864.

Description

The holotype (Fig. 35I) is a relatively well-preserved part of a nearly complete mature body chamber and phragmocone. The conch surface is nearly smooth, ornamented with partly distinct, irregularly spaced growth lines or rugae (Fig. 31B). At the base of the body chamber, the conch height and width are 48 mm and 45 mm, respectively (CHI = 1.07). Hence, the conch cross section is slightly compressed. At the aperture, the conch cross section is not fully preserved, and a measurement of the conch width is not possible. The apertural height is 52 mm. With its total length of ca 80 mm, the body chamber is nearly tubular and straight. In cross section, the prosiphuncular side is more narrowly rounded, drop-shaped. In lateral view, the margins are almost straight.

The phragmocone is slightly endogastrically curved with a conch height increasing from 36 mm to 47 mm over a length of 60 mm (angle of expansion = 11°). A conspicuous constriction occurs at ca 30 mm adapically of the base of the body chamber with a conch height of ca 38 mm. At the adapical end of the specimen, the conch height is 33 mm, the corresponding width is 32 mm. The sutures are nearly transverse at the adapical end of the specimen and with shallow lateral lobes near the base of the mature body chamber. The septal foramen is close to the conch margin on the concave side of the conch. It has a diameter of ca 3 mm (RSH = 0.09). Traces of expanded siphuncular segments are preserved.

A second specimen (TUG 47-864) is a poorly preserved, slightly curved, fragment of a phragmocone and body chamber with a length of ca 130 mm of which only half of the conch is preserved. The siphuncle is missing, and the septa are fragmentary. The conch, however, shows the irregular constrictions of the phragmocone present in the holotype. The base of the body chamber has a height of 44 mm. The conch height expands with angles of expansion between 13° (heights 37 mm to 42 mm) and 22° (heights 30 mm to 37 mm).

Comparison

This species has a smaller adult size than *K. frognoyense* (mature body chamber height 68 mm), it has a less compressed conch cross section than *K. heryoense* Strand, 1934 (CHI = 1.15), and a longer body chamber than *K.* (?) *ormsoense* sp. nov. (mature body chamber height = 54 mm, RBL = 1).

Kiaeroceras sp. A
Fig. 40A, D

Material examined

ESTONIA • 1 spec.; Hiumaa Island, Kõrgessaare quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 895-69.

Description

The specimen is a fragment of a mature body chamber and phragmocone. The conch height and width at the base of the body chamber are 41 mm and 37 mm, respectively (CHI = 1.1). The conch is nearly straight. The conch cross section is elliptical. The length of the body chamber is not fully preserved, it was longer than 37 mm. In lateral view, margins of the body chamber are slightly convex; the body chamber reaches its greatest height of 42 mm ca 23 mm from the base. At the base of the body chamber, a ca 3 mm thin band of oncomyarian muscle scars is preserved. Five chambers of the phragmocone are preserved, indicating a low angle of expansion, which cannot be measured because of the incomplete preservation. Septal crowding of the adoral-most septa indicates maturity of the specimen. The sutures form very shallow lateral lobes. The siphuncle is located close to the conch margin and expands between the septal foramens toward a width of ca 5 mm. The width of the septal foramen is ca 4 mm where the conch height is 38 mm (RSH = 0.11, RSS = 1.25), and the septal distance is 5 mm (RCL = 0.13, SCR = 1).

Remarks

This fragment differs from *K. kaebliki* sp. nov. in its larger in adult size, and less compressed, more equally rounded conch cross section.

Kiaeroceras sp. B
Fig. 35A–B

Material examined

ESTONIA • 1 spec.; Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-161.

Description

The specimen is an almost tubular, almost straight fragment of a mature body. The conch surface is poorly preserved but apparently smooth. The conch cross section is drop-shaped with a widely rounded antisiphuncular and a narrower prosiphuncular side. The conch height and width are 43 mm and 37 mm, respectively (CHI = 1.4). The body chamber is 63 mm long, without constriction. The remaining peristome appears to be straight and directly transverse. The base of the body chamber indicates that the sutures formed shallow lateral lobes. The siphuncle is nearly marginal, and the septal foramen has a width of 4 mm (RSH = 0.09).

Remarks

The fragment is relatively strongly compressed compared with other Estonian specimens of *Kiaeroceras*. Its adult body chamber height is smaller than in the Norwegian species.

Kiaeroceras sp. C
Fig. 35E, G

Material examined

ESTONIA • 1 spec.; Niibi hillock; Moe Formation, Pirgu Regional Stage; GIT 225-997.

Description

The specimen is a nearly complete mold of a mature body chamber with height, width, and length of 53 mm, 44 mm and 75 mm, respectively (CHI = 1.11). The conch is straight and tubular. The conch cross section is oval compressed with a relatively narrow, drop-shaped margin on the prosiphuncular side. The peristome is nearly straight and a very shallow (5 mm) hyponomic sinus occurs on the prosiphuncular side. The siphuncle is nearly marginal with a septal foramen ca 8 mm in diameter, located ca 3 mm from the conch margin (RSH = 0.15, RSP = 0.16).

Comparison

This specimen differs from *K. ormsoense* sp. nov., to which it is otherwise similar, in having a compressed conch cross section and a longer, perfectly tubular body chamber (RBL = 1.4 as compared with RBL ca 1 in *K.* (?) *ormsoense*).

Kiaeroceras sp. D
Fig. 40B, E

Material examined

ESTONIA • 1 spec.; Kärdla quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 1745-201.

Description

The specimen is a fragment of a very slightly endogastrically curved mature body chamber with conch height, and width at its base of 61 mm and 49 mm, respectively (CHI = 1.44). The preserved part of the body chamber is 65 mm long and tubular in lateral view. The conch cross section is oval with a narrower prosiphuncular side. The siphuncle is close to the conch margin and ca 7 mm wide (RSH = 0.11).

Remarks

In its dimensions, this specimen is most similar to the Norwegian species of *Kiaeroceras* but differs in having a more compressed conch (*K. frognoyense* has a CHI of 1.15, and *K. heroyense* a CHI of 1.25).

Kiaeroceras sp. E
Figs 37A, 40F

Material examined

ESTONIA • 1 spec.; Vormsi Island, Saxby shore (N); Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-21.

Description

The specimen is a fragment of a mature body chamber and nine chambers of the phragmocone (Fig. 40F). The body chamber is straight and tubular with a conch height of ca 48 mm. The phragmocone is slightly endogastrically curved. The adoral-most two septa are crowded. The phragmocone increases in height from 44 mm to 47 mm at a length of 34 mm (angle of expansion = 5°). The sutures are directly transverse and straight. The siphuncle is near the conch margin, its segments are strongly expanded within the chambers with a height of 8 mm where the conch height is 46 mm, and the chamber length is 5 mm (SCR = 1.6). The septal necks are cyrtochoanitic. Endosiphuncular bullettes occur (Fig. 37A).

Remarks

The specimen is similar to *K. urgense* sp. nov. with respect to the low angle of expansion of the phragmocone and the size and shape of the mature body chamber. It differs from the former in lacking the constriction at the phragmocone and in having a smaller angle of expansion. It cannot fully be compared with other species of the genus because the conch cross section is not preserved, and the specimen is therefore left in open nomenclature.

Genus ***Lyckholmoceras*** Teichert, 1930

Type species

Lyckholmoceras estoniae Teichert, 1930, from Saaremõisa (Lyckholm), N of Haapsalu, Läänemaa, Estonia, Kõrgessaare Formation, Vormsi Regional Stage; by monotypy.

Emended diagnosis

Slightly endogastrically curved, large brevicones with slightly compressed conch cross section, conch margin narrower at ventral side; mature body chamber uncontracted or at mid-length, with distinct hyponomic sinus; sutures with shallow lateral lobe; siphuncle marginal with slightly expanded segments; endosiphuncular bullettes occur.

Remarks

The genus was placed within the Cyrtogomphoceratidae by Flower in Flower & Teichert (1957) and without further discussion classified within the Diestoceratidae in Sweet (1964b: K295). Both families contain genera with swollen siphuncles and with annulosiphonate deposits or endosiphuncular bullettes. However, here I follow Teichert (1964b) to restrict the cyrtogomphoceratids to endogastrically curved and the diestoceratids to straight and exogastrically curved forms (see above). Hence, *Lyckholmoceras* is interpreted as a member of the Cyrtogomphoceratidae, herein.

The original diagnosis is emended herein regarding the presence of endosiphuncular deposits. In Teichert (1930: 301) it is stated “Keine Ausfüllungen des Siphos bekannt” (translated from German: “Endosiphuncular deposits unknown”. This statement was emended by Sweet (1964b: K295) to “actinosiphonate deposits not known”. In the Estonian material, assigned to *Lyckholmoceras*, studied herein, endosiphuncular bullettes occur. The genus diagnosis is changed accordingly.

Lyckholmoceras norvegiae Strand, 1934
Figs 37G, 38A–B

Lyckholmoceras norvegiae Strand, 1934: 88–91, pl. 11 figs 1a–b, 2.
Beloitoceras heterocurvatum Strand, 1934: 77, pl. 10 fig. 11 (non pl. 10 figs 8–10).
Parryoceras strandi Sweet, 1959: 58–59, pl. 9 figs 5–6, pl. 10 fig. 6.

Lyckholmoceras norvegiae – Flower in Flower & Teichert 1957: 59, text-figs c, g. — Dzik 1984: 67, text-fig. 18.13.

Diagnosis

Lyckholmoceras with compressed conch cross section (CHI ca 1.5), in longitudinal direction moderately curved; mature body chamber almost straight with uncontracted aperture and well-marked hyponomic sinus; sutures with shallow lateral lobes; siphuncular segments slightly expanded within chambers, narrowing adorally, with SCR of ca 1; ornamented with faint, densely irregularly spaced lirae. Small endosiphuncular bullettes are present. (Compiled from Strand 1934: 89–90.)

Material examined

ESTONIA • 1 spec.; Haapsalu holm; Adila Formation, Pirgu Regional Stage; TUG 1745-2 • 4 specs; Vormsi Island, Hosholm shore (tower locality); Adila Formation, Pirgu Regional Stage; GIT 878-166, GIT 878-167, GIT 878-187, GIT 878-226.

Description

The most complete specimen is GIT 878-226, which preserves parts of the mature living chamber and a 70 mm long mold of the phragmocone (Fig. 39A–B). The conch height cannot be measured in this specimen because the prosiphuncular side of the conch is not preserved but the preserved parts show the general conch shape. In lateral view, the body chamber appears straight, the adoral ca 35 mm of the phragmocone has a convex outline at the antisiphuncular side and the adapical part is straight. The straight part of the phragmocone has a conch width of < 37 mm. The conch cross section is ovally compressed with a narrow margin at the antisiphuncular side. At the base of the body chamber, the conch width is 38 mm and the height is approximately 50 mm (CHI = 1.3). The peristome is straight and simple on the antisiphuncular side. It is ca 40 mm distant from the base of the body chamber. The part of the phragmocone with width < ca 35 mm is distinctly longitudinally striated; ca 60 striae occur around the circumference. The sutures are 5 mm apart where the conch width is 28 mm, they form shallow lateral lobes.

The conch cross section is preserved in specimen GIT 878-167, which is a small fragment of a phragmocone with only one chamber completely preserved. There, the conch height and width are 32 mm and 25 mm respectively (CHI = 1.28), and the conch cross section is elliptically compressed with narrow dorsal and ventral margins. The septal foramen is located ca 1–2 mm from the conch margin and has a diameter of 3 mm (RSH = 0.09, RSP ca 0.07).

The angle of expansion can be measured in specimen TUG 1745-2, which is a fragment of a phragmocone in which the conch height increases from 20 mm to 32 mm in 37 mm (angle of expansion = 18°). Specimens GIT 878-166, GIT 878-167, GIT 878-187, and TUG 1745-2 have conch heights of less than 40 mm and all show the characteristic longitudinal striation on the mold of the outer shell of the phragmocone (e.g., Fig. 38A–B).

The details of the siphuncle and septal necks are preserved in GIT 878-187 (Fig. 37G), and GIT 878-167. In both specimens, the siphuncle is located close to the margin at the concave side of the conch. The siphuncular segments are expanded tubular. The connecting ring is relatively thick and adnate on the adapical surface of the septum on the siphuncular side nearest to the conch center and adnate at the adoral side of the septa at the siphuncular side nearest to the conch margin. Where the conch width is 32 mm, the chamber length is 4.5 mm, the maximum height of the siphuncle is 4 mm, and the septal foramen is 2 mm (GIT 878-187, RSS = 2, SCR = 0.89). The septal necks are cyrtochoanitic; they are recumbent and adnate at the side of the siphuncle nearest to the conch margin. Small bullettes occur, which expand in adapical direction.

Remarks

The specimens described above are slightly less compressed in conch cross section than the types of the species described by Strand (1934), which have a CHI of 1.36–1.49. This difference can be interpreted as taphonomic effect or as an effect of ontogenetic change in CHI and measurement at different growth stages. More material is needed to evaluate the intraspecific and ontogenetic variability of the CHI. The Estonian specimens are nevertheless placed within *L. norvegiae*, based on the general similarities in conch dimensions and conch shape with this species.

The specimen described under *Parryoceras strandi* Sweet, 1959 is identical in conch shape, dimensions, and with regard of the shape and size of the siphuncle-septal neck complex and must be synonymized with *L. norvegiae*. It remains an open question how the closely related *Parryoceras* Sweet & Miller, 1957 compares in detail to *Lyckholmoceras*, because the details of the septal necks and connecting rings are poorly known in the former. *Parryoceras euchari* Sweet & Miller, 1957, the type of the genus, apparently differs from species of *Lyckholmoceras* in having a more strongly constricted mature body chamber than species of *Lyckholmoceras*.

Genus ***Strandoceras*** Flower, 1946

Type species

Protophragmoceras tyriense Strand, 1934, from Stavnestangen, Ringerike, Norway, Bønsnes Formation, Late Katian; by original designation.

Diagnosis

Endogastric cyrtocones with compressed conch cross section, ventral side of cross section more narrowly rounded than the dorsal side; mature body chamber less curved than the rest of the conch; peristome with small sinus on concave and wide sinus on convex side of conch; sutures with shallow lateral lobes slightly shifted adapically at the dorsal side; siphuncle near conch margin with broadly expanded segments and endosiphuncular bullettes. (Adopted from Flower 1946: 434.)

Strandoceras sphynx (Schmidt, 1858)
Figs 31C–D, 41A, F, 42A

Phragmoceras sphynx Schmidt, 1858: 200.

Phragmoceras sphynx – Eichwald 1860: 1272–1273. — Roemer 1861: 61. — Strand 1934: 93, 107. — Flower 1946: 434. — Flower in Flower & Teichert 1957: 57, 114, text-figs 15e, g–h.
Protophragmoceras sphinx (sic) – Teichert 1930: 270, 299–301, pl. 7 fig. 20, pl. 8 fig. 24, text-figs 3–4. — Balashov 1953a: 212. — Dzik 1984: 48, 52, 65, text-fig. 14.5, pl. 7 fig. 7.

Diagnosis

Large *Strandoceras* with mature conch height of more than 70 mm; conch cross section oval compressed with narrower ventral conch margin; mature body chamber slightly endogastrically curved, up to ca 80 mm long, nearly tubular or slightly gibbous with maximum conch height near base; ornamented with fine transverse lirae.

Material examined

ESTONIA • 1 spec.; Vormsi Island; Saxby old quarry; Moe Formation, Pirgu Regional Stage; TUG 1672-29 • 1 spec.; Raplamaa, Pahkla; Moe Formation, Pirgu Regional Stage; TUG 1745-195 • 1 spec.; Läänemaa, Niibi hillock; Moe Formation, Pirgu Regional Stage; TAM G432:68 • 2 specs; Sutlepa quarry; Adila Formation, Pirgu Regional Stage; TAM G149:27, TAM G149:28.

Type locality and horizon

Niibi, Estonia; Moe Formation, Pirgu Regional Stage.

Description

Specimen TUG 1672-29 is a nearly complete endogastrically curved conch preserving the outer shell and part of the mature body chamber (Figs 31D, 41A). The conch surface is ornamented with slightly

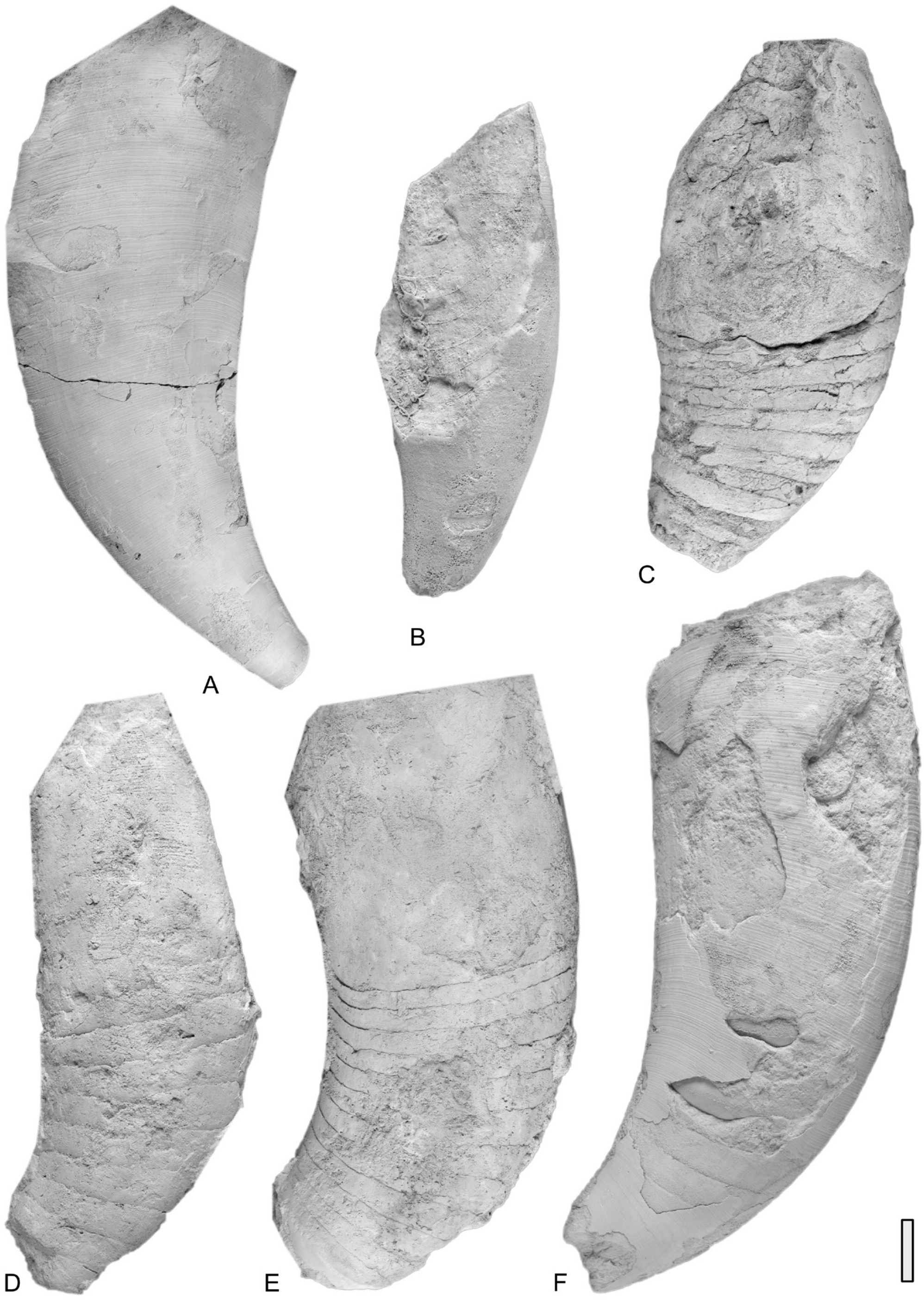


Fig. 41. Large species of *Strandoceras* Flower, 1946 of the Vormsi–Pirgu regional stages, Estonia. **A**. *Strandoceras sphynx* (Schmidt, 1858), specimen TUG 1672-29 from Saxby village, Vormsi Island, Pirgu Regional Stage. **B**. *Strandoceras sulevipoegi* sp. nov., holotype TUG 1745-209, from Salu, Pirgu Regional Stage. **C**. *Strandoceras muhvi* sp. nov., holotype TUG 42-432, from Kohila quarry, Vormsi Regional Stage. **D**. *Strandoceras sulevipoegi*, paratype TUG 42-399, from Vormsi Island, Vormsi–Pirgu regional stages. **E**. *Strandoceras kalevipoegi* sp. nov., holotype TUG 42-431, from Kohila quarry, Vormsi Regional Stage. **F**. *Strandoceras sphynx* (Schmidt, 1858), specimen TAM G432:68 from Niibi hillock, Läänemaa, Pirgu Regional Stage. Scale bar = 20 mm, same scale in all figures, all in lateral view.

irregularly spaced, distinct growth bands and / or lirae, which are adapically shifted at the antisiphuncular side of the conch curvature, and which form a hyponomic sinus on the prosiphuncular side. The conch cross section is preserved only at the apical end of the specimen. There, the conch height and width are 17 mm and 15 mm, respectively (CHI = 1.13) and the cross section oval compressed with a narrow margin on the prosiphuncular side. In lateral view, the antisiphuncular conch margin is convex throughout the entire length, the prosiphuncular conch margin is concave in early growth stages and straightens at a position where the conch height is ca 55–60 mm, resulting in an overall inflated conch shape. The conch reaches a maximum height of ca 72 mm at ca 55 mm from the peristome, adorally of which, the conch height decreases to ca 68 mm at the peristome (Fig. 42A; supplementary data 4). The conch is also inflated in width, although, the extent of the inflation cannot be measured in this or other available specimens. The angles of expansion reach a maximum with ca 27° between conch heights of 17 mm and 25 mm.

Where visible, the sutures are straight and directly transverse on the lateral sides and form deep narrow saddles on the prosiphuncular side; they are 7 mm apart where the conch height is 37 mm (RCL = 0.19).

Another nearly complete specimen is TAM G432:68 (Figs 31C, 41F). This specimen is similarly ornamented to specimen TUG 1672-29 (Fig. 31D). The conch cross section is not preserved. In lateral view, the antisiphuncular conch margin is convex throughout the entire length, the prosiphuncular conch margin is concave in early growth stages and straightens at a position where the conch height is ca 65 mm, resulting in an overall bulged conch shape. The conch reaches a maximum height of ca 73 mm at ca 55 mm from the peristome. Adorad of this, the conch height decreases toward ca 70 mm at the peristome. The conch is also inflated in width. The angles of expansion reach a maximum of ca 37° between conch heights of 31 mm and 43 mm. The sutures are straight and directly transverse on the lateral sides and are 11 mm apart where the conch height is 52 mm (RCL = 0.21). At the base of the body chamber, the conch height is 70 mm. The body chamber has a length of ca 80 mm and is only faintly curved.

Remarks

In the Lyckholm strata, at least three relatively similar species of *Strandoceras* occur (*S. sphynx*, *S. kalevipoegi* sp. nov., and *S. sulevipoegi* sp. nov.). Schmidt's (1858: 200) original description does not allow to specify, which of the three species he referred to. Possibly, Schmidt (1858), more generally referred to the slender morphotype of *Strandoceras*, which these three species represent, but a lectotype designation is not possible because the Schmidt type-material could not be identified. The slender morphotype is also figured in Teichert (1930) under this species (see list of synonymy). For simplicity, it is suggested here, that this slender morphotype is synonymized with *S. sphynx*.

Comparison

Strandoceras kalevipoegi sp. nov. is larger (conch height ca 80 mm), and more strongly curved. *Strandoceras tyriense* (Strand, 1934) and *S. sulevipoegi* sp. nov. is smaller (conch heights are ca 55 mm and 65 mm, respectively) and has a lower angle of expansion during late ontogeny. *Strandoceras schmidti* (Teichert, 1930) and *S. muhvi* sp. nov. differ in having a shorter, more rapidly enlarging conch (compare in Fig. 42A–B).

Strandoceras kalevipoegi sp. nov.
urn:lsid:zoobank.org:act:23EA0987-FD52-4193-98AA-54A085118FB8
Fig. 41E, 42A

Diagnosis

Large *Strandoceras* reaching conch heights of 80 mm; phragmocone strongly endogastrically curved with angle of expansion of up to 35°; mature body chamber ca 80 mm long, contracted, and nearly straight with greatest height at the adapical half of its length; conch surface smooth or with very fine growth lines.

Etymology

From Kalevipoeg, the main hero in the Estonian national epic, Friedrich R. Kreutzwald's (1803–1882) poem ”Kalevipoeg”, referring to the large size of this species.

Type material

Holotype

ESTONIA • Kohila quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 42-431.

Paratypes

ESTONIA • 2 specs; Vormsi Island, Saxby shore (S); Kõrgessaare Formation, Vormsi Regional Stage; TUG 899-54, TUG 899-89 • 1 spec.; Sutlepa quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 80-509.

Description

The holotype is a fragment of parts of an endogastrically curved phragmocone and a mature body chamber, partly preserving the outer shell. The conch surface is preserved near the base of the peristome, where it is smooth or with very fine growth lines, only. In lateral view, the conch margin at the antisiphuncular side is convex throughout the entire length. The prosiphuncular side of the conch margin is concave on the phragmocone and nearly straight on the body chamber. At the base of the body chamber, the conch height is 75 mm. The greatest conch height of 80 mm is located in the lower part of the body chamber, ca 30 mm from its base. The body chamber is ca 80 mm long. The conch cross section of the specimen is not preserved but it was apparently compressed with an oval shape, slightly narrower on the prosiphuncular side with a reconstructed CHI of ca 1.6 at the base of the body chamber. The phragmocone expands with an angle of expansion of up to 14°at conch heights between 62 mm and 72 mm. The sutures form very shallow lateral lobes and distinct narrow saddles on the prosiphuncular

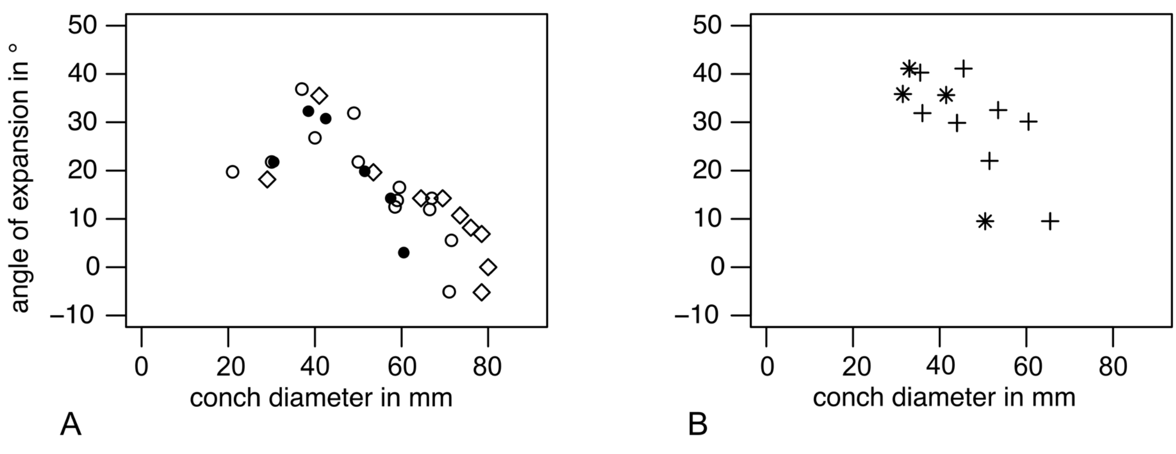


Fig. 42. Diagrams of variability in conch growth in species of *Strandoceras* Flower, 1946. **A**. *S. kalevipoegi* sp. nov. = diamonds; *S. sphynx* (Schmidt, 1858) = white circles; *S. sulevipoegi* sp. nov. = black circles. **B**. *S. muhvi* sp. nov. = crosses; *S. schmidti* = stars. Note that distinction of species in conch fragments with conch heights < 50 mm is not possible based on angle of expansion. Negative angles indicate decreasing conch heights.

side of the conch; they are ca 9 mm apart where the conch height is 72 mm (RCL = 0.13). The peristome is straight and simple with a deep (ca 15 mm) hyponomic sinus on the prosiphuncular side.

The more strongly curved apical sections of the phragmocone are preserved in specimen TUG 899-89. The conch cross section is oval compressed with a narrower margin on the prosiphuncular side. The conch height and width are 36 mm and 32 mm, respectively (CHI = 1.13). The conch expands with an angle of expansion of 35° between conch heights 33 mm and 49 mm.

The details of the siphuncle and the septal necks are well-preserved in specimen TUG 80-509. There, the siphuncle is marginal, the septal foramen has a width of 9 mm, the siphuncular segments expand to 15 mm in height, and the chamber length is 5 mm, where the conch height is 66 mm (RSH = 0.14, RSS = 0.6, SCR = 3). The septal necks are cyrtochoanitic and thick endosiphuncular bullettes are present.

Comparison

This species is unique among *Strandoceras* in reaching adult conch heights of 80 mm, in having a nearly smooth conch surface, and in having a long, nearly straight mature body chamber, which contrasts with the curved rapidly expanding phragmocone.

Strandoceras kohilense sp. nov.
urn:lsid:zoobank.org:act:8C055DE8-1F47-4517-8965-EA9C4D8E8EF5
Figs 43C, 44B

Diagnosis

Strandoceras with drop-shaped conch cross section, narrower at the dorsal conch margin; mature body chamber nearly tubular in shape, slightly curved with maximum conch height of ca 50 mm; distinct hyponomic sinus on concave conch margin.

Type material

Holotype

ESTONIA • Kohila quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 47-883.

Paratypes

ESTONIA • 2 specs; Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-1136, GIT 878-79.

Description

The most complete specimen is TUG 47-883 (Fig. 44C), which is an endogastrically curved fragment of a mature body chamber and four chambers of the phragmocone. The conch surface is not preserved. At the base of the body chamber the height and width are ca 47 mm and 27 mm, respectively (CHI = 1.74), and the elliptically compressed conch cross section has narrow dorsal and ventral margins. The specimen is probably slightly deformed (compressed). The body chamber is in its length of 47 mm completely preserved (RBL = 1). At the aperture, a distinct hyponomic sinus is present on the prosiphuncular side. In lateral view, the prosiphuncular margin is concave and the antisiphuncular margin convex, resulting in a curved tubular shape of the mature body chamber. The angle of expansion of the phragmocone near the base of the body chamber is low (3°), increasing in height between 46 mm and 47 mm at a length of 18 mm. The sutures form shallow lateral lobes and distinct, narrow saddles near the location of the siphuncle; they are 7 mm apart where the conch height is 47 mm (RCL = 0.15). The siphuncle and the septal foramen are too poorly preserved to be measured. The position of the siphuncle is nearly marginal.

Specimen GIT 426-1136 is a fragment of four chambers of the phragmocone and a mature body chamber of nearly identical to TUG 47-883. It is less deformed, and details of the septal foramen are better preserved. At the base of the body chamber, the height and width are 48 mm and 35 mm, respectively (CHI = 1.37). The body chamber is 47 mm long, curved and nearly tubular in lateral view. The sutures form wide lateral lobes and narrow, distinct saddles at the location of the siphuncle, they are 7 mm apart where the conch height is 50 mm (RCL = 0.14). The septal foramen is near the conch margin.

The details of the siphuncle and septal neck are preserved in specimen GIT 878-79 (Fig. 44B). At a conch height of 47 mm, a chamber is 6 mm long, the septal foramen in 4.5 mm high, and the siphuncular segments expand toward a height of 9 mm (RSH = 0.1, RSS = 2, SCR = 1.5). The connecting ring is thin, and the septal necks are cyrtochoanitic. Simple, small endosiphuncular bullettes are present. The connecting ring is hyposeptally adnate.

Remarks

The adult size of *S. kohilense* sp. nov. (mature conch height ca 50 mm) is smaller than in *S. kalevipoegi* sp. nov., *S. sphynx*, *S. sulevipoegi* sp. nov., *S. tyriense*, and *S. muhvi* sp. nov. The species *S. schmidti* differs from *S. kohilense* in having a wider angle of expansion. *Strandoceras kohilense* differs from the other species in having at the base of the mature body chamber, a drop-shaped conch cross section with a margin which is narrower at the dorsal side than on the ventral side. This difference could suffice to erect a new genus. However, nothing is known about the ontogenetic change of the conch cross section in this species, and it cannot be ruled out that the conch cross section is slightly deformed by taphonomic

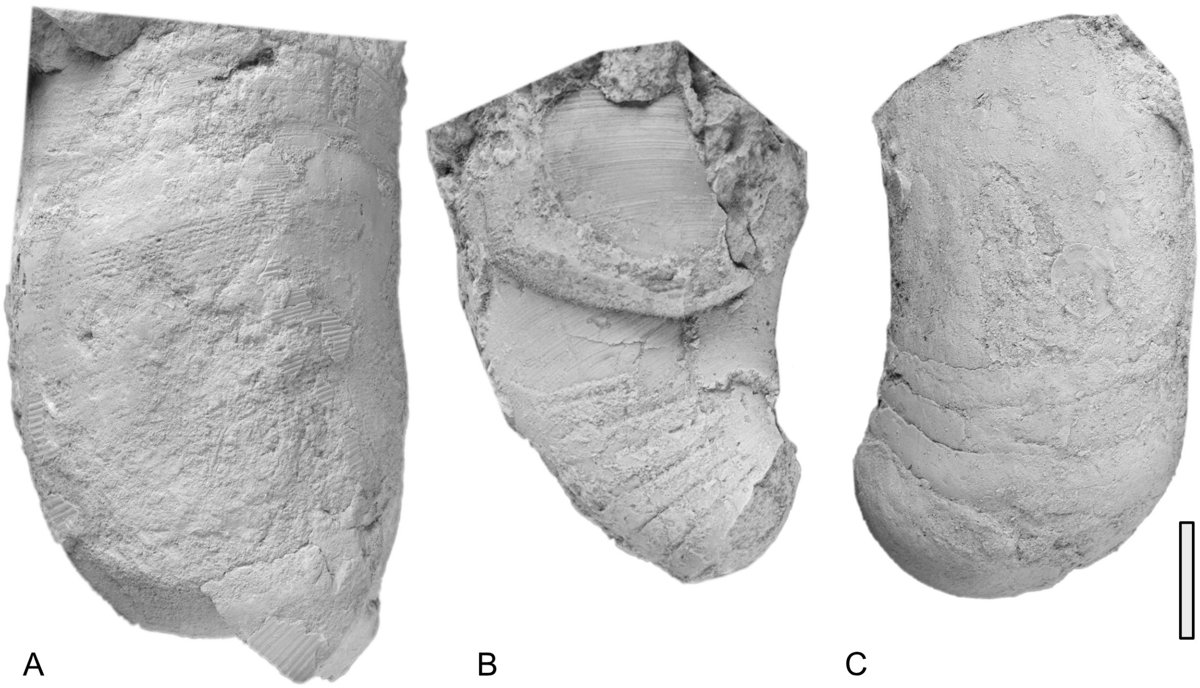


Fig. 43. Fragments of *Strandoceras* Flower, 1946 of the Vormsi–Pirgu regional stages, Estonia. **A**. *Strandoceras sulevipoegi* sp. nov., paratype TUG 899-55, from Saxby shore, Vormsi Island, Vormsi Regional Stage. **B**. *Strandoceras schmidti* (Teichert, 1930), specimen TUG 1745-25, from Salu, Pirgu Regional Stage. **C**. *Strandoceras kohilense* sp. nov., holotype TUG 47-883, from Kohila quarry, Vormsi Regional Stage. Scale = 20 mm, same scale in all figures, all in lateral view.

processes. More material is needed to evaluate the differences between this species and the type species of *Strandoceras*.

Strandoceras muhvi sp. nov.
urn:lsid:zoobank.org:act:06217430-05D8-4FDB-829D-06E6E44D3E05
Figs 41C, 42B, 44A

Diagnosis

Short *Strandoceras* with angle of expansion of up to ca 40°; conch cross section elliptically compressed; maximum conch height ca 65 mm; mature body chamber ca 70 mm long, slightly curved and contracted; ornamented with fine transverse lirae and / or growth bands.

Etymology

Refers to Muhv, a small troll in Eno Raud's (1928–1996) children-book series "Naksitrallid".

Type material

Holotype

ESTONIA • Kohila quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 42-432.

Paratypes

ESTONIA • 1 spec.; Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; TUG 939-58 • 1 spec.; same data as for preceding; GIT 878-27.

Fig. 44. Median sections of phragmocones of *Strandoceras* Flower, 1946, from Saxby shore, Vormsi Island, Vormsi Regional Stage, Estonia. **A**. *Strandoceras muhvi* sp. nov., paratype TUG 939-58. **B**. *Strandoceras kohilense* sp. nov., paratype GIT 878-79. Scale bars = 5 mm.

Description

The most complete specimen is TUG 42-432 (Fig. 41C), which preserves parts of the phragmocone of the adult body chamber, and part of the outer shell. The conch surface is poorly preserved. Near the peristome, traces of transverse lirae or growth bands occur, which are ca 2 mm apart. The complete conch cross section is only preserved at the adapical end. There, the conch height and width are 29 mm and 27 mm, respectively (CHI = 1.07) and it is rounded elliptical in shape. At the base of the body chamber, the conch width can be reconstructed. There, the height and width are 67 mm and 54 mm, respectively (CHI = 1.25). In lateral view, the antisiphuncular margin is convex throughout. The prosiphuncular conch margin is only preserved in the phragmocone, which is concave throughout but with a lower curvature than the antisiphuncular conch margin, resulting in an inflated conch shape with a maximum conch height of ca 65 mm reached at ca 60 mm from the peristome. The complete length of the body chamber is ca 70 mm (RBL = 1.04). The phragmocone expands with an angle of 14°–41° with a maximum reached at conch heights of 41–50 mm (see supplementary data 1 for measurements). The sutures are straight and directly transverse and shallow and narrow, but distinct saddles occur on the prosiphuncular side. Throughout the preserved part of the phragmocone, the sutures are 5–7 mm apart (RCL: 0.12–0.17).

Details of the siphuncle and septal necks are preserved in specimen TUG 939-58 (Fig. 44A). The siphuncle is marginal in position, with a wide septal foramen (ca 9 mm) where the conch height is ca 50 mm (RSH = 0.18). The maximum width of the siphuncle is 15 mm where the chamber length is 4 mm (RSS = 1.7, SCR = 3.75). Thick endosiphuncular bullettes occur. The septal necks are cyrtochoanitic.

Remarks

This species of *Strandoceras* is unique to the genus regarding its high angle of expansion. *S. schmidti* (Teichert, 1930) differs in having a less expanded conch and a smaller adult size (see below).

Strandoceras schmidti (Teichert, 1930)
Fig. 42B, 43B

Codoceras schmidti Teichert, 1930: 297, pl. 8 figs 25–26.

Codoceras schmidti – Strand 1934: 88. — Miller & Youngquist 1947: 13. — Balashov 1953a: 207. — Barskov 1972: 66.
Strandoceras schmidti – Flower in Flower & Teichert, 1957: 57.

Diagnosis

Small, short *Strandoceras* with angle of expansion of up to ca 35°; conch cross section oval compressed, narrower at ventral side; maximum conch height ca 55 mm; mature body chamber slightly curved and contracted; ornamented with fine transverse lirae.

Material examined

ESTONIA • 1 spec.; Salu; Pirgu Regional Stage; TUG 1745-25 • 1 spec.; Lääne-Virumaa, Tapa; Moe Formation, Pirgu Regional Stage; GIT 426-440.

Type locality and horizon

Kose-Uuemõisa, Harju county, Estonia; Vormsi–Pirgu regional stages (“Lyckholm Stufe” of Teichert 1930).

Description

TUG 1745-25 is a fragment of an endogastrically curved phragmocone and body chamber with parts of the outer shell preserved (Fig. 43B). The conch surface is nearly smooth, ornamented only with fine growth lines or growth bands. At the apical end of the specimen, the conch cross section is preserved; it is oval compressed with a narrower margin on the prosiphuncular side, with a conch height and width of 26 mm and ca 24 mm, respectively (CHI = 1.13). The conch height expands with an angle of ca 36° between conch heights of 25 mm and 46 mm. At the base of the body chamber, the conch height is 54 mm. The preserved part of the body chamber is 50 mm long. In lateral view, the antisiphuncular margin is convex throughout the entire length of the conch. The conch margin of the prosiphuncular side is preserved only on the phragmocone and the basal ca 15 mm of the body chamber, it is concave throughout, but straightens adorally. The sutures are straight and directly transverse, 5 mm apart, where the conch height is 34 mm (RCL = 0.15).

The second specimen is less well-preserved, and reliable measurements of angle of expansion and CHI are not possible. The base of the body chamber at this specimen has a height of 43 mm.

Remarks

The type specimen figured in Teichert (1930: pl. 8 figs 25–26), is incompletely preserved, not allowing for a quantification of the angle of expansion, and measurements are not given in Teichert (1930). The diagnosis given herein, therefore, is based on the material described herein combined with the original descriptions in Teichert (1930). A specimen from the Eichwald collection of St Petersburg is described and figured as "*Strandoceras oryx* (Eichwald, 1861)" (sic) in Kiselev (1991), referring to *Phragmoceras oryx* Eichwald, 1857. This specimen, collected from an unspecified locality at Hiiumaa, is similar to *S. schmidti* (Teichert, 1930) in general shape and size. It is therefore possible that *S. schmidti* (Teichert, 1930) is a subjective junior synonym of *Phragmoceras oryx* Eichwald, 1857, and that the specimens described herein under *S. schmidti* should be better placed within Eichwald's (1857) species. However, because the Eichwald material is currently inaccessible, this problem needs to be solved in a future work.

Strandoceras sulevipoegi sp. nov.

urn:lsid:zoobank.org:act:8846BE74-EF9D-437F-B22A-493CB44C1E89

Figs 31E, 41B, D, 42A, 43A

Diagnosis

Strandoceras with relatively slender conch; angle of expansion up to 34°; mature body chamber nearly tubular, slightly endogastrically curved, ca 60–65 mm high and 75 mm long, with an oval compressed conch cross section (CHI ca 1.3) with a narrower prosiphuncular conch margin; ornamented with fine transverse lirae.

Etymology

From Sulevipoeg, a hero in the Estonian national epic, Friedrich R. Kreutzwald's (1803–1882) poem "Kalevipoeg", a friend of Kalevipoeg. See *Strandoceras kalevipoegi* sp. nov.

Type material

Holotype

ESTONIA • Salu; Pirgu Regional Stage; TUG 1745-209.

Paratypes

ESTONIA • 1 spec.; same data as for holotype; TUG 1745-209 • 1 spec.; Förby shore; Pirgu Regional Stage; TUG 1745-176 • 1 spec.; Niibi quarry; Moe Formation, Pirgu Regional Stage; TUG 42-433

• 1 spec.; Paluküla quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-565 • 1 spec.; Salutaguse; Moe Formation, Pirgu Regional Stage; TUG 1745-292 • 1 spec.; Saxby old quarry; Moe Formation, Pirgu Regional Stage; TUG 1745-198 • 1 spec.; Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; TUG 899-55 • 1 spec.; Sutlepa quarry; Adila Formation, Pirgu Regional Stage; TAM G149:26 • 1 spec.; Tapa; Moe Formation, Pirgu Regional Stage; GIT 426-48 • 1 spec.; same data as for preceding; TUG 1239-6 • 1 spec.; Vormsi Island; Vormsi–Pirgu regional stages; TUG 42-399.

Description

Only relatively incomplete fragments are known from this species. They differ from other species of this genus in being more slender. The most complete outline of the relatively weak conch curvature is preserved in specimen TUG 42-399 (Fig. 41D), which is a fragment of the mature body chamber and eight chambers of the phragmocone, but in which the internal characters and the conch width are not preserved. The mature body chamber is preserved in six specimens with conch heights of 62–64 mm (TUG 42-399, TUG 899-55, TUG 1745-176, GIT 426-565, and widths of 48 mm (TUG 899-55, TUG 1239-6) at their bases (CHI = 1.3). The conch cross section is oval with a narrower prosiphuncular conch margin. The total length of the mature body chamber is 75 mm (TUG 42-399, TUG 899-55, TUG 1745-176) (see Fig. 43A). The mature body chamber is slightly endogastrically curved and in lateral view has a convex margin at the antisiphuncular side and a concave margin on the prosiphuncular side. The conch height at the mature aperture is ca 65 mm (specimen TUG 1745-176).

The holotype is a fragment of a phragmocone with a length of ca 140 mm, preserving its relatively weak curvature and low angle of expansion which is 22° between conch heights of 28 mm and 33 mm, and 32° between conch heights of 33 mm and 44 mm (Fig. 41B). The outer shell is preserved in the holotype. It is ornamented with fine transverse lirae or growth bands, similar to those present in *S. sphynx*, but coarser (Fig. 32E). The sutures form shallow lateral lobes, and are 8 mm apart where the conch height is 35 mm (RCL = 0.23). The siphuncle is marginally positioned at the concave side of the conch curvature (endogastric curvature) with widely expanded segments. The width of the septal foramen is ca 6 mm, the width of the siphuncular segment 14 mm, and the chamber length 8 mm where the conch height is ca 50 mm (RSH = 0.12, RSS = 2.3, SCR = 1.75).

Specimen TUG 42-433 is a relatively complete fragment of a phragmocone without outer shell preserved which permits measurement of the trajectory of the angle of expansion (Fig. 42A); it expands with a minimum angle of 3° between conch heights of 60 mm and 61 mm and a maximum angle of 31° between conch heights of 37 mm and 48 mm.

Comparison

This is a relatively slender *Strandoceras*. The conch height at the base of the mature body chamber is 60–65 mm, which is considerably smaller than in *S. kalevipoegi* sp. nov. with a conch height of ca 75 mm, and in *S. sphynx*, which measures ca 70 mm at the base of the body chamber. *Strandoceras tyriense* is smaller (conch height at base of mature body chamber is ca 55 mm) and its phragmocone is more strongly curved.

Discosorida fam., gen. et sp. indet. A
Fig. 45A–B

Material examined

ESTONIA • 3 specs; Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage; GIT 878-188 to GIT 878-190 • 1 spec.; Salu; Pirgu Regional Stage; TUG 1745-26.

Description

All four specimens are isolated, endogastrically curved mature body chambers, without phragmocone parts. They are identical in size and shape. At the base, their height is 44–45 mm, at the aperture the height measures 36–37 mm, and the total length from base to aperture is ca 50 mm. The three specimens from Vohilaid Island are likely to be slightly deformed (compressed) with a width of ca 29 mm at the body chamber base (CHI = 1.5). In specimen TUG 1745-26, the width is 30 mm where the height is 42 mm (CHI = 1.4). The conch cross section is rounded elliptical at mid body chamber position. At the base of the body chamber, the antisiphuncular margin is more narrow, almost rounded angular. In this latter specimen, traces of a fine transverse annulation are preserved, which is directly transverse, indicating that no hyponomic sinus occurs at the peristome. In lateral view, the antisiphuncular margin is convex and the prosiphuncular margin concave. The conch height decreases nearly continuously toward the aperture resulting in maximum conch heights at or near the base of the body chamber. The siphuncle is nearly marginal, but in all specimens is too poorly preserved to be measured in all specimens.

Remarks

The endogastrically curved and contracted body chambers indicate that these belong to an unknown discosorid species, probably a cyrtogomphoceratid. The form of the body chamber (curved, contracted) in combination with a marginal siphuncle is unknown from any multiceratoid genus. However, because details of the siphuncle and the phragmocone remain unknown a firm determination and erection of a new taxon is not possible with the available material.

Discosorida fam., gen. et sp. indet. B
Fig. 46A–B

Material examined

ESTONIA • 1 spec.; Hiiumaa Island, Paluküla quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-1100.

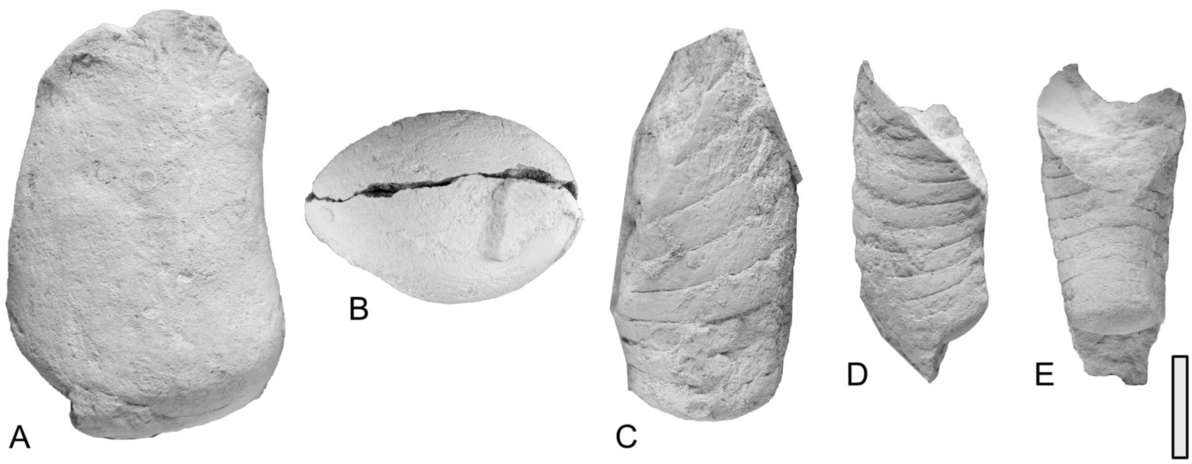


Fig. 45. Fragments of indeterminate Multiceratoidea Mutvei, 2013 of the Vormsi–Pirgu regional stages, Estonia. **A–B**. Discosorida fam., gen., et sp. indet. A, Vohilaid shore (E), Vohilaid Island, Pirgu Regional Stage. **A**. Specimen GIT 878-188, lateral view. **B**. Specimen GIT 878-189, adapical view, position of the siphuncle toward the right. **C–E**. Multiceratoidea fam., gen., et sp. indet. A. **C**. Specimen GIT 840-269, from Hosholm shore (tower) Pirgu Regional Stage, lateral view. **D–E**. Specimen GIT 878-76, from Saxby shore, Vormsi Island, Vormsi Regional Stage. **D**. Lateral view. **E**. View of the concave side of conch curvature, position of siphuncle unknown. Scale bar = 20 mm, same scale in all figures.

Description

The specimen is a fragment of a slightly endogastrically curved body chamber and two chambers of the phragmocone. The outer shell is not preserved. At the base of the body chamber, the conch height is 60 mm. The reconstructed width is 48 mm (CHI = 1.25). The conch cross section is elliptically shaped with narrow dorsal and ventral margins. In lateral view, the prosiphuncular side is concave and the antisiphuncular side convex, resulting in a slightly curved shape and a decreasing conch height. At the adoral-most parts, ca 20–30 mm from the aperture, the margins are slightly more curved, resulting in a slightly ventrally shifted apertural opening. At the aperture, the height is 52 mm. At its base a ca 7 mm wide band with oncomyarian, buttressed muscle scars is present. A hyponomic sinus is preserved on the prosiphuncular side, it is ca 10 mm deep. The body chamber is 53 mm long (RBL = 0.88).

The sutures are straight and slightly deflected adorally at the antisiphuncular side, with shallow saddles at the antisiphuncular side. The two adoral-most sutures are crowded (ca 5 mm apart), the second chamber has a length of ca 8 mm at a conch height of 60 mm (RCL = 0.13). On the adoral-most septum the septal foramen is 9 mm wide and traces of the siphuncular segments indicate a maximum expansion of the siphuncular segments to at least 15 mm (RSH = 0.15, RSS = 1.7, SCR = 1.9).

Remarks

The endogastric condition and the widely expanded siphuncle with weak or absent bullettes indicate that this specimen probably represents an unknown cyrtogomphoceratid species. The specimen differs from species of *Strandoceras* in having a short, contracted mature body chamber. The size of the specimen and the position and size of the siphuncle suggest that this specimen could be related to *Westonoceras estonicum* Balashov, 1959, another likely cyrtogomphoceratid species (not related to *Westonoceras*), which is known only from a single fragmentarily preserved phragmocone from late Katian strata of Tapa, Estonia. More material is needed to test this hypothesis.

Discosorida fam., gen. et sp. indet. C

Fig. 46C–D

Material examined

ESTONIA • 1 spec.; Hiiumaa Island; Kõrgessaare quarry, Vormsi Regional Stage; TUG 1745-284.

Description

The specimen is a mold of a complete mature body chamber. The outer shell is not preserved. The base of the body chamber has a height and width of 40 mm and 28 mm, respectively (CHI = 1.43). The body chamber is 28 mm long (RBL = 0.7). In lateral view, the antisiphuncular margin is convex and the prosiphuncular margin straight or only slightly convex near the aperture. The peristome is simple and straight, a faint hyponomic sinus is present on the prosiphuncular side. The adoralmost ca 5 mm of the body chamber are contracted. At the base, a ca 5 mm a wide band of oncomyarian, buttressed muscle scars is present. The suture is straight and directly transverse. The septal foramen is 5 mm wide and imprints on the septal mode suggest an expanded siphuncular segment with a width of at least 10 mm (RSH = 0.13, RSS = 2).

Remarks

This specimen (probably a cyrtogomphoceratid) is very similar in shape to GIT 426-1100 (Discosorida fam., gen. et sp. indet. B) but it is smaller (height at base of body chamber: 40 mm, against 60 mm in the latter). More, and better persevered material is needed to evaluate the features of the siphuncle to assign this specimen to a (new) species.

Discosorida fam., gen. et sp. indet. D
Fig. 46E–F

Material examined

ESTONIA • 1 spec.; Sutlema old quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 1827-162.

Description

The specimen is a 50 mm long, fragment of a mature body chamber; it is slightly endogastrically curved with a circular conch cross section. At its base, the conch diameter is 40 mm. The suture, as reconstructed from the base of the body chamber, is straight and transverse with a distinct narrow saddle at the position of the siphuncle. The septal foramen is almost marginal with a width of 5 mm (RSH = 0.125). No traces of the outer shell are preserved.

Remarks

This relatively incomplete fragment of a mature body chamber (likely from a cyrtogomphoceratid) is documented herein, because it cannot be assigned to any of the known genera or species known from

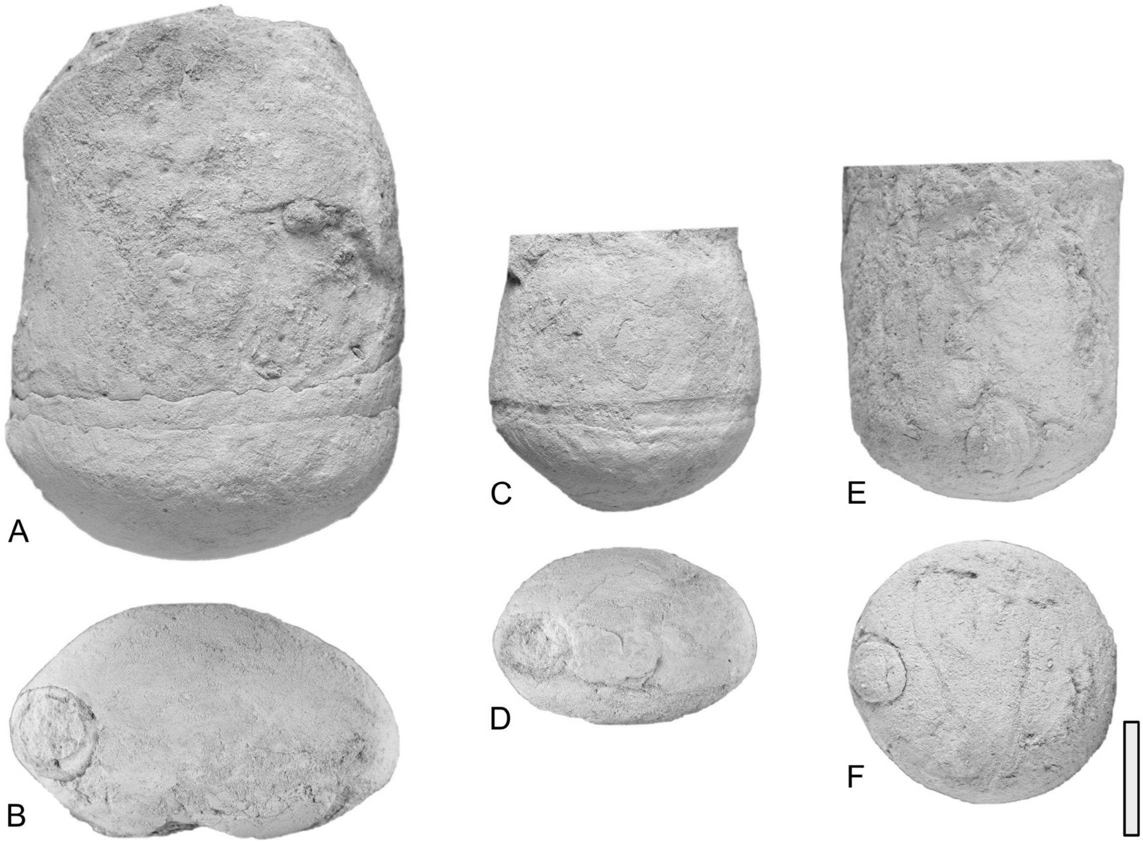


Fig. 46. Fragments of indeterminate Discosorida Flower, 1950 of the Vormsi Regional Stage, Estonia. **A–B**. Discosorida fam., gen. et sp. indet. B, specimen GIT 426-1100 from Paluküla quarry. **A**. Lateral view. **B**. Adapical view. **C–D**. Discosorida fam., gen. et sp. indet. C, specimen TUG 1745-284 from Kõrgessaare quarry, Hiiumaa Island. **C**. Lateral view. **D**. Adapical view. **E–F**. Discosorida fam., gen. et sp. indet. D, specimen TUG 1827-162 from Sutlema old quarry. **E**. View of the prosiphuncular side. **F**. Adapical view, note the discosoroid-like siphuncle. **G**. Adoral view, note the *Kiaeroceras*-like cross-section. Scale bar = 20 mm, same scale in all figures.

Estonia or from the literature. It differs from species of *Kiaeroceras* in being more strongly curved and in lacking the characteristic narrowly rounded prosiphuncular margin. It differs from species of *Strandoceras* in having a circular conch cross section.

Order Tarphycerida Flower in Flower & Kummel, 1950
Family Trocholitidae Chapman, 1857

Genus ***Discoceras*** Barrande, 1867

Type species

Clymenia antiquissima Eichwald, 1842, Kärdla, Hiiumaa Island, Estonia; Vormsi–Pirgu regional stages ("Lyckholm Stufe" of Teichert 1930), late Katian; by secondary designation (Schröder 1891).

Diagnosis

Tarphycerid with slightly to moderately depressed evolute shell with variously spaced frills; caecum subcentral, shifted toward ventral side, the siphuncle shifts in second and third chambers toward dorsal side, its final dorsal or subdorsal position is attained in third septum. (From Manda & Turek 2018: 414.)

Remarks

The genus *Discoceras* was originally erected to encompass species with a subquadratic cross section and a dorsal siphuncle, which are either strongly annulated, such as in the type species or smooth such as in *Lituites angulatus* Saemann, 1853 (Barrande 1867). Subsequently, *Discoceras* has been restricted to the annulated *D. antiquissimum*, and smooth or slightly ribbed forms have been assigned to *Schroederoceras* Hyatt, 1894.

The high ontogenetic and intraspecific variability in ornamentation and whorl cross section led Strand (1934) and Sweet (1958) to the conclusion that it is not possible to distinguish between a smooth or slightly ribbed *Schroederoceras* and a strongly ribbed *Discoceras*. Following Strand (1934: 32–33), *Discoceras* comprises closely coiled forms, with subquadratic to trapezoidal conch cross sections and with a sculpture "formed by imbricate lamellae which overlap in apical direction (…) and ribs, which are either strongly elevated or weaker and more closed set." This concept of *Discoceras* was adopted in the *Treatise* (Furnish & Glenister 1964) and is followed herein. It was not accepted by, e.g., Balashov (1953b), Stumbur (1962), and Dzik (1984).

Furthermore, to tackle the high intrageneric and intraspecific variability of *Discoceras*, Stumbur (1962) erected two new genera (*Rectanguloceras* Stumbur 1962; and *Sweetoceras* Stumbur, 1962), rejected Sweet's (1958) synonymisation of *Discoceras* and *Schroederoceras*, and developed a phylogenetic hypothesis based on these genera (or vice versa). However, Stumbur's (1962) genus diagnoses do not permit effective differentiation between these two novel genera and between *Discoceras* and *Schroederoceras*, respectively. His diagnoses of the two genera are so vague, that they are inapplicable in practice.

In several specimens assigned to *D. roemeri*, and *D. saemanni* the ornamentation is preserved: The external shell is ornamented with finely crenulated, imbricate lamellae, costae or frills (see, e.g., Strand 1934: 37, 44). Additionally, a faint lateral band is visible in a specimen assigned to *D. roemeri* by Kröger (2013: fig. 31a, see below). Several external casts and fragments of the outer shell of species of *Discoceras* are preserved in the Estonian collections, which also show a longitudinal banding, which in a glance resembles a preserved color stripe. Closer examination, however, reveals that this band results from different strengths of the imbricate lamellae: at approximately mid-flank a narrow band is present with exceptionally prominent costae. Ventrally, the frills are more distinct and long: overlapping more strong than dorsal of the band.

Without doubt, the peculiar ornamentation, with a lateral band of elevated costae is a character of taxonomic value. However, it is preserved only under exceptional circumstance and, therefore, probably has never been explicitly described or included within the diagnoses of species of *Discoceras*, it occurs in specimens assigned to *D. saemanni* and *D. roemeri*. The feature probably is related to the "lateral furrow" described in two Silurian species of *Discoceras* by Manda & Turek (2018).

Strand (1934) distinguished two pairs of species of *Discoceras* in the latest Katian strata of Norway based on the shape of the whorl cross section (*D. angulatum*–*D. hyatti*; *D. roemeri*–*D. saemanni*). Each pair supposedly contains a species with a relatively narrow venter (*D. angulatum*, *D. roemeri*) and a species with a broadly trapezoidal cross section and a broad venter (*D. hyatti*, *D. saemanni*). The two pairs, in turn were distinguished by their expansion rate and relative whorl cross section width. However, the new data available from the Estonian material show that the high variability of the shape of the whorl cross section during ontogeny, within and between individual specimens does not permit distinctions between *D. saemanni* and *D. hyatti*, respectively (see below). Herein, *D. hyatti* is interpreted as a junior synonym of *D. saemanni*, leaving three late Katian species to be distinguished: one with a whorl cross section with broadly trapezoidal venter (*D. saemanni*) and two with a relatively narrow venters (*D. angulatum*, *D. roemeri*). *Discoceras angulatum* remains restricted to its genotype until revision. Hence, it is possible that these species represent sexual dimorphs because in many specimens, the relatively broad venter only occurs during late growth stages. A similar distinction between a species of *Discoceras* with a narrow venter and a species with a wide venter can be seen in *D. amtjaernense* Kröger & Aubrechtová, 2019 and *D. nilssoni* Kröger & Aubrechtová, 2019 from the early Katian Kullsberg Limestone, Sweden.

Discoceras antiquissimum (Eichwald, 1842)
Fig. 47C–D, 48A, 49A, 50A

Clymenia antiquissima Eichwald, 1840: 15 (nomen nudum).
Clymenia antiquissima Eichwald, 1842: 33, pl. 3 figs 16–17.
Lituites trapezoidalis Lossen, 1860: 25, pl. 1 fig. 2.

Lituites (*Trocholites*) *antiquissimus* – Schmidt 1861: 62, pl. 6 fig. 2a–g.
Lituites antiquissimus – Roemer 1861: 62, pl. 6 fig. 2f–g (non pl. 6 fig. 2a–e = *Discoceras roemeri* Strand, 1934, see below); 1885: 68, pl. 4 fig. 12. — Karsten 1869: 53, pl. 19 fig. 7a–c.
Discoceras antiquissimum – Foerste 1925: 17, 58, pl. 18 fig. 1. — Strand 1934: 32, pl. 2 figs 4, 11, pl. 4 figs 2–3, pl. 13 fig. 9. — Thorslund 1936: pl. 2 fig. 11. — Balashov 1953b: 265, pl. 12 fig. 1a–b. — Sweet 1958: 99, text-fig. 13q. — Stumbur 1959: fig. d. — Neben & Krueger 1973: pl. 77 figs 24–25. — Dzik 1984: 42, text-figs 9c–d, 12.39, pl. 7 fig. 1.
Discoceras antiquissima — Hucke & Voigt 1967: 58, pl. 15 fig. 1.

Diagnosis

Discoceras with adult conch diameters more than 130 mm, WER of ca 1.9, decreasing with increasing conch size; whorl cross section slightly depressed with WWI 1.2–1.5 becoming less depressed in maturity, broadly reniform in juvenile stages, rounded trapezoidal with venter wider than dorsum in later groth stages; free mature body chamber with constriction near aperture; ornamented with prominent ribs, distance between ribs is one to two times the distance between two septa; siphuncle close to dorsal conch margin, ca 0.15–0.17 of whorl height, septal necks orthochoanitic. (Adopted from Strand 1934.)

Material examined

ESTONIA • 1 spec.; sine loco; Pirgu Regional Stage; GIT 878-152 • 5 specs; Haapsalu holm; Adila Formation, Pirgu Regional Stage; GIT 225-1005, GIT 225-973, GIT 225-974, GIT 426-138, GIT 426-375 • 3 specs; same data as for preceding; TUG 107-43, TUG 46-150, TUG 47-882 152 • 1 spec.;

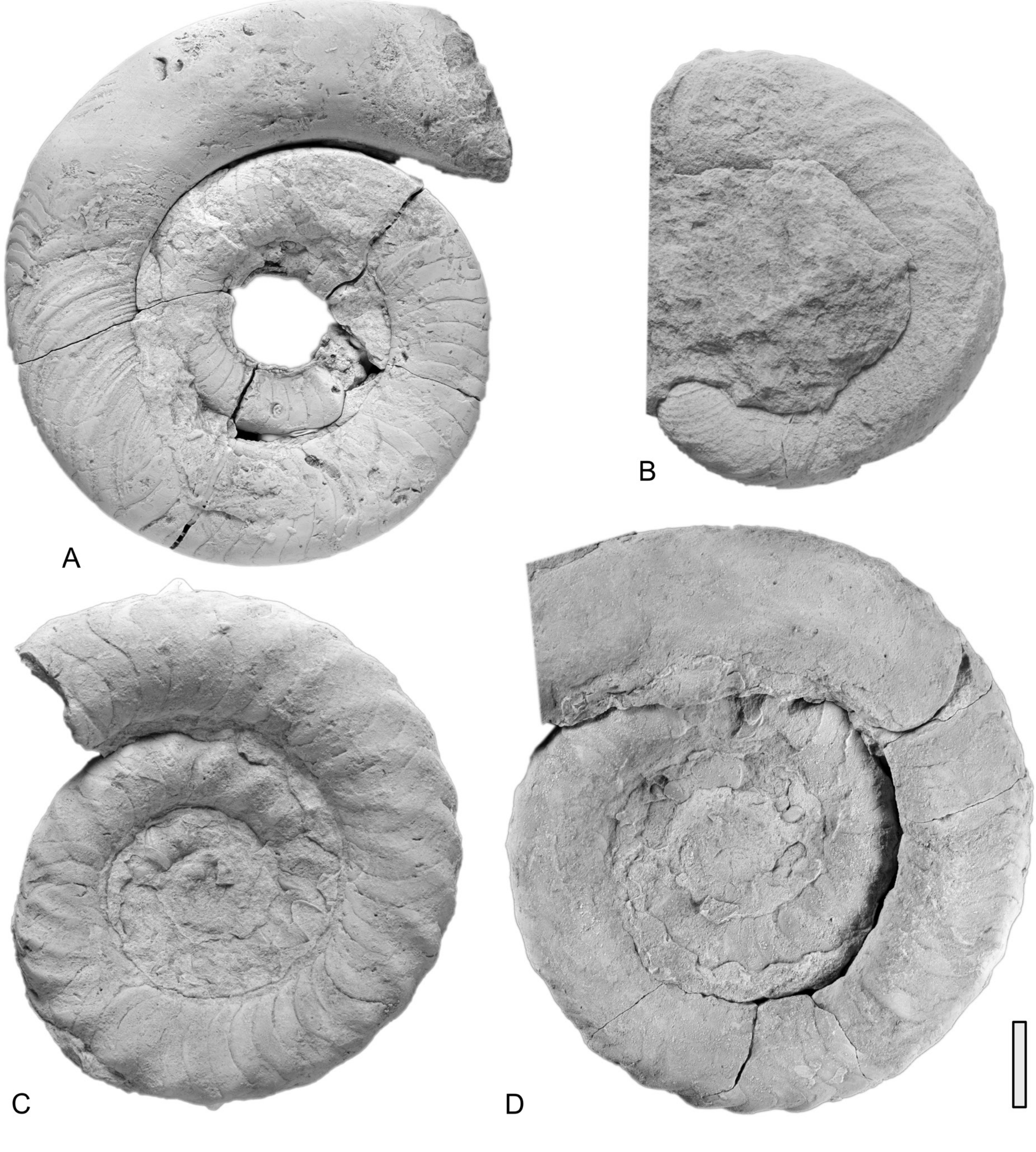


Fig. 47. Annulated species of *Discoceras* Barrande, 1867 of the Vormsi–Pirgu regional stages, Estonia. **A–B**. *Discoceras paopense* sp. nov. from Vormsi Regional Stage. **A**. Paratype TUG 2-730, from unknown locality, Estonia**. B**. Holotype TUG 2-719, Paope limestone quarry, Vormsi Regional Stage. **C–D**. *Discoceras antiquissimum* (Eichwald, 1842) from Pirgu Regional Stage. **C**. Specimen GIT 878-208, from Hosholm shore (tower), Vormsi Island. **D**. GIT 878-148, from Vohilaid (E), Vohilaid Island. Scale bar = 20 mm, same scale in all figures.

Hiiumaa Island, east shore between Heltermaa and Vahtrepa; Pirgu Regional Stage; TUG 66-288 • 6 specs; Vormsi Island, Hosholm shore; Adila Formation, Pirgu Regional Stage; GIT 840-246, GIT 840-247, GIT 840-257, GIT 840-64, GIT 840-90, GIT 840-91 • 2 specs; same data as for preceding; TUG 1743-59, TUG 39-814 • 10 specs; Vormsi Island, Hosholm shore (tower locality); Adila Formation, Pirgu Regional Stage; GIT 840-255, GIT 878-140, GIT 878-141, GIT 878-208 to GIT 878-212, GIT 878-214, GIT 878-221 • 1 spec.; Inju-Meriküla quarry; Ärina Formation, Porkuni Regional Stage; GIT 426-384 • 1 spec.; Kersleti quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 939-67 • 1 spec.; Kohila; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-382 • 1 spec.; Küti, near Viru-Jaagupi; Kõrgessaare Formation, Vormsi Regional Stage; TUG 1745-322 • 1 spec.; Lohu (Pontiaki) springs; Adila Formation, Pirgu Regional Stage; GIT 878-137 • 1 spec.; Mahtra; Pirgu Regional Stage; GIT 426-1080 • 1 spec.; Piirsalu quarry; Moe Formation, Pirgu Regional Stage; TAM G1:170 • 1 spec.; Paluküla quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 225-1017 • 1 spec.; Piirsalu quarry; Moe Formation, Pirgu Regional Stage; GIT 426-381 • 1 spec.; same data as for preceding; TUG 46-153 • 1 spec.; Pirgu river outcrops; Adila Formation, Pirgu Regional Stage; GIT 426-383 • 1 spec,; same data as for preceding; TUG 1745-298 170 • 1 spec.; Rabivere quarry; Moe Formation, Pirgu Regional Stage; TUG 56-113 • 2 specs; Uuemõisa; Adila Formation, Pirgu Regional Stage; TAM G432:504, TAM G432:505 113 • 1 spec.; Vohilaid Island, Vohilaid outcrop 2 (2 and 3 after B. Stein); Adila Formation, Pirgu Regional Stage; GIT 878-145 • 1 spec.; same data as for preceding; TUG 66-287 • 15 specs; Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage; GIT 878-147, GIT 878-148, GIT 878-197, GIT 878-199 to GIT 878-201, GIT 878-204 to GIT 878-206, GIT 878-207, GIT 878-225, GIT 878-313 to GIT 878-316.

Type locality and horizon

Kärdla, Hiiumaa Island, Estonia; Vormsi–Pirgu regional stages (“Lyckholm Stufe” of Teichert 1930).

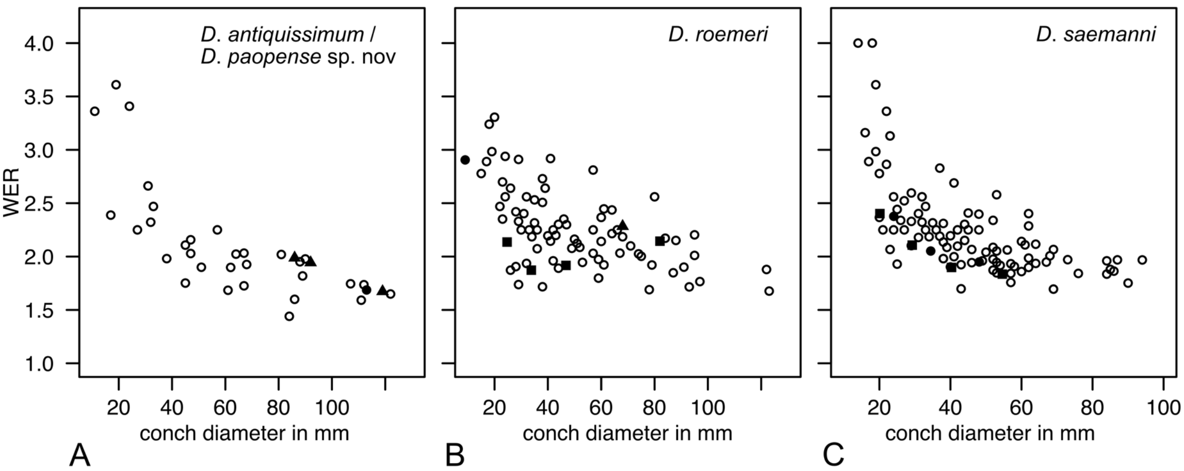


Fig. 48. Whorl expansion rate of species of *Discoceras* Barrande, 1867 of the Vormsi–Pirgu regional stages, Estonia. **A**. WER of *D. antiquissimum* (Eichwald, 1842) (= circles) and *D. paopense* sp. nov. (= black triangles). White circles = Estonian specimens described herein; black circles = specimens described in Strand (1934). **B**. WER of *D roemeri* Strand, 1934. White circles = Estonian specimens described herein; black circles = specimens described in Strand (1934), and in Balashov (1953b); black squares = specimens described as *D. angulatum* (Saemann, 1853) in Strand (1934); black triangles = specimens described as *Schroederoceras balaschovi* Stumbur, 1956 in Stumbur (1956). **C**. WER of *D. saemanni* (Hyatt, 1894). White circles = Estonian specimens described herein; black circles = specimens described in Strand (1934); black squares = specimens described as *D. hyatti* Strand, 1934 in Strand (1934).

Description

The species has been described in detail by Strand (1934). Additional measurements, described herein, contribute to an understanding of the variability of WER and WWI (Figs 48A, 49A; supplementary data 5). The relative whorl width (WWI) decreases with conch size from ca 1.5 at whorl heights of ca 10 mm to 1.0–1.2 in nearly adult specimens (whorl heights 30–35 mm).

The whorl expansion rate (WER) is 1.5–2.0 in nearly adult specimen, but it is considerably higher during early growth stages (maximum 3.6 in specimen GIT 426-138 at a conch diameter of 19 mm).

The largest specimen in the collections is specimen TAM G1:170 (described also in Strand 1934), a complete, mature specimen from Piirsalu, Estonia, Pirgu Regional Stage, with a diameter of 145 mm, a whorl height of 31 mm and a conch width of 31 mm. Whorl heights of 33 mm, and 31 mm, and respective widths of 36 mm and 31 mm, are known from specimen GIT 225-1005, TUG 46-153 from Pirgu Regional Stage.

Remarks

This species is unique to *Discoceras* because of its prominent juvenile to adult annulation. However, the strength of annulation varies between specimens, it appears to be absent in earliest growth stages (Fig. 50A), as well as during latest growth stages (Fig. 47D). The possibility exists that some variants with stronger or weaker annulation represent different species. However, the available material does not permit differentiation between species with different annulation patterns.

Discoceras paopense sp. nov.

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Figs 47A–B, 48A, 49A, 51C

Diagnosis

Discoceras with large adult conch diameters of more than 120 mm, adult WER ca 1.7–2, decreasing with increasing conch size; whorl cross section slightly compressed with WWI 0.8–0.9 in mature stages, with flattened venter not wider than dorsum; free whorl in mature growth stages; ornamented with irregularly spaced costae and distinct shallow ribs, ca three to four costae occur between two ribs, the ribs and the costae run obliquely across the umbilical margin and form a deep U-shaped hyponomic sinus.

Etymology

Refers to the type locality.

Type material

Holotype

ESTONIA • Paope quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 2-719.

Paratypes

ESTONIA • 3 specs; same data as for holotype; GIT 426-114, GIT 426-35, GIT 426-373 • 1 spec.; sine loco; Kõrgessaare Formation, Vormsi Regional Stage; TUG 2-730 • 1 spec.; Vormsi Island, Saxby shore; Kõrgessaare Formation Vormsi Regional Stage; GIT 426-160.

Description

The holotype, TUG 2-719, consists of ⅔ of a mold of a whorl with a conch diameter of 88 mm of which only the apical 33 mm of the phragmocone are preserved in 3D (Fig. 47B). The other parts are strongly flattened, without inner septa and siphuncle preserved. The whorl height at the maximum diameter is 28 mm. At a whorl width of 19 mm, the corresponding whorl height is 19 mm. There, the conch cross section is rounded, subquadratic. At a whorl width of 19 mm, the septal distance is 2–3 mm. The conch surface is ornamented with shallow annulations in a distance of 3–4 mm at the venter combined with distinct striae, which run parallel to the annuli with ca 4–5 striae per cycle of annulations. The annuli and striae form a deep and broadly rounded hyponomic sinus (in the inner whorls of the specimen ca 5 mm deep) and exhibit an apically deflected, curved path over the flanks.

The largest and most complete specimen is TU 2-730 (Fig. 47A). This specimen is a mold of a nearly mature individual with a maximum diameter of 119 mm. The preserved part of the body chamber is 105 mm long and spans nearly 45°, it is detached from the rest of the conch at a diameter of ca 114 mm. The whorl cross section of the adoralmost part of the body chamber has a width of ca 28 mm and a height of 32 mm, at the base of the body chamber the width is 25 mm and the height 28 mm, its umbilical flanks are rounded with the greatest width near the dorsum, the venter is flattened with the flattened part narrower than the umbilical margin. The cross section in a juvenile part of the conch is rounded with a width and height of 14 mm.

The septal distance at the base of the body chamber is 4–5 mm. The sutures form shallow, wide lobes on the umbilical flanks and on the venter and a pointed saddle at the ventrolateral shoulders.

The ornamentation consists of shallow, irregularly spaced, but distinct annuli (at the base of the body chamber ca three occur at a length of 10 mm). Between the annuli, ca two to four costae are present. The ornamentation runs obliquely across the umbilical margins of the whorl and forms a deep broad hyponomic sinus.

Specimen GIT 426-114 is a 75 mm long fragment of a mold of a body chamber with a rounded subquadratic cross section with a whorl width of 30 mm and a whorl height of 26 mm. The specimen

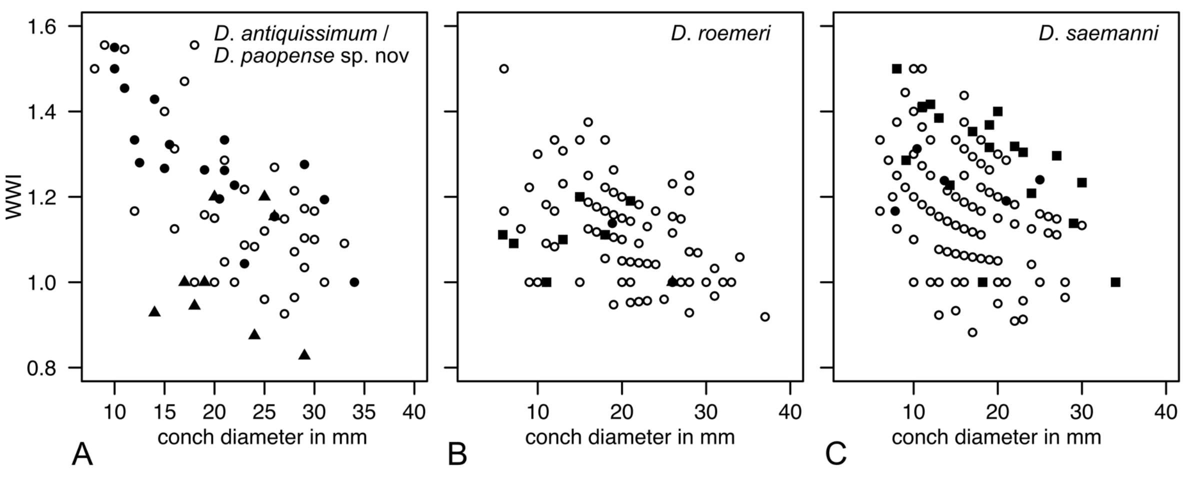

Fig. 49. Whorl width index species of *Discoceras* Barrande, 1867 of the Vormsi–Pirgu regional stages, Estonia. **A**. WWI of *D. antiquissimum* (Eichwald, 1842) (= circles) and *D. paopense* sp. nov. (= black triangles). White circles = Estonian specimens described herein; black circles = specimens described in Strand (1934). **B**. WWI of *D roemeri* Strand, 1934. White circles = Estonian specimens described herein; black circles = specimens described in Strand (1934), and in Balashov (1953b); black squares = specimens described as *D. angulatum* (Saemann, 1853) in Strand (1934); black triangles = specimens described as *Schroederoceras balaschovi* Stumbur, 1956 in Stumbur (1956). **C**. WWI of *D. saemanni* (Hyatt, 1894). White circles = Estonian specimens described herein; black circles = specimens described in Strand (1934); black squares = specimens described as *D. hyatti* Strand, 1934 in Strand (1934).

is ornamented with annuli (ca 3 in a distance of 10 mm) which run obliquely, curved at the flanks adapically and form a deep and U-shaped hyponomic sinus (> 10 mm deep).

Specimen GIT 426-351 is a well-preserved mold of a phragmocone with a rounded subquadratic to trapezoidal cross section with greatest whorl width of 23 mm near the flattened venter and with a whorl height of 20 mm. The ornamentation is identical to that of specimen GIT 426-114. The siphuncular foramen is located at the dorsal margin of the septum and has a diameter of 4.5 mm (RSH = 0.23).

Specimen GIT 426-373 is a fragment of a phragmocone with a rounded subquadratical conch cross section with whorl width 13 mm and corresponding whorl height of 11 mm. The septal distance is 2.5 mm and the siphuncular foramen is located at the dorsal margin with a diameter of 2 mm (RSH = 0.18). The specimen is ornamented with distinct annuli, which run obliquely over the flanks and form a deep U-shaped hyponomic sinus, ca 4 annuli occur per 10 mm.

Remarks

The most complete specimen (TUG 2-230) of this new species cannot serve as a holotype, because it is from an unknown locality (although its stratigraphy, Vormsi Regional Stage, is stated on the label, which is coherent with the distinct Kõrgessaare Formation lithology of the specimen).

Comparison

The new species differs from *D. antiquissimum* in ornamentation. In contrast to the latter, the path of the ornament follows a broad curve obliquely across the umbilical margin of the whorl, forming a deep U-shaped hyponomic sinus. It consists of a succession of alternating strong annuli and weaker costae (ca two to three) in between two ribs. The ornamentation is more similar to that of *D. boreale* Sweet,

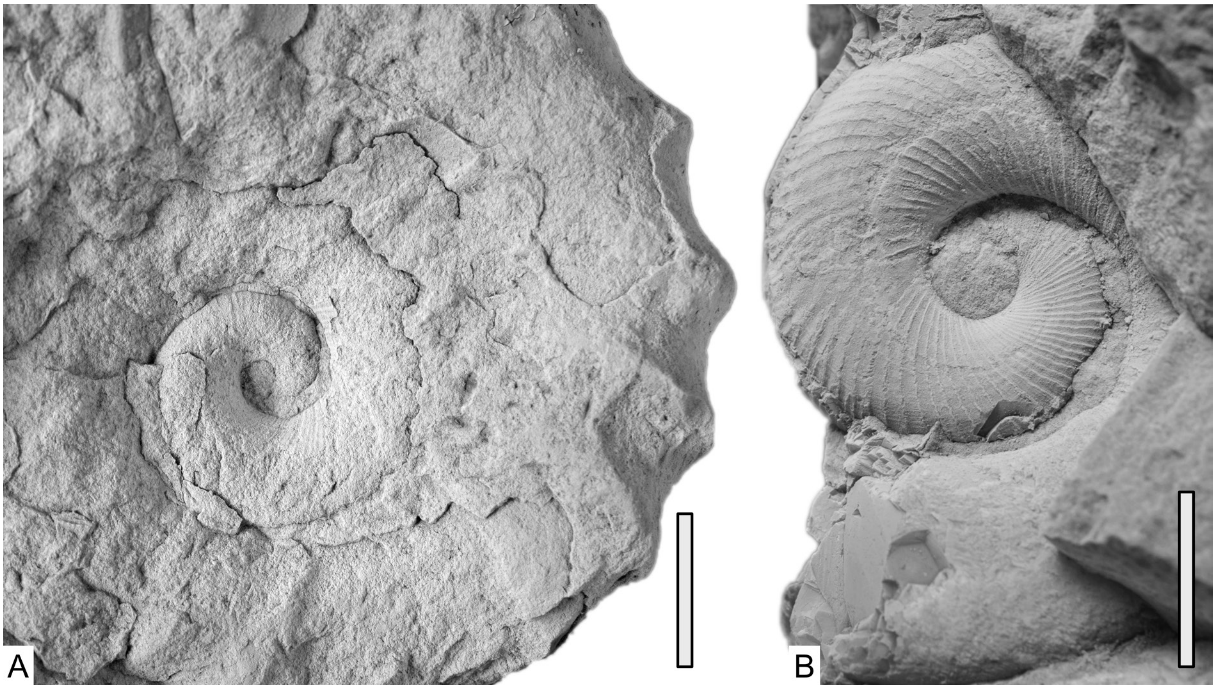

Fig. 50. Early growth stages of species of *Discoceras* Barrande, 1867 of the Pirgu–Porkuni regional stages, Estonia. **A**. *D. antiquissimum* (Eichwald, 1842), specimen GIT 425-375, from Haapsalu holm, Pirgu Regional Stage. **B**. *D. saemanni* (Hyatt, 1894), specimen GIT 426-425, from Röa-Jakobi quarry, Porkuni Regional Stage. Scale bars = 10 mm.

1958, and *D. arcuatum* (Lossen, 1860). *Discoceras paopense* sp. nov. differs from both these species, in having a whorl cross section of the aspect of *D. roemeri* with a flattened venter. The relatively low WWI of *D. paopense* sp. nov. is similar to that of *D. rarospira* (Eichwald, 1860), but the latter species differs in having a more rounded whorl cross section and a siphuncle that is further from the dorsal conch margin.

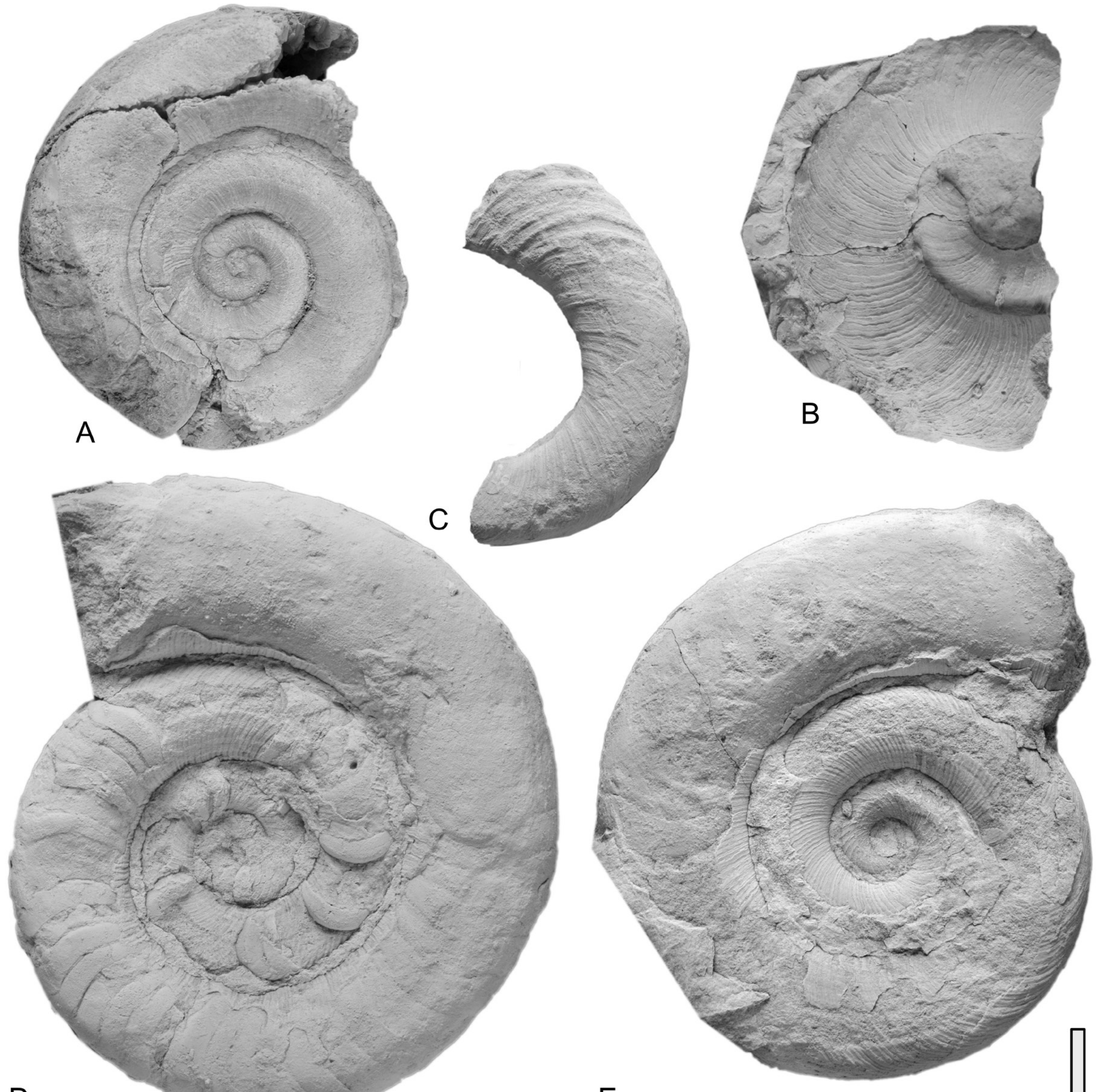

Fig. 51. Species of *Discoceras* Barrande, 1867 of the Vormsi–Pirgu regional stages, Estonia. **A**. *D. saemanni* (Hyatt, 1894), 1934, specimen GIT 426-345, from Saxby shore, Vormsi Island, Vormsi Regional Stage. **B**. *D. roemeri* Strand, 1934, specimen TUG 39-711, from Niibi hillock, Pirgu Regional Stage. **C**. *D. paopense* sp. nov., paratype GIT 426-160, from Saxby shore, Vormsi Island, Vormsi Regional Stage. **D**. *D. roemeri*, specimen TUG 1723-27, from Vohilaid (E), Vohilaid Island, Pirgu Regional Stage. **E**. *D. roemeri*, specimen GIT 878-230, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage. Scale bar = 20 mm, same scale in all figures.

Probably, the specimen assigned to *D. antiquissimum*, and figured in Dzik (1984: pl. 7.1.) from erratic boulders of Poland (collection of Roemer 1861) belongs to *D. paopense* sp. nov. because it has a similar ornamentation. This specimen, however, differs in having a (taphonomically?) depressed whorl cross section.

Discoceras roemeri Strand, 1934
Figs 48B, 49B, 51D, E, 52E, 53

Discoceras roemeri Strand, 1934: 38, 42–43, pl. 2 figs 6a–b, 7, pl. 5 figs 1–2.
Schroederoceras balaschovi Stumbur, 1956: 181, pl. 1 figs 5–6.

Lituites antiquissimus – Roemer 1861: 62, pl. 6 fig. 2a–e (non pl. 6 fig. 2f–g = *Discoceras antiquissimum* (Eichwald, 1840)).
Schroederoceras angulatum – Teichert 1930: 276. — Balashov 1953b: 263, pl. 13 figs 1a–b, 2a–b.
Discoceras angulatum – Mutvei 1957: text-fig. 12, pl. 8.
Discoceras roemeri – Sweet 1958: 99, 102, text-fig. 13p. — Dzik 1984: 41, 44, text-figs 10, 12.43, pl. 6 figs 5–6.
Schroederoceras roemeri – Stumbur 1962: 136, text-fig. 2.4.
Rectanguloceras balaschovi – Stumbur 1962: 142, text-fig. 2.9.
Rectanguloceras (*Discoceras*) cf. *roemeri* – Neben & Krueger 1973: pl. 65 figs 1–2.

Diagnosis

Discoceras with large adult conch diameters of > 140 mm, WER ca 1.9–2.5, decreasing with increasing conch size; whorl cross section slightly depressed with WWI ca 1.1–1.3, rounded, subquadratic with venter not wider than dorsum; body chamber nearly 180° long, free in mature growth stages and becoming markedly higher during mature stages; ornamented with imbricated lamellae, irregularly spaced costae and shallow ribs. (From Kröger 2013.)

Material examined

ESTONIA • 1 spec.; Aulepa quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 895-149 • 1 spec.; sine loco; Vormsi–Pirgu regional stages; GIT 426-379 • 1 spec.; same data as for preceding; TAM G432:597 • 1 spec.; Förby shore; Pirgu Regional Stage; TUG 1745-175 • 1 spec.; Haapsalu holm; Adila Formation, Pirgu Regional Stage; TUG 939-74 • 1 spec.; Vormsi Island, Hosholm shore; Adila Formation, Pirgu Regional Stage; GIT 840-250 • 1 spec.; same data as for preceding; TUG 119-624 • 1 spec.; Vormsi Island, Hosholm shore (tower locality); Adila Formation, Pirgu Regional Stage; GIT 878-230 • 8 specs; Jootma ditch; Moe Formation, Pirgu Regional Stage; GIT 426-368, GIT 426-369, GIT 426-385, GIT 426-403 to GIT 426-405, GIT 426-441, GIT 426-442 • 1 spec.; Kernu quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-380 • 1 spec.; Kohila; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-424 • 1 spec.; Kolu quarry; Pirgu Regional Stage; GIT 426-364 • 4 specs; Kõrgessaare quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-396, GIT 426-400 to GIT 426-402 • 1 spec.; same data as for preceding; TUG 895-68 • 1 spec.; Küti, near Viru-Jaagupi; Kõrgessaare Formation, Vormsi Regional Stage; TUG 1745-324 • 1 spec.; Lehtse; Kõrgessaare Formation, Vormsi Regional Stage; TAM G432:593 • 1 spec.; same data as for preceding; TUG 42-368 • 1 spec.; Moe, Pirgu Regional Stage; GIT 426-366 • 1 spec.; Moe trench; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-106 • 2 specs; Niibi hillock; Moe Formation, Pirgu Regional Stage; TUG 39-711, TUG 42-290 • 1 spec.; Odulemma old quarry; Nabala Regional Stage; GIT 426-365 • 5 specs; Paluküla quarry; Kõrgessaare Formation, Vormsi Regional; Stage; GIT 426-419, GIT 426-420, GIT 426-434, GIT 426-435, GIT 878-135 • 1 spec.; same data as for preceding; TUG 2-732 • 11 specs; Paope quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-1076 to 426-1078, GIT 426-349, GIT 426-350, GIT 426-353, GIT 426-406, GIT 426-407, GIT 426-410, GIT 426-415, GIT 426-417

• 1 spec.; same data as for preceding; TUG 1745-206 • 1 spec.; Röa-Jakobi quarry; Ärina Formation, Porkuni Regional Stage; GIT 426-425 • 1 spec.; Saaremõisa (Lyckholm); Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-122 • 1 spec.; same data as for preceding; TAM G432:680 • 1 spec.; same data as for preceding; TUG 1745-172 • 1 spec.; Saksi manor; Pirgu Regional Stage; TUG 2-284• 1 spec.; Salu; Pirgu Regional Stage; GIT 426-362 • 1 spec.; same data as for preceding; TUG 939-77 • 3 specs; Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-113, GIT 426-343, GIT 426-348 • 1 spec.; same data as for preceding; TUG 44-41 • 8 specs; Vormsi Island, Saxby shore (N); Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-1068, GIT 426-1069, GIT 878-24, GIT 878-29, GIT 878-38, GIT 878-48, GIT 878-52, GIT 878-73 • 1 spec.; Sutlema old quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 1827-164 • 1 spec.; Sutlepa quarry; Adila Formation, Pirgu Regional Stage; TUG 2-651 • 1 spec.; Tapa; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-98 • 2 specs; Vohilaid Island, Vohilaid shore (E); Adila Formation, Pirgu Regional Stage; GIT 878-202, 2GIT 878-203 • 1 spec.; same data as for preceding; TUG 1723-27.

Type locality and horizon

Herøya, near Porsgrunn, Norway; Herøya Formation ("Gastropod limestone"), latest Katian Stage (Strand 1934).

Description

Specimen GIT 878-230 is an exceptionally well-preserved, complete mature specimen (Figs 51E, 52E). This specimen has a conch diameter of 123 mm, the base of the body chamber is at a conch diameter of 105 mm. The body chamber is 107 mm long and extends around ca ¼ of a volution. The body chamber diverges from the rest of the conch at ca 112 mm. The sutures form wide lobes over the umbilical margin and are nearly straight at the venter. They are ventrally 10 mm apart where the corresponding conch diameter is 105 mm. At the aperture, the whorl is slightly constricted and forms wide U-shaped hyponomic sinus. At the aperture, the whorl cross section is subquadratic with a rounded venter, the whorl cross section has a distinctively flattened venter at the base of the body chamber. There, the whorl width, and height are 33 mm, and the umbilical margins are slightly rounded with their greatest width near the mid-flank. At a conch diameter of 69 mm, the whorl cross section has a width of 29 mm and a height of 27 mm, and the venter is distinctively flattened. There, the umbilical margins are rounded with greatest width at mid-flanks. The path of the ornament follows a broad U-shaped hyponomic sinus on the venter (Fig. 52E). The costae are irregularly spaced: at a conch diameter of 80 mm, ca six to seven occur at a length of 10 mm at the venter. On the first three whorls at ca mid-flank position, a 2–3 mm wide band is present in which the lamellae are slightly more pronounced and thicker. Ventrally of that band, the lamellae generally appear to be slightly longer, creating a stronger relief. On the external cast of this specimen, parts of the shell are attached at the position of the longitudinal band and ventrally, giving the false impression of a longitudinal color banding (see also Fig. 52C).

Four specimens are preserved with the mature divergence of the body chamber; in one of them the divergence occurs at a conch diameter 93 mm (TUG 1745-175); in the others it occurs at diameters 118 mm (GIT 878-230), 124 mm (TUG 1723-27) (Fig. 51D), and 125 mm (TUG 2-651). The only complete adult specimens in the collection are GIT 878-230, and TUG 1723-27 with adult diameters of 124 mm and 128 mm, respectively.

Remarks

The specimens described by Balashov (1953b) under *Schroederoceras roemeri*, represent a different species. Based on similarities in ornamentation and siphuncular position, they are probably related to *D. boreale* Sweet, 1958.

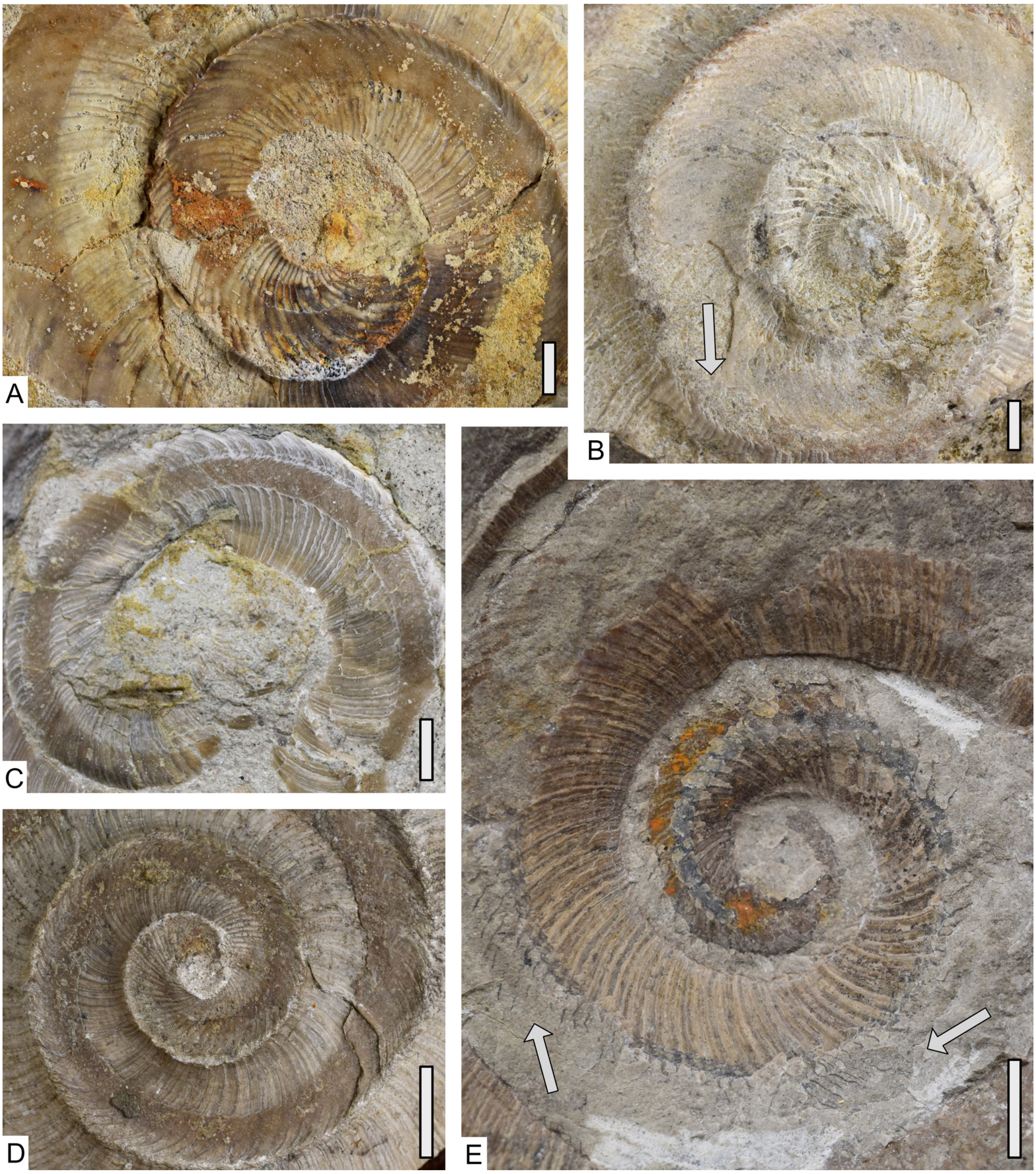

Fig. 52. Details of the ornamentation of species of *Discoceras* Barrande, 1867 of the Vormsi–Pirgu regional stages, Estonia. **A–D**. *Discoceras* sp. **A**. Specimen TUG 42-371, from Kohila, Vormsi Regional Stage. **B**. Specimen TUG 1745-212, from Saxby shore, Vormsi Island, Vormsi Regional Stage. **C**. Specimen TUG 1745-203, from Paope quarry, Vormsi Regional Stage. **D**. Specimen TUG 2-726, from Saaremõisa (Lyckholm), Vormsi Regional Stage. **E**. *D. roemeri* Strand, 1934, specimen GIT 878-230, from Hosholm shore (tower), Vormsi Island, Pirgu Regional Stage. Arrows mark areas in which the partly imbricated strong crenulation is well-preserved and visible. Scale bars = 5 mm in all figures.

The finely transversely lamellate or costate conch surface (Fig. 52) is not preserved in most specimens because it is often firmly attached to the external sediment. During natural weathering or artificial preparation, the shell splits from the smooth, inner cast of the specimen and the surface of its external side remains invisible. In few, exceptionally preserved specimens, a peculiar ornamentation is visible: in superficial view it is longitudinal banded, giving the impression of a color band at approximately mid-flank position (compare, e.g., Kröger & Aubrechtová 2019: fig. 5). The apparent banding, however, is produced by subtle differences in ornamentation between the dorsal part of the flank and the ventral part of the flank and the venter: the frills or crenulate lamellae are deeper and more pronounced at the ventral section of the flank.

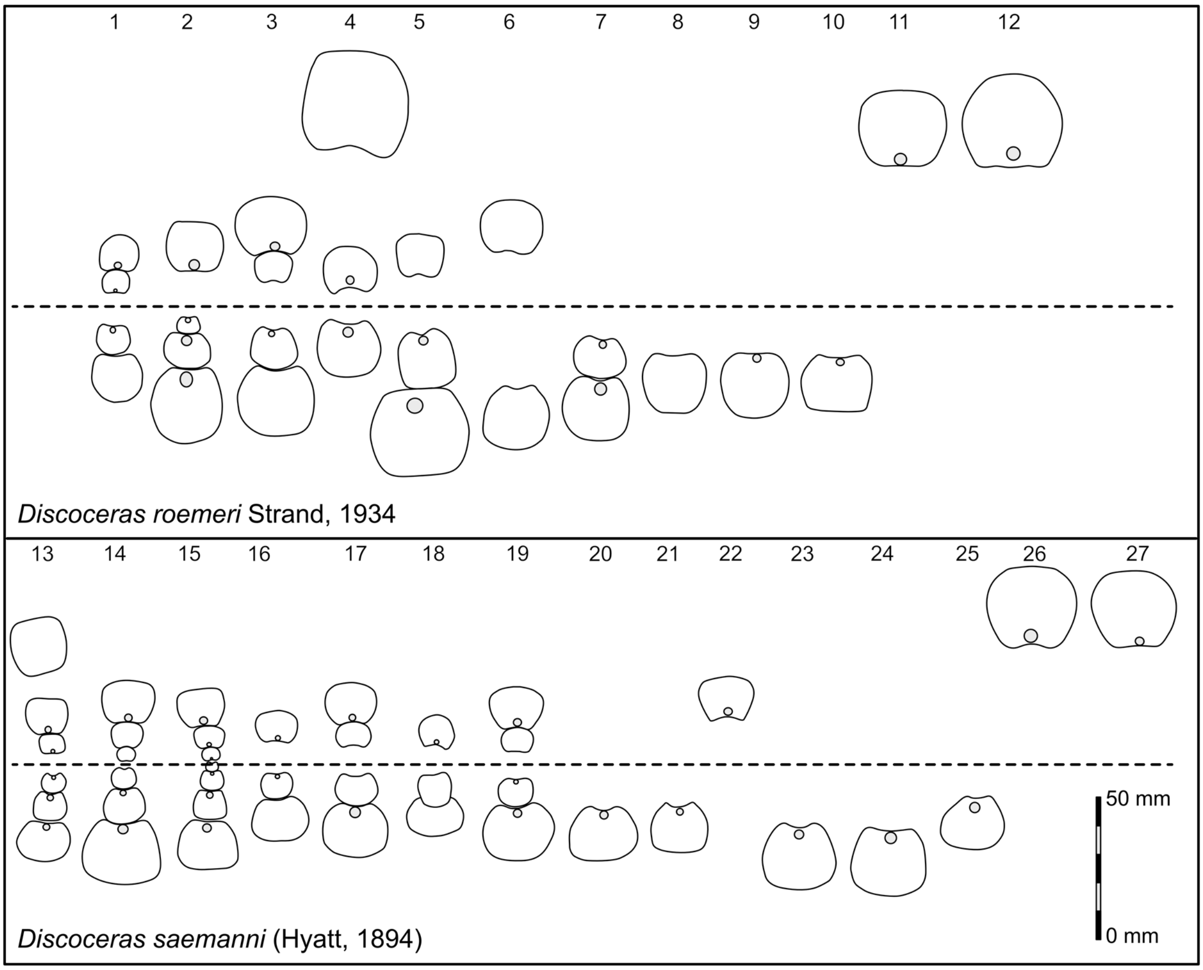

Fig. 53. Camera lucida drawings of whorl cross-sections of specimens assigned to *Discoceras roemeri* Strand, 1934 or *Discoceras saemanni* (Hyatt, 1894) of the Vormsi–Pirgu regional stages, Estonia. Note the high ontogenetic and interspecific variability, and the taphonomic distortion among the specimens. Numbers refer to specimens: **1**. GIT 426-348. **2**. GIT 840-250. **3**. GIT 878-68. **4**. TUG 1745-175. **5**. GIT 426-425. **6**. GIT 426-109. **7**. GIT 426-357. **8**. GIT 426-365. **9**. GIT 426-364. **10**. GIT 426-1074. **11**. GIT 426-343. **12**. TUG 42-290. **13**. TUG 939-65. **14**. TUG 72-342. **15**. TUG 1745-59. **16**. GIT 878-69. **17**. GIT 426-358. **18**. GIT 878-56. **19**. TAM G432:598. **20.** GIT 426-361. **21**. GIT 426-355. **22**. TUG 42-367. **23**. TAM G432:503. **24**. GIT 426-354. **25**. TUG 939-66. **26**. GIT 426-107. **27**. GIT 426-363 (see file 1 for specimen details).

Comparison

The holotype of *D. roemeri* is a large, mature specimen (conch diameter ca 140 mm, Strand 1934: 45). In comparison, the holotype of *D. angulatum*, which also is a complete mature specimen and the only type specimen of this species (see Strand 1934), is small (diameter ca 90 mm, Strand 1934: 37). The shape of the whorl cross section of *D. roemeri* is described as "rounded quadrangular" (Strand 1934: 43), whilst that of *D. angulatum* was described as "subquadrangular […] with the venter narrower than the dorsum" (Strand 1934: 37). Additionally, the length of the mature body chamber differs between the types of the two species: in *D. roemeri* it is ca ½ of a volution, whilst it is only ¼ of a volution in *D. angulatum*. The types of *D. angulatum* and *D. roemeri* differ also in WWI, with *D. angulatum* having a smaller WWI at a comparable conch size (Fig. 49B; supplementary data 5). Despite these differences in the types, it is impossible to distinguish between the two species in the Estonian material.

The WWIs of the Estonian specimens assigned to *D. roemeri*, herein, are generally lower than of the Norwegian types of this species at comparable growth stages, and are more similar to that of the type of *D. angulatum* (Fig. 49B). However, several of the measured specimens in the Estonian collections are also larger than 90 mm in conch diameter, and therefore could only be placed within *D. angulatum* after emending the diagnosis of this species and accepting larger adult conch diameters. To distinguish different species based on WWI is not possible, as no sharp boundaries exist between the two groups.

Distinction between the two species based on the whorl cross sections is also not possible in the Estonian material. Many interspecific and ontogenetic variations of *D. angulatum*-like and *D. roemeri*-like whorl cross section shapes occur in the Estonian material, with a flattened, slightly rounded venter, and subquadratic to broadly reniform shapes (Fig. 53; also compare Strand 1934: pl. 2 figs 3, 5–7). This is also the case in a specimen figured by Kröger (2013: fig. 32a) assigned to *D. roemeri*, where the premature whorl cross section is almost identical to that of the adult *D. angulatum*. It is therefore impossible to distinguish between *D. angulatum* and *D. roemeri* in premature specimens with conch diameters < 90 mm.

Furthermore, the available material does not permit distinctions between two or more size classes of maturity. Among the seven type specimens of *D. roemeri* described by Strand (1934), four have a conch diameter of more than 130 mm. The Estonian material contains four mature specimens belonging to the *D. angulatum*–*D. roemeri* group, three of them have mature conch diameters of more than 120 mm (see above). An additional specimen with a mature conch diameter of ca 100 mm is known from Balashov 1953b: pl. 13 fig. 1a–b, described under *Schroederoceras angulatum*. With these data it is not possible to distinguish between clearly constrained size-groups of *D. roemeri* and *D. angulatum*.

Too little is known about the intraspecific and ontogenetic variability of the length of the body chamber. Significant differences exist between specimens described, herein (compare Fig. 51D–E). However, the low number of specimens with complete body chambers available does not permit the detection of sets of features covarying with the body chamber length. Future work (that includes the Norwegian material) may show whether *D. roemeri* is a subjective junior synonym of *D. angulatum* or if both species represent distinct groups. Therefore, for practicality, herein, we assign specimens with a *D. angulatum*–*D. roemeri* aspect to the latter and reserve *D. angulatum* to specimens with small adult size and an adult conch cross section identical to the type of this species.

Discoceras roemeri differs from *D. saemanni*, which also has a distinctively flattened venter, in having a whorl cross section with greatest width between the venter and the dorsum, but not strictly at the venter. Throughout the entire length of the conch, the umbilical margins are generally more rounded in *D. roemeri* compared to *D. saemanni*. The average WER of mature *D. roemeri* is ca 1.8–1.9; slightly lower than that of mature *D. saemanni* (WER ca 2.0) (compare Fig. 48B–C for ontogenetic trends; supplementary data 5).

Discoceras saemanni (Hyatt, 1894)
Figs 48C, 49C, 50B, 51A, 53

Lituites angulatus Saemann, 1853: 166, pl. 21 fig. 1c–d, (not 1a–b).
Trocholites undosus Foord, 1891: 45.
Schroederoceras saemanni Hyatt, 1894: 462.
Discoceras hyatti Strand, 1934: 38–39, pl. 2 fig. 2, pl. 5 fig. 3a–b.

Discoceras sp. – Foerste 1929: 176, pl. 20 fig. 2a.
Discoceras saemanni – Strand 1934: 40–42, pl. 2 fig. 1a–b, pl. 4 fig. 1. — Sweet 1958: 102, fig. 13n.
Discoceras hyatti – Sweet 1958: 102, fig. 13g. — Dzik 1984: 44, text-fig. 12.43.
Schroederoceras hyatti – Stumbur 1959: 26, fig. 1v.
Schroederoceras saemanni – Stumbur 1962: 137.

Emended diagnosis

Discoceras with adult conch diameters of up to ca 125 mm; mature WER of ca 2.0; mature whorl cross section with WWI ca 1.1–1.2, subtrapezoidal with flattened venter, venter considerably wider than dorsum except at adult aperture and in juvenile growth stages; WER and WWI decrease with conch size; free mature body chamber with constriction near aperture; ornamented with crenulated costae and distinct growth lines that form a U-shaped hyponomic sinus, low ribs can occur.

Material examined

ESTONIA • 1 spec.; sine loco; Vormsi Regional Stage; TAM G432:598 • 2 specs; same data as for preceding; TUG 1745-59, TUG 666-298 • 3 specs; Hosholm shore; Adila Formation, Pirgu Regional Stage; GIT 426-354 to GIT 426-356 • 1 spec.; Imastu old quarry; Kõrgessaare Formation, Vormsi Regional Stage; TUG 42-366 • 1 spec.; Jootma ditch; Moe Formation, Pirgu Regional Stage; GIT 426-1137 • 1 spec.; Kersleti; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-377 • 3 specs; Kõrgessaare quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-361, GIT 426-395, GIT 426-429 368 • 1 spec.; Moe stratotype outcrop; Moe Formation, Pirgu Regional Stage; TUG 42-367 • 1 spec.; Moe trench; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-107 • 2 specs; Niibi hillock; Moe Formation, Pirgu Regional Stage; GIT 426-357, GIT 426-358 • 3 specs; same data as for preceding; TAM G432:423, TAM G432:424, TUG 939-66 • 1 spec.; Oru manor; Kõrgessaare Formation, Vormsi Regional Stage; TUG 2-715 • 1 spec.; Paluküla quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-422 • 2 specs; same data as for preceding; TUG 47-880, TUG 66-294 • 8 specs; Paope quarry; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-159, GIT 426-352, GIT 426-408, GIT 426-413 to GIT 426-416, GIT 426-1074, GIT 426-1075 • 1 spec.; Rannaküla old quarry; Adila Formation, Pirgu Regional Stage; GIT 426-360 • 1 spec.; Saaremõisa (Lyckholm); Kõrgessaare Formation, Vormsi Regional Stage; TUG 72-342 • 1 spec.; Salu; Pirgu Regional Stage; GIT 426-36377 • 20 specs; Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; GIT 426-107, GIT 878-155, GIT 426-109, GIT 426-112, GIT 426-342, GIT 426-344, GIT 426-345, GIT 426-347, GIT 878-155, GIT 426-1071 to GIT 426-1073, GIT 878-17, GIT 878-22, GIT 878-56, GIT 878-64, GIT 878-66 to GIT 878-69 • 12 specs; same data as for preceding; TUG 39-710, TUG 44-40, TUG 66-290 to TUG 66-292, TUG 119-625, TUG 666-296, TUG 939-65, TUG 1666-16, TUG 1743-36, TUG 1743-5, TUG 1745-214 • 1 spec.; Sutlepa quarry; Adila Formation, Pirgu Regional Stage; GIT 426-359 • 2 specs; same data as for preceding; TAM G432:502, TAM G432:503 • 1 spec.; same data as for preceding; TUG 39-706 • 1 spec.; Tapa; Kõrgessaare Formation, Vormsi Regional Stage; TUG 1745-22.

Table 2. Results from a two sample Student's t-test between x: combined measurements from Strand's (1934) type specimens of *Discoceras hyatti* Strand, 1934, and *Discoceras saemanni* (Hyatt, 1894) (n = 25) and y: Estonian specimens assigned to *Discoceras saemanni*, herein (n = 157). The null hypothesis that the means of the two populations are equal cannot be rejected for WER.

	t-statistic	degrees of freedom	p-value	mean x	mean y
WER	-1.69	9.19	0.13	2.09	2.25
WWI	4.00	37.7	<0.005	1.28	1.72

Type locality and horizon

Herøya, near Porsgrunn, Norway; Herøya Formation ("Gastropod limestone"), latest Katian Stage (Strand 1934).

Description

The species has been described by Strand (1934) based on Saemann's (1853) specimen of *Lituus angulatus* and three additional specimens of *D. saemanni*, all of them have conch diameters of more than 100 mm, the largest has a mature diameter of 125 mm. The two specimens, described by Strand (1934) under *D. hyatti*, are smaller, with mature conch diameters of 84 mm and 95 mm, respectively. In three specimens of the Estonian material, the mature divergence of the body chamber is preserved; it occurs at a conch diameter of 74 mm in TUG 1745-214, and at 110 mm in GIT 426-425.

GIT 426-425 is a fragment of a mature specimen with the complete adult body chamber preserved (Fig. 50B). The diameter at the base of the body chamber is ca 100 mm. The body chamber is ca 100 mm long and has a trapezoidal cross section at its base. There, it is widest at the venter with a width of 34 mm and a height of 30 mm (WWI = 1.13). The adult aperture has a subquadratic, rounded cross section and a width of 32 mm. The specimen has a subquadratic conch cross section at a diameter of 33 mm with a conch width of 15 mm and corresponding conch height of 11 mm (WWI = 1.36). At a conch diameter of 51 mm, the conch cross section is rounded subquadratic with a flat venter and a maximum width at mid-flank of 18 mm, and with a corresponding height at 17 mm (WWI = 1.06).

A change from a subquadratic whorl cross section with maximum width at mid-flank to trapezoidal whorl cross section with its maximum width at the venter occurs at conch diameters of ca 40–50 mm and corresponding conch widths of 16–17 mm (e.g., TUG 1745-59, GIT 426-345, GIT 426-354, GIT 426-425, GIT 426-1072).

The ornamentation is well-preserved in specimens GIT 426-425 and 426-391, where it forms well-developed, irregularly spaced, crenulated costae or frills which are imbricated toward the aperture, and which form a wide U-shaped hyponomic sinus. The costae are more regularly spaced in juvenile portions (first one–two volutions), with a distance of ca 1 mm at the venter; they are less distinct in later growth stages and on the mature body chamber with a distance of ca 1–1.5 mm at the venter. In specimen GIT 426-425, a distinct band is apparent at mid-flank in the first two whorls, where the frills appear to be more elevated and broken off the remainder of the shell. On the initial ca two volutions of specimen GIT 878-67, the costae are developed more strongly at distances of 3–4 mm, forming low ribs. In specimen GIT 878-67, the mold preserves the ornamentation and the septa and shows that ca three costae occur in the distance between two successive septa on the second volution. Identical features of the ornamentation are best preserved and figured, in specimens assigned herein to *Discoceras* sp. (Fig. 52A–C).

The features of the siphuncle and septal neck are well-preserved in specimen GIT 426-107. The siphuncle is located at the dorsal margin of the whorl throughout its preserved length (conch diameter 41–92 mm). At a conch diameter of 92 mm, the whorl height is 24 mm, and the diameter of the septal foramen is 4 mm (RSH = 0.17), and the septal distance is 4.5 mm. At a position with whorl height 19 mm, the septal foramen is 2.5 mm in diameter (RSH = 0.13); the septal distance is 4 mm. The septal neck is straight, suborthochoanitic and 1.5 mm long. The connecting ring is 0.7 mm thick, reaching its greatest thickness near the adapical part of the segment.

Remarks

The emendation herein regards the variability of the adult size (given as ca 120 mm in Strand 1934), and the WWI (given as 1.2–1.5 in Strand 1934). Because of the high ontogenetic variability of this character, the range of the mature WWI rather than its total range throughout the growth of the conch (as used by Strand 1934) is included in the diagnosis. The maximum adult size is taken from the largest of the types described by Strand (1934: 41) under this species.

Strand (1934) distinguished *D. saemanni* from *D. hyatti* based on the whorl cross section (wider in the former) and by the expansion rate (lower in the latter). However, a comparison of the WWI and WER of the types of Strand (1934) reveals that these differences are well within the variability of the Estonian sample (see Fig. 48C). The combined samples of *D. saemanni* and D. *hyatti* from Norway (i.e., the Strand 1934 types) and from Estonia differ in WWI but not in WER (see Table 2). However, the variation between specimens appears to form a continuum between the extremes. Therefore, a distinction between two species based on expansion rate and whorl shape is practically impossible with the available material.

Additionally, the ontogenetic trends between the types of *D. saemanni* and *D. hyatti* differ, their WWI decreases with conch size in the former, and it remains relatively constant in the latter (see, e.g., Strand 1934: pl. 2 figs 1–2; Fig. 49C). However, the Estonian material contains specimens with decreasing, increasing, and nearly constant WWI trends, and specimens in which WWI initially increases and later decreases. In total, these trends result in a decreasing WWI–conch size relation (Fig. 49C) and it is impossible to distinguish morphologically well-delimited groups among them.

Strand (1934) also mentioned the ornamentation as a feature that distinguishes *D. saemanni* from *D. hyatti*, but it remains unclear what exactly these differences are. In both species, he described similar distinct costae and growth lines and the occurrence of low ribs during juvenile growth stages. In the Estonian material, it was not possible to distinguish two or more groups based on differences in ornamentation. Consequently, *D. hyatti* is interpreted as a junior synonym of *D. saemanni* herein.

Comparison

Discoceras saemanni differs from *D. roemeri* and *D. angulatum* in having a whorl cross section with greatest width at the venter. In *D. roemeri* and *D. angulatum*, the greatest width occurs at a position of the umbilical shoulders but not at the venter. In *D. roemeri* and *D. angulatum*, the umbilical shoulders are generally more rounded throughout their conch lengths.

In several specimens of *D. saemanni*, the whorl cross section changes during ontogeny from rounded, subquadratic or depressed reniform in early growth stages to trapezoidal with greatest width at the venter during later ontogeny (Fig. 53). This change occurs at diameters of smaller than ca 50 mm, and at whorl widths smaller than 17 mm. It is therefore impossible to distinguish between *D. saemanni*, *D. roemeri*, and *D. angulatum* in specimens with diameters below ca 50 mm, and with whorl widths below 17 mm when the whorl cross section is not unambiguously trapezoidal. However, in several specimens assigned to *Discoceras saemanni* (including a specimen figured in Strand 1934: pl. 2 fig. 1a), a trapezoidal whorl cross section with its greatest width at venter appears already from the first volution onward, making such a distinction possible. As a general ontogenetic trend, a change from a more rounded toward a more flattened venter occurs in all specimens (Fig. 53). In mature specimens, however, the aperture, again, is rounded and has no flattened venter. A considerable intraspecific and ontogenetic variation occurs also in ornamentation of *D. saemanni*, with at least one specimen (GIT 426-1072), showing an annulation on the inner two whorls.

The embryonic shells of specimens assigned to *D. hyatti* and *D. antiquissimum* have been described by Stumbur (1959). In both species, the first whorl is tightly coiled, leaving no or only a very narrow umbilical window and comprising five (*D. hyatti*) to seven (*D. antiquissimum*) chambers. The diameters of the embryonal shell are 10.1 mm for *D. hyatti*, and 14.7 mm for *D. antiquissimum* (Stumbur 1959). In both species the siphuncle starts near the venter in the first chamber, perforates the first septum slightly ventral from the whorl center and reaches a nearly dorsal position at the 3rd to 4th septum (Stumbur 1959).

Multiceratoidea gen. et sp. indet. A
Fig. 45C–E

Material examined

ESTONIA • 1 spec.; Pirgu River outcrops; Adila Formation, Pirgu Regional Stage; TUG 1745-299 • 1 spec.; Vormsi Island, Hosholm shore (tower outcrop); Adila Formation, Pirgu Regional Stage; GIT 840-269 • 1 spec.; Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stage; GIT 878-76.

Description

GIT 840-269 (Fig. 45C) is a fragment of a phragmocone, exogastrically curved with an angle of expansion of 20° at a conch height between 37 mm and 26 mm. At its apical end, the height and width are 26 mm and 23 mm, respectively (CHI = 1.13). The septa are 6 mm apart where the conch height is 31 mm (RCL = 0.19), and the sutures form lateral lobes. The siphuncle is marginally positioned and expands into the chambers. The septal foramen is 2.5 mm wide where the conch height is 26 mm (RSH = 0.1).

GIT 840-76 (Fig. 45D–E) is an exogastrically curved fragment of a phragmocone with a conch height and width of 20 mm and 18 mm, respectively, at its apical end (CHI = 1.11) with sutures which form lateral lobes. The sutures are 5 mm apart where the conch height is 23 mm (RCL = 0.22). The conch curvature, CHI, RCL and curvature of the suture line are similar to that of GIT 840-269.

TUG 1745-299 is a fragment of a phragmocone of an apparently exogastric cyrtocone with a conch width of 24 mm. It is closely similar to the two specimens, but too poorly preserved to be measured.

Remarks

These three specimens are described in order to document the presence of a relatively large, exogastrically curved brevicone, different from the genera and species described herein, but not well enough known to determine the order, genus, or species.

Multiceratoidea gen. et sp. indet. B
Fig. 39C

Material examined

ESTONIA • 1 spec.; Vormsi Island, Saxby shore; Kõrgessaare Formation, Vormsi Regional Stag; TUG 1743-37.

Description

The specimen is a fragment of a curved adoral part of a mature body chamber. The complete length of the fragment is 63 mm. At the aperture, the conch is 50 mm high and slightly compressed, a shallow apertural sinus (hyponomic?) occurs at the side of the conch which in lateral profile forms the convex conch margin. Otherwise, the peristome was apparently straight, transverse. At its apical end, 47 mm from the aperture, the conch has a diameter of 55 mm and is circular in cross section. In lateral view, on the convex side of the conch curvature shallow, irregularly spaced ribs occur, which are ca 15 mm apart. The conch surface is ornamented with distinct growth lines.

Remarks

The available information about this species, i.e., the contracted curved body chamber, compressed conch cross section, hyponomic sinus on the convex side of the conch curvature suggest that it belongs to an unknown annulated multiceratoid. More complete material is needed for a definite determination.

Multiceratoidea gen. et sp. indet. C
Fig. 28K–L

Material examined

ESTONIA • 1 spec.; Vormsi Island, Hosholm shore (tower locality); Adila Formation, Pirgu Regional Stage; GIT 878-234.

Description

The specimen is an exogastrically curved fragment of a body chamber and one chamber of the phagmocone. The outer shell is not preserved but the surface was apparently smooth or ornamented with faint transverse lirae. At the base of the body chamber, the conch height and width are 17 mm and 14 mm, respectively (CHI = 1.21). The conch cross section is oval compressed with a narrower conch margin on the prosiphuncular side. The conch has an angle of expansion of 18°. The body chamber has a preserved length of ca 15 mm. In lateral view, both conch margins are curved, convex on the prosiphuncular and concave on the antisiphuncular side. The two preserved septa are 2.2 mm apart (RCL = 0.13), and their sutures form shallow lateral lobes. The siphuncle is located near the convex margin of the conch with a septal foramen which is too poorly preserved to be measured.

Remarks

The fragmentary character of this specimen does not allow further determination. It is not clear whether this fragment represents a mature individual or a juvenile specimen. *Cyrtorizoceras tenue* Strand, 1934 has a similar angle of expansion (18°) and a CHI of 1.25 but is too poorly known to be compared with the specimen described herein.

Results of the faunal analysis

Completeness of the record

As a result of this review, 90 species are known from the Vormsi–Pirgu regional stages, 36 of them are left in open nomenclature because of insufficient material. The relatively large number of these insufficiently known species and the large number of species, known only from a single specimen (42 species) indicate the presence of a large number of rare species in the Vormsi–Pirgu strata of Estonia, many of which are probably to be discovered.

The relative size of this cohort of unknown species can be statistically estimated using the coverage-based extrapolated Hill numbers (see methods) for the total sample and for the extensively sampled localities

Table 3. Observed (S_{obs}), and coverage-extrapolated species richness (qD) of cephalopod samples from Estonia (combined specimens from Teichert (1930) and herein), Saxby shore (combined localities Saxby (N) and Saxby (S)), Vormsi Regional Stage, Hosholm (= Mõisaholm) shore (combined Hosholm shore and Hosholm shore (tower)), Pirgu Regional Stage, and Vohilaid (E), Pirgu Regional Stage. The % of unknown species refers to qD as 100%. Lower (lcl) and upper (ucl) 95% confidence are given for qD. Note the different sample sizes. The Boda Limestone sample of cephalopods of Kröger (2013) is given for comparison.

locality	sample size	S_{obs}	qD (lcl–ucl)	% unknown
Estonia total	646	90	127 (76–177)	30
Saxby shore	147	31	44 (10–78)	30
Hosholm shore	124	27	36 (0–77)	25
Vohilaid shore (E)	70	21	29 (0–59)	28
Boda Lst	561	65	80 (62–98)	19

(Saxby shore, Hosholm shore, Vohilaid shore (E), Table 3). A comparison of the different samples shows that the combined Saxby shore outcrops are the most completely sampled. However, compared with the collections from the Boda Limestone (late Katian–early Hirnantian, Sweden) the sampling is still relatively poor. Additionally, it should be noted that except for the Hosholm and Vohilaid samples, which were systematically sampled, it can be expected that the sampling effort was uneven for different higher taxa. The beautiful and compact coiled discocerids where more frequently collected than, e.g., large, poorly preserved fragments of endocerids or small, inconspicuous fragments of *Isorthoceras*. This influences the shape of the species abundance distribution (SAD), which, based on empirical findings, is expected to fit a log-series distribution (Baldridge *et al.* 2016).

A comparison between the SADs of the systematically collected Hosholm shore sample and the Saxby shore sample supports the assumption of a biased collection-practice at Saxby shore (Fig. 54A) and a random collection-practice at Hosholm shore (Fig. 54B). The SAD of Hosholm shore has a good fit to a log-series distribution. In contrast, the Saxby collection has too many abundant (e.g., discocerids and *P. senckenbergi*, Table 4) and too few less abundant species compared to the model distribution. The log-series model also shows a very good fit with the SAD of the Boda Limestone sample (Fig. 54C),

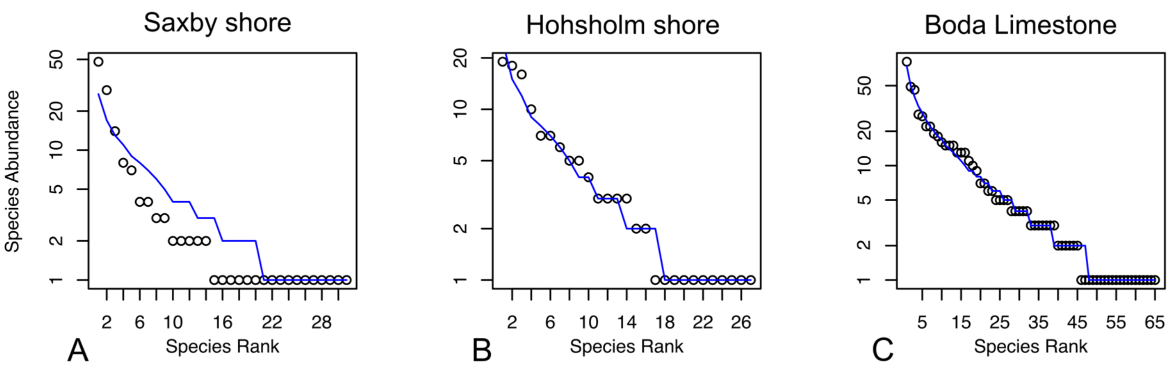

Fig. 54. Species-abundance-rank plots for cephalopod occurrences. **A**. Saxby shore localities, Vormsi Island, Vormsi Regional Stage. **B**. Hosholm shore localities, Vormsi Island, Pirgu Regional Stage. **C**. Boda Limestone, Siljan area, Sweden (data from Kröger 2013). Blue line: fitted log-series model distribution, y-axis in log-scale.

Table 4 (continued on next page). Species abundance rank lists of cephalopod samples from Saxby shore (combined localities Saxby (N) and Saxby (S)), Vormsi Regional Stage, Hosholm (= Mõisaholm) shore (combined Hosholm shore and Hosholm shore (tower)), and Vohilaid (E), all Pirgu Regional Stage.

	Saxby shore		Hosholm shore		Vohilaid shore (E)	
rank	**species**	**n**	**species**	**n**	**species**	**n**
1	*Palaeodawsonocerina senckenbergi*	48	*Danoceras piersalense* comb. nov.	19	*Discoceras antiquissimum*	17
2	*Discoceras saemanni*	29	*Discoceras antiquissimum*	18	*Hosholmoceras ovalis* sp. nov.	10
3	*Discoceras roemeri*	14	*Beloitoceras sinuososeptatum*	16	*Beloitoceras sinuososeptatum*	8
4	*Isorthoceras saaremense* comb. nov.	8	*Gorbyoceras clathratoannulatum* comb. nov.	10	*Diestoceras stensioei*	4
5	*Isorthoceras luhai* comb. nov.	7	*Charactoceras estonicum*	7	*Ephippiorthoceras vormsiense* sp. nov.	4
6	*Isorthoceras* sp. D	4	*Striatocycloceras hosholmense* sp. nov.	7	*Gorbyoceras textumaraneum*	4
7	*Pleurorthoceras* sp.	4	*Gorbyoceras textumaraneum*	6	*Danoceras vohilaidense* sp. nov.	3
8	*Kiaeroceras kaebliki* sp. nov.	3	*Diestoceras stensioei*	5	*Discoceras roemeri*	3
9	*Redpathoceras saxbyense* sp. nov.	3	*Hosholmoceras ovalis* sp. nov.	5	Discosorida gen. et sp. indet. A	3
10	*Nybyoceras bekkeri*	2	*Lyckholmoceras norvegiae*	4	*Charactoceras estonicum*	2
11	*Saxbyoceras kingpooli* gen. et sp. nov.	2	*Discoceras roemeri*	3	*Cyrtorizoceras* sp. A	1
12	*Strandoceras kalevipoegi* sp. nov.	2	*Discoceras saemanni*	3	*Dalecarlioceras* sp.	1
13	*Strandoceras kohilense* sp. nov.	2	*Ephippiorthoceras vormsiense* sp. nov.	3	*Danoceras piersalense* comb. nov.	1
14	*Strandoceras muhvi* sp. nov.	2	*Hosholmoceras triangulatum* sp. nov.	3	*Deckeroceras balticum* sp. nov.	1
15	*Cameroceras hasta*	1	*Striatocycloceras* cf. *hosholmense*	3	*Dowlingoceras* sp. A	1
16	*Cyrtorizoceras hariense* sp. nov.	1	*Dalecarlioceras constrictum*	2	*Gorbormoceras vohilaidense* gen. et. sp. nov.	1
17	*Danoceras oviforme* sp. nov.	1	*Beloitoceras* cf. *sinuoseptatum*	2	*Gorbyoceras clathratoannulatum* comb. nov.	1
18	*Discoceras paopense* sp. nov.	1	*Dowlingoceras tornense* sp. nov.	2	*Hosholmoceras triangulatum* sp. nov.	1
19	*Geisonoceras saksbyense*	1	*Charactoceras* sp. A	1	*Kallholnoceras* sp.	1
20	*Gorbyoceras clathratoannulatum* comb. nov.	1	*Charactoceras* sp. B	1	*Redpathoceras saxbyense* sp. nov.	1
21	*Gorbyoceras stumburi*	1	*Cyrtorizoceras* sp. B	1	*Schuchertoceras deformis*	1
22	*Isorthoceras* sp. C	1	*Danoceras oviforme* sp. nov.	1		
23	*Isorthoceras* sp. E	1	*Danoceras* sp. A	1		
24	*Kiaeroceras* cf. *oermsense* sp. nov.	1	*Diestoceras* sp.	1		
25	*Kiaeroceras ormsoense* sp. nov.	1	*Gorbyoceras stumburi*	1		
26	*Kiaeroceras* sp. B	1	*Dowlingoceras kallholnense*	1		
27	*Kiaeroceras* sp. E	1	*Isorthoceras luhai* comb. nov.	1		

Table 4 (continued). Species abundance rank lists of cephalopod samples from Saxby shore (combined localities Saxby (N) and Saxby (S)), Vormsi Regional Stage, Hosholm (= Mõisaholm) shore (combined Hosholm shore and Hosholm shore (tower)), and Vohilaid (E), all Pirgu Regional Stage.

	Saxby shore		**Hosholm shore**		**Vohilaid shore (E)**	
rank	**species**	**n**	**species**	**n**	**species**	**n**
28	Multiceratoidea gen. et sp. indet. A	1	*Kallholnoceras* sp.	1		
29	Multiceratoidea gen. et sp. indet. B	1	Multiceratoidea gen. et sp. indet. A	1		
30	*Ormoceras heckeri*	1	*PalaeodawsonocerinA* ? sp.			
31	*Rizosceras teres* sp. nov.	1		1		
32	*Strandoceras sulevipoegi* sp. nov.	1				

a result which supports an unbiased sampling in the reef limestone of the Siljan area, Sweden. This is expected, because cephalopods occur in the Boda Limestone predominantly in pocket concentrations yielding easily collectable species mixings (Kröger 2013; Kröger & Ebbestad 2014).

Cephalopod richness

The coverage standardized richness of the total cephalopod assemblage in Estonia reaches its maximum in the strata of the Vormsi and Pirgu regional stages with an extrapolated richness (qD) of 71 species, respectively (Fig. 55, Table 5). These assemblages by far are the most diverse cephalopod assemblages known from Baltoscandia.

Beyond that, a quantitative comparison of the total richness of the Estonian Vormsi–Pirgu stage cephalopod assemblages with well-known assemblages of other regions of the same time interval (e.g.,

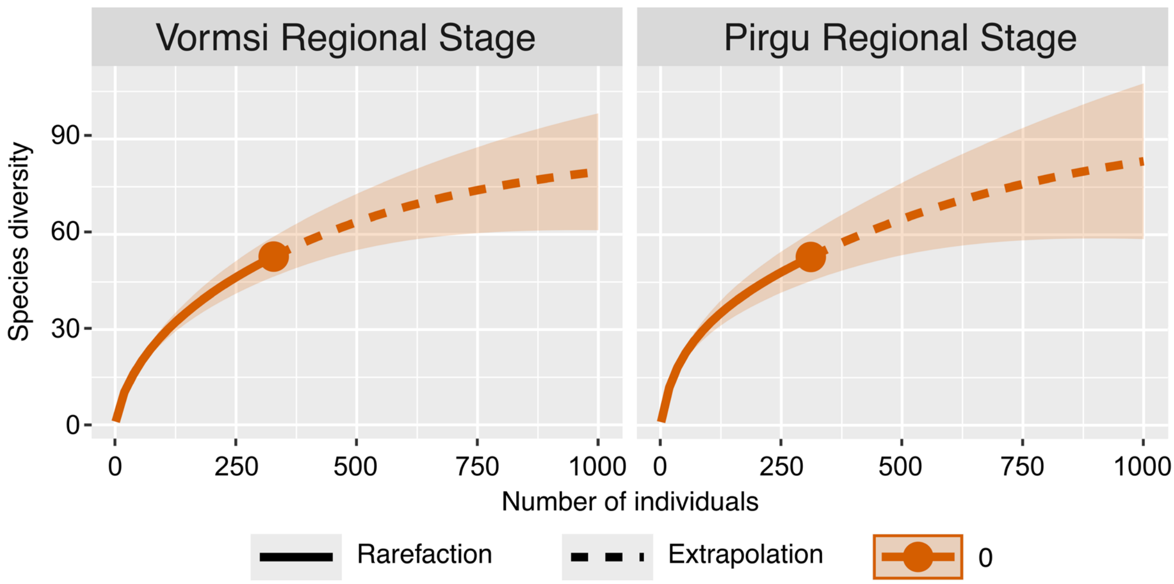

Fig. 55. Coverage-rarefied and extrapolated species richness of Estonian cephalopod collections. **A**. Vormsi Regional Stage **B**. Pirgu Regional Stage. Based on 336 specimens (individuals) from Vormsi Regional Stage and 315 specimens (individuals) from Pirgu Regional Stage.

Table 5. Observed richness (Sobs) and richness estimates of cephalopods for the Vormsi and Pirgu regional stages (RS) of Estonia. Coverage-extrapolated species richness (qD) based on twice the sample size with lower (lcl) and upper (ucl) 95% confidence level.

	sample size	S_{obs}	qD	lcl qD	ucl qD
Vormsi RS	311	53	71	40	101
Pirgu RS	328	53	71	42	100

Boda Limestone, Sweden, see Kröger & Ebbestad 2014) or from other time intervals of the same region (e.g., the late Sandbian Vasalemma Limestone, see Kröger & Aubrechtová 2017) is difficult, because of the different sampling areas and the confounding species-area effect (see, e.g., Antell *et al.* 2024). Herein, therefore, only relative differences in abundance and richness will be compared.

Within the Estonian assemblages striking differences exist between Vormsi and Pirgu stages (Fig. 56). The abundances of the Vormsi Stage assemblages are strongly dominated by the combined orthocerids and pseudorthocerids (39%, mainly *Palaeodawsonocerina* and *Isorthoceras*) and tarphycerids (35%, *Discoceras*) while the Pirgu Stage assemblages are less strongly dominated by a single group, and oncocerids (30%, mainly *Beloitoceras*), and tarphycerids (28%, *Discoceras*) dominate, while combined orthocerids and pseudorthocerids are subordinate (18%). This difference is also partly reflected in the richness of the different groups. In both stages, the combined discosorids and oncocerids are the most diverse group (Vormsi = 23 species, Pirgu = 30 species). However, in the Pirgu Stage orthocerids and pseudorthocerids are less diverse than in the Vormsi Stage, with a total of 8 species in the former and 16 species in the latter. The species turnover of 81% of the total number of counted species (n = 86) between the two stages is very high, and results from a ca 40% of species disappearance during the Vormsi Stage and ca 41% new appearances during the Pirgu Stage. Most range-through-species are pseudorthocerids and all three *Discoceras* species range through. The highest turnover occurs within the oncocerids and discosorids (Table 6).

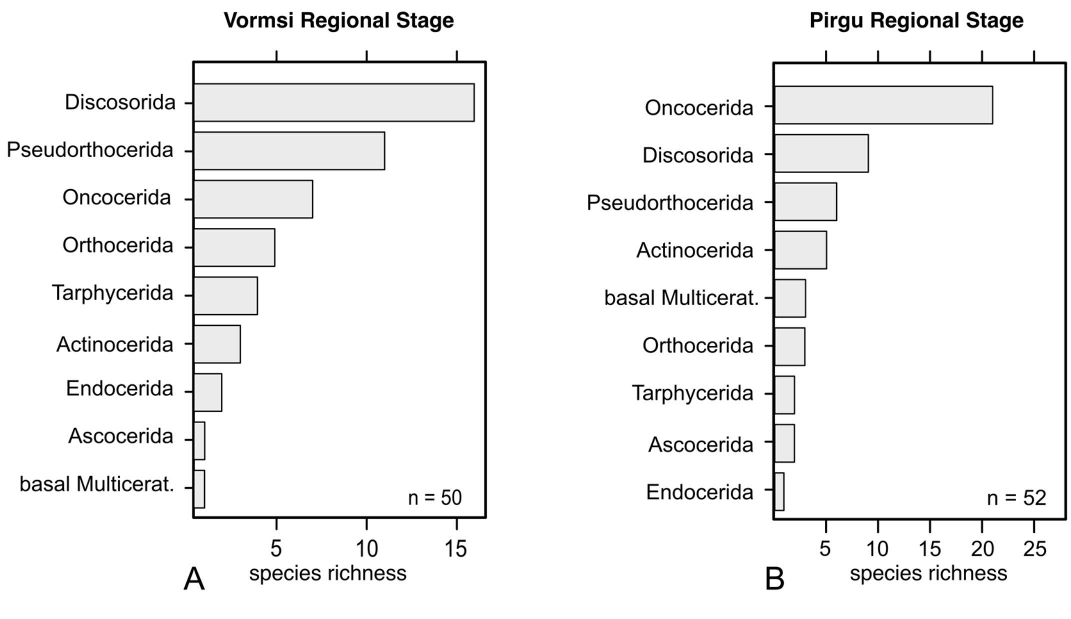

Fig. 56. Abundance rank plots for cephalopod occurrences at order level. **A**. Vormsi Regional Stage. **B**. Pirgu Regional Stage.

Table 6. Species turnover between Vormsi and Pirgu regional stages per cephalopod order. Note the high turnover (70 of 86 species change between the two stages).

Order	disappearances Vormsi	appearances Pirgu	range through
Actinocerida	1	3	2
Ascocerida	0	1	1
Discosorida	14	7	2
Endocerida	1	0	1
Oncocerida	6	20	1
Orthocerida	4	1	1
Pseudorthocerida	6	1	5
Tarphycerida	1	0	3
basal Multiceratoidea	1	3	0
Total	**34**	**36**	**16**

Spatial cluster analysis

The Estonian late Katian cephalopod occurrences can be compared with late Katian cephalopod assemblages elsewhere. A close similarity of the Lyckholm cephalopod fauna with North American assemblages has already been noted by Teichert (1930). Strand (1934), in discussing the late Katian cephalopod taxa of Norway, emphasized the close similarity of the Norwegian and Estonian assemblages with those of North America. A relatively close similarity of the Estonian assemblage to the cephalopod taxa found in the late Katian Killey Bridge Formation of Ireland has been detected by Evans (1993). Herein, therefore, a compilation of major late Katian cephalopod occurrences from across North America, Greenland, Baltoscandia, and Ireland, has been analyzed. The compilation comprises 517 species of 109 genera from 27 geological units (supplementary data 6). Of the 108 genera, 69 are informative for a cluster analysis (= non-endemic). Two different analyses reveal different aspects of similarity among the assemblages. The genus-level analysis emphasises palaeogeographic relationships, because it is assumed that similar genera occur in palaeogeographically related assemblages. Comparison of observed genus-richness per cephalopod order also reveals similarities in the original habitat (e.g., climate, habitat depth, nutrient availability), because cephalopod orders differ in their original habitats and habits (e.g., Westermann 1998; Kröger *et al.* 2009a).

The results (Fig. 57) show that the Estonian occurrences are strongly similar to that of the Boda Limestone, Siljan area, Sweden, which is no surprise given their palaeogeographic proximity and their similar stratigraphic age (Kröger & Ebbestad 2014; Kröger *et al.* 2016). Next in similarity are the Norwegian occurrences, supporting Strand’s (1934) early findings. The Baltoscandian cluster, in turn, is most similar to late Katian assemblages of Quebec, Canada (Vauréal and Ellis Bay formations, Anticosti Island; White Head Formation, Gaspé Peninsula) and to the Maquoketa Formation of Iowa, USA. Surprisingly, the cephalopod fauna of the Cape Calhoun group (Greenland) and the assemblage of the Killey Bridge Limestone (Ireland) cluster not with the Estonian assemblage. The Killey Bridge cephalopods are more similar to the Richmondian assemblages of the Cincinnatian area (USA), and the Cape Calhoun assemblage is more closely related to the cephalopods of the Bighorn Group of the northwestern USA. In a cluster analysis published by Evans (1993: fig. 6) the Killey Bridge fauna is closer related to the Quebec / Baltoscandia group.

Fig. 57. Presence / absence plot of cephalopod genus occurrences of selected Late Ordovician strata. The clustering based on the Raup-Crick dissimilarity index and calculated with "average" method (see text for details). Abbreviation: lst = limestone. (see Supp. file 6 for data and References).

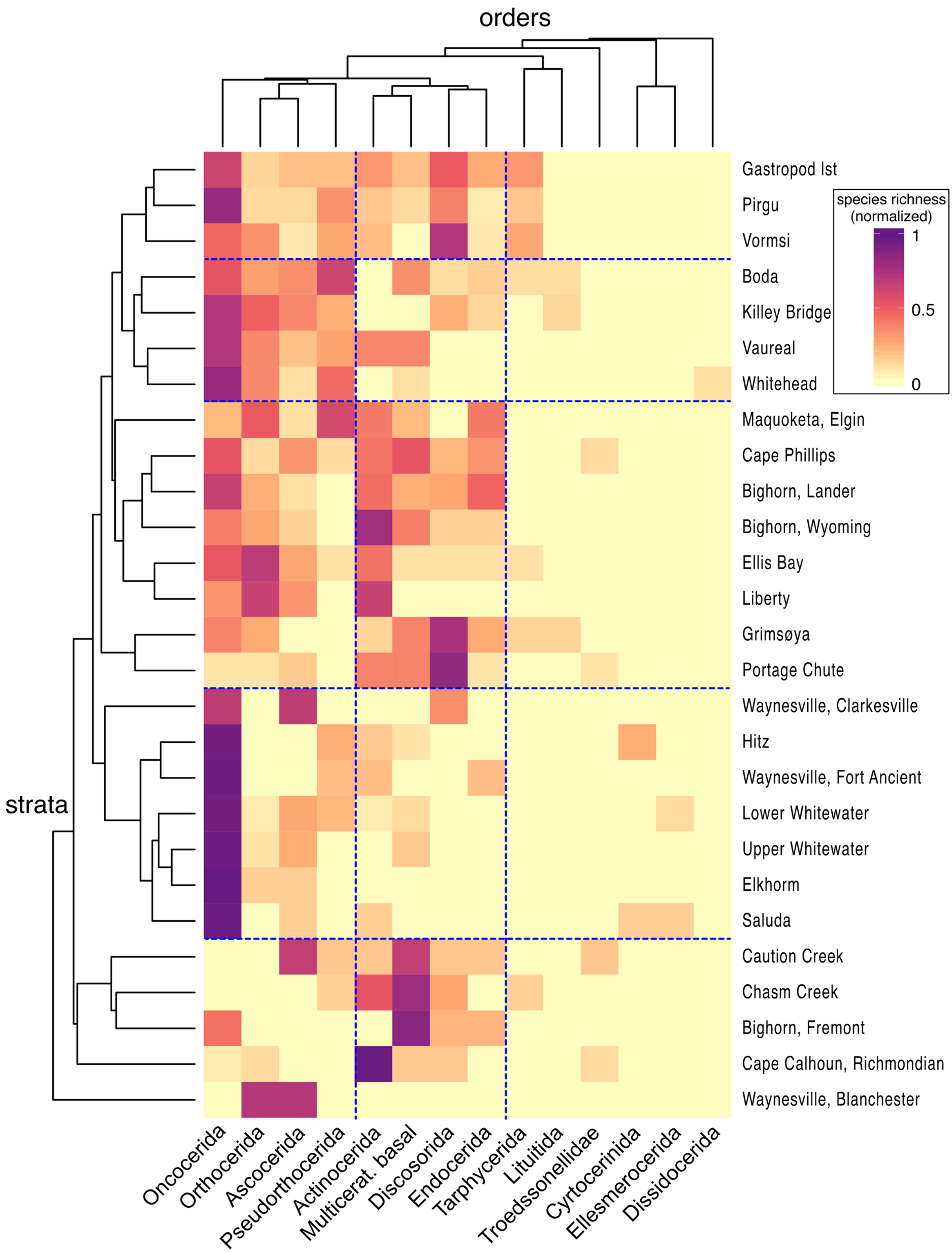

Fig. 58. Heatmap of genus richness of cephalopod orders in selected Late Ordovician strata. Richness values were normalized before clustering for each stratum. The clustering is based on the Bray-Curtis dissimilarity index and calculated with "average" method. Abbreviation: lst = limestone. (For data and references see file 6.)

The analysis of the relative genus-richness of the orders of the different assemblages results in a different pattern (Fig. 58). There, the Estonian assemblages cluster with the Norwegian occurrences, and the Boda Limestone cephalopods cluster with that of the Vauréal Formation of Anticosti Island, the White Head and the Killey Bridge occurrences. The common theme here is the relative richness of the orthocerids and pseudorthocerids in the latter, and the relative richness of actinocerids and discosorids in the former cluster.

Discussion

Sampling and species delineation

Despite the large amount of material available for this study, several problems remain. These concern an obvious bias in sampling, and the inherent difficulties in delineating cephalopod species and higher taxa. As a result, the diversity picture, emerging from the analysis presented herein, is affected by different biases at different taxonomic levels.

Many species, described herein needed to be left in open nomenclature because they are known from only single, poorly preserved fragments. This suggests a high number of rare, yet undescribed, species. Additionally, some species, described herein, such as *Beloitoceras hetercurvatum*, *Discoceras roemeri*, and *Discoceras saemanni* comprise an intraspecific morphological variety, which suggests that splitting would be possible with better-preserved material available, which would then permit the delineation of groups based on, e.g., ornamentation, or mature body chamber modifications.

These species currently represent morphological groups based on features, which are practically available from most specimens (angle of expansion, conch curvature, etc.). In many specimens, details of, e.g., the ornamentation are not preserved but may vary significantly. This problem probably exists for many Late Ordovician cephalopod assemblages of moderate preservation quality, such as those known from several North American localities in palaeotropical settings. The species count presented herein and in comparable settings, therefore is necessarily only a rough estimation of a potentially much higher original richness. This potential species lumping probably affects the observed species abundance distribution, increasing the abundance of species of, e.g., *Discoceras*, which form the dominant fraction in the assemblages from Saxby shore.

At higher taxonomic levels, a sampling bias occurs toward mid-sized, aesthetically attractive specimens from genera such as *Discoceras* or *Striatocycloceras*. Large endocerids, and small, simple, orthoconic genera, such as *Isorthoceras*, generally appear to be undersampled in the Late Ordovician strata of Estonia. This results in collections, which contain too many singletons (rare specimens) and an inflated dominance fraction (see Fig. 54A) compared with SADs-model expectations.

Finally, when comparing distribution patterns of cephalopods at family and order level, problems need to be considered that persist in higher cephalopod classification. Several higher groups are now known to be para-, or polyphyletic (such as the Barrandeocerida and Oncocerida, see Pohle *et al.* 2022). When compared in rank-abundance plots, they should be treated with care, because they may reflect a variety of different morphotypes, and hence potential ecological roles. These groups also frequently contain genera which have an unstable position in the respective reconstructed clades and consequently have been classified differently by different authors (e.g., Uranoceratidae, see Kröger 2013, and herein).

The classification of orthocones with very short septal necks into either the Orthocerida or Pseudorthocerida is a problem which concerns the unresolved question of the origin and early evolution of the Pseudorthocerida (see, e.g., Pohle *et al.* 2022). An additional problem, which becomes evident with the material presented herein, is the transitional character of endogastrically curved forms with endosiphuncular bullettes (such as in cyrtogomphoceratids), straight forms with endosiphuncular bullettes that form adapical projections (such as *Kiaeroceras*, see e.g., Fig. 37F, H), and exogastrically curved forms with actinosiphonate siphuncles (such as in valcouroceratids, see e.g., *Mixosiphonoceras norvegicum* Strand, 1934). This suggests a reevaluation of the valcouroceratid and cyrtogoomphoceratid families, which is beyond the scope of this work.

These problems currently limit to a certain degree the information value of the richness estimations (at genus and order level) presented herein. Nevertheless, some general conclusions on the distribution patterns can be drawn from the available data. This is because a more and more consistent picture emerges with a growing body of studies of cephalopod occurrences showing that higher cephalopod groups, such as Actinocerida, Orthocerida and breviconic Multiceratoidea, are dependent on depositional environment (including conditions, such as palaeotemperatures, palaeo-water depth).

Palaeoecology and palaeogeography

The Vormsi–Pirgu interval yields by far the most diverse Ordovician cephalopod fauna of Baltoscandia. This conclusion can be drawn by comparing assemblages, described from other Ordovician intervals (Kröger 2007; Kröger *et al.* 2009b, 2011; Kröger & Ebbestad 2014; Kröger & Rasmussen 2014; Kröger & Aubrechtová 2017, 2019; Aubrechtová & Meidla 2020). Unfortunately, the published fossil record of cephalopods remains patchy. To date, only single, well-exposed, and well-preserved but geographically or taxonomically restricted assemblages have been described. At the same time, systematic revisions, especially of the cephalopods of the Haljala-Kukruse, Oandu-Nabala, and Hirnantian regional stages, are missing. A reliably quantitative time series of the Baltoscandian cephalopod diversity, therefore, is still out of reach. The conclusion of a Vormsi–Pirgu stage Baltoscandian diversity maximum, therefore, is largely based on my decades-long field experience, an overview on the museum collections of the region, and the fact that the cephalopod assemblages that have been described so far, represent exceptionally rich examples from the relevant time intervals. Cephalopods are comparatively rare and species poor in the remaining strata. Hence, the described fauna (herein and elsewhere) permits a sketch of a general picture: one of a successively increasing Ordovician cephalopod diversity, peaking within the Pirgu Regional Stage, a diversification, which is termed the “Lyckholm acme”, herein.

This peak diversification is largely due to the diversification of multiceratoids, which classically have been classified within the Oncocerida, Discosorida and Barrandeocerida and are characteristic faunal elements of shallow, warm water depositional environments (Westermann 1998) rich in remains of skeletal colonial organisms such as bryozoans, corals, and stromatoporoids. The cephalopod diversification was therefore tightly connected to the development of a widespread carbonate platform in the region, containing reef-ecosystems (see also Penny *et al.* 2022). The cephalopods described herein were collected from localities of non-reefal depositional environments (except the cephalopods from the Niibi locality, Pirgu Regional Stage, see e.g., Kröger *et al.* 2019) but rugose and tabulate corals, stromatoporoids, and bryozoans are an important component of the localities which yielded the richest cephalopod faunas (e.g., Hosholm and Vohilaid shores, Pirgu Regional Stage, see above). These localities represent tropical, relatively shallow neritic environments with clear (nutrient poor, Kiipli *et al.* 2010) palaeo-water conditions.

The regional conditions also need to be seen within the global context of a climate that underwent, under a general cooling trend, strong changes with repeated cooling-warming intervals (i.e., Boda-cooling and warming events, Melchin *et al.* 2013; Young *et al.* 2023), and was accompanied by drastic regional sea level changes (see e.g., Nielsen 2011). In this context, the Kõrgessaare Formation of the Vormsi Regional stage, exposed in Saxby shore, represents a deeper depositional environment than e.g., the coral rich strata of the Adila Formation, Pirgu Regional Stage, at Hosholm and Vohilaid shore. This is clearly reflected in the respective cephalopod assemblages, which are relatively rich in pseudorthocerids and orthocerids in the former and strongly dominated by oncocerids and discocerids in the latter.

Apart from this shift in dominance, the high rate of turnover across the stratigraphic levels (i.e., temporal turnover) is remarkable. The important role of temporal turnover for the diversity dynamic of Late Ordovician marine fauna has already been emphasized by Penny *et al.* (2022). Here, it can be shown that temporal turnover was an important factor during the Late Ordovician cephalopod diversification. Differences in temporal turnover also could explain the diverging Late Ordovician diversity trends between the microphytoplankton (Hints *et al.* 2010) and the fauna, i.e., high turnover rates in the former and lower turnover rates in the latter. This hypothesis needs to be tested in future work.

A similarly highly dynamic spatio-temporal eco-evolutionary mosaic, like that of the Estonian late Ordovician palaeo-shelf, is better known from coeval strata of North America, where repeated intervals of drastic regional faunal shifts have been described under the term of the "Richmondian invasion" (see Stigall 2023 for a review). The cephalopod aspect of this faunal shift has been already noted by Foerste (1924) and Flower (1946). The cephalopod fauna, described herein, gives a glimpse into a possible global dimension of late Katian spatio-temporal turnover events and faunal shifts. Several of the "Lyckholm"-genera have their first occurrences in low-palaeolatitude regions of North America, such as *Beloitoceras* and *Diestoceras* (Foerste 1924), while *Redpathoceras* (Flower 1963), *Schuchertoceras* (Flower 1946) probably immigrated from there during warmer periods, combined with a northward palaeogeographic shift of the Baltica palaeocontinent. It seems that the strong Laurentian affinities of the Vormsi–Pirgu stage Baltoscandian cephalopods presented herein contrast with the stronger Avalonian affinities of brachiopods (Harper *et al.* 2013; Candela 2015). The reasons for these differences are not clear. This open question and the many other open questions mentioned herein demonstrate that the details of the Late Ordovician global faunal shifts of cephalopods need to be analyzed in more detail in future work, particularly including Chinese and Siberian occurrences.

Conclusions

A revision of ca 660 specimens of cephalopods from Estonian limestone strata of the Vormsi–Pirgu regional stages revealed a rich fauna of 90 species belonging to 35 genera, and 17 families. Four genera are new: *Gorbormoceras* gen. nov., *Hiiumoceras* gen. nov., *Hosholmoceras* gen. nov. *Saxbyoceras* gen. nov.

23 species are new: *Beloitoceras uuemoisense* sp. nov., *Cyrtorizoceras hariense* sp. nov., *Danoceras oviforme* sp. nov., *D. vohilaidense* sp. nov., *Deckeroceras balticum* sp. nov., *Discoceras paopense* sp. nov., *Dowlingoceras tornense* sp. nov., *Ephippiorthoceras vormsiense* sp. nov., *Gorbormoceras vohilaidense* gen. et sp. nov. *Hiiumoceras hiiuense* sp. nov., *Hosholmoceras* ovalis sp. nov., *H. triangulatum* sp. nov., *Kiaeroceras kaebliki* sp. nov., *K. ormsoense* sp. nov., *K. urgense* sp. nov., *Redpathoceras saxbyense* sp. nov., *Rizosceras teres* sp. nov., *Saxbyoceras kingpooli* gen. et sp. nov., *Strandoceras kalevipoegi* sp. nov., *S. kohilense* sp. nov., *S. muhvi* sp. nov., *S. sulevipoegi* sp. nov., *Striatocycloceras hosholmense* sp. nov.

Six species are placed in new combinations: *Danoceras piersalense* (Teichert, 1930) comb. nov., *Isorthoceras luhai* (Stumbur, 1956) comb. nov., *Isorthoceras saaremense* (Balashov, 1959) comb. nov., *Gorbyoceras clathratoannulatum* (Roemer, 1861) comb. nov., *Richardsonoceras priscum* (Eichwald, 1860) comb. nov., *Schuchertoceras deformis* (Eichwald, 1860) comb. nov.

36 species are left in open nomenclature.

The revision revealed difficulties in delineating species of *Discoceras* and a probability of the existence of several undetected species within the material of that genus because critical characters, such as length of mature body chamber and details of the ornamentation are commonly not preserved. The revision also revealed forms, which may be transitional between the Valcouceratidae and Cyrtogomphoceratidae

(*Kiaeroceras*), and it provided evidence that *Piersaloceras* (which is currently classified within the Graciloceratidae) could be a member of the Uranoceratidae or Probillingsitidae and therefore could provide additional evidence for the origin of Ascocerida.

An analysis of the species abundance distribution in rank-abundance plots shows that sampling practice and species delineation differently affected distributions of cephalopod assemblages from the three main sampling localities. Species lumping and preferential collection of coiled and aesthetically ornamented specimens probably leads to an inflation of the dominance fraction in the assemblage of a locality (Saxby shore, Vormsi Island, Vormsi Regional Stage) that was sampled by generations of collectors.

An estimation of the coverage-extrapolated species richness of cephalopods of the Vormsi and Pirgu stage strata of Estonia shows that this time interval yields by far the most diverse of the Ordovician cephalopod assemblages in Baltoscandia. This richness peak within the time interval is historically known as the "Lyckholm stage" therefore is termed herein "Lyckholm acme of cephalopods." The richness is partly an effect of a high temporal turnover within the interval but can also be attributed to favourable warm water palaeo-conditions with a rich and abundant co-occurrence of, partly reef-forming, colonial skeletal anthozoans, bryozoans, and stromatoporoids.

Finally, a cluster analysis and comparison of the Estonian cephalopod assemblage with contemporary late Katian assemblages from strata elsewhere in Baltoscandia, and of the Laurentia and Avalonia palaeocontinent reveals much overlap at genus level. Most similar are the late Katian cephalopod occurrences of the Boda Limestone (Sweden), the Gastropod Limestone (Norway) and of Quebec, Canada (Ellis Bay and Vauréal formations, Anticosti Island, and Whitehead Formation, Percé Peninsula). The comparison at order level gives some information about the palaeo-environment favourable for the different orders. Here, the Estonian occurrences cluster with those from Norway, and in contrast, the similarities of the occurrences from the Boda Limestone and from the Killey Bridge Formation of Ireland are distinctive.

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Data availability statement

All data generated or analysed during this study are available on Zenodo (https://doi.org/10.5281/zenodo.14833042), and consist of: (1) list of all determined specimens of cephalopods of Vormsi–Pirgu regional stages of Estonia with SARV identifier, related stratum and locality of collection, and taxonomic opinion; (2) list of collection localities of cephalopods of Vormsi–Pirgu regional stages of Estonia with geographic coordinates given in the decimal degree (WGS84) coordinate system; (3) measurements taken from orthoconic cephalopods of Vormsi–Pirgu regional stages of Estonia; (4) measurements taken from breviconic cephalopods of Vormsi–Pirgu regional stages of Estonia; (5) measurements taken from coiled cephalopods of Vormsi–Pirgu regional stages of Estonia; (6) list of species compiled for cluster analysis, with references.

References

Achab A., Asselin E., Desrochers A., Riva J.F. & Farley C. 2011. Chitinozoan biostratigraphy of a new Upper Ordovician stratigraphic framework for Anticosti Island, Canada. *GSA Bulletin* 123 (1–2): 186–205. https://doi.org/10.1130/B30131.1

Ainsaar L., Truumees J. & Meidla T. 2015. The position of the Ordovician–Silurian boundary in Estonia tested by high-resolution δ13C chemostratigraphic correlation. *In*: Ramkumar M. (ed.) *Chemostratigraphy*: 395-412. Elsevier, New York. https://doi.org/10.1016/B978-0-12-419968-2.00015-7

Angelin N.P. & Lindström G. 1880. *Fragmenta Silurica*. Samson and Wallin, Stockholm. https://doi.org/10.5962/bhl.title.63278

Antell G.T., Benson R.B.J. & Saupe E.E. 2024. Spatial standardization of taxon occurrence data—a call to action. *Paleobiology* 50 (2):177–193. https://doi.org/10.1017/pab.2023.36

Aubrechtová M. & Meidla T. 2020. Lituitid cephalopods from the upper Darriwilian and basal Sandbian (Middle–Upper Ordovician) of Estonia. *GFF* 142 (4): 267–296. https://doi.org/10.1080/11035897.2020.1762723

Balashov Z.G. 1953a. Stratigraficheskoe rasprostranenie nautiloidej v ordovike Pribaltiki. *In*: Sokolov B.S. & Obut A.M. (ed.) *Stratigraphy and Fauna of the Ordovician and Silurian of the Western Part of Russian platform*: 197–216. Gostoptehizdat, Leningrad.

Balashov Z.G. 1953b. Svernutye i polisvernutye nautiloidei ordovika pribaltiki. *Trudy Vsesoyuznogo Neftyanogo Nauchno-Issledovatel'skogo Geologo-Razvednoknogo Instituta* 78: 217–268.

Balashov Z.G. 1955. Some new genera and species of Nautiloidea from the Ordovician of the Baltic Area. *Voprosy Paleontologij* 2: 45–54.

Balashov Z.G. 1959. Nekotorye novye vidy nautiloidej ordovika, silura i devona SSSR. *Materialy k "Osnovam paleontologii"* 3: 37–46.

Balashov Z.G. 1962a. Nadotrâd Endoceratoidea. Endoceratoidei. *In*: Orlov Û.A. (ed.) *Osnovy paleontologii. Spravočnik dlâ paleontologov i geologov SSSR. Mollûski - golovonogie. Nautiloidei, èndoceratoidei, aktinoceratoidei, baktritoidei, ammonoidei (agoniatidy, goniatidy, klimenii)*: 173–203. Izdatel'stvo Akademii Nauk, Moskva.

Balashov Z.G. 1962b. *Nautiloidei ordovika sibirskoi platformy*. Izdatel'stvo Leningradskogo Universiteta, St Petersburg.

Balashov Z.G. 1962c. Otrâd Tarphyceratida. *In*: Orlov Û.A. (ed.) *Osnovy paleontologii. Spravočnik dlâ paleontologov i geologov SSSR. Mollûski - golovonogie. Nautiloidei, èndoceratoidei, aktinoceratoidei, baktritoidei, ammonoidei (agoniatidy, goniatidy, klimenii)*: 77–82. Izdatel'stvo Akademii Nauk, Moskva.

Balashov Z.G. 1968. *Endoceratoidei ordovika SSSR*. Isdatelstvo Leningradskogo Universiteta, Leningrad.

Balashov Z.G. 1974. Endoceratida. *In*: Ruzhentsev V.E. (ed.) *Fundamentals of Paleontology Vol. V, Mollusca – Cephalopoda I Vol. V*: 74–81. Smithsonian Institution Libraries Translations Program, Jerusalem.

Balashov Z.G. 1975. Cefalopody molodovskogo i kitayogorodskogo gorizontov Podolii. *Voprosy Paleontologii* 7: 63–101.

Balashov Z.G. & Zhuravlyeva F.A. 1962. Otrâd Orthoceratida. *In*: Orlov Û.A. (ed.) *Osnovy paleontologii. Spravočnik dlâ paleontologov i geologov SSSR. Mollûski – golovonogie. Nautiloidei, èndoceratoidei,* *aktinoceratoidei, baktritoidei, ammonoidei (agoniatidy, goniatidy, klimenii)*: 82–93. Izdatel'stvo Akademii Nauk, Moskva.

Balashov Z.G. & Zhuravleva F.A. 1974. Order Orthoceratida. *In*: Ruzhentsev V.E. (ed.) *Fundamentals of Paleontology, Vol. V, Mollusca – Cephalopoda I, Vol. V*: 106–123. Smithsonian Institution Libraries Translations Program, Jerusalem.

Baldridge E., Harris D.J., Xiao X. & White E.P. 2016. An extensive comparison of species-abundance distribution models. *PeerJ* 4: e2823. https://doi.org/10.7717/peerj.2823

Barrande J. 1866. *Système Silurien du centre de la Bohême, I.ère partie, Recherches Paléontologiques, vol. II, Classe de Mollusques, Ordre des Céphalopodes, ser. 7*. Privately published, Praha. https://doi.org/10.5962/bhl.title.14776

Barrande J. 1867. *Système Silurien du centre de la Bohême, I.ère partie, Recherches Paléontologiques, vol. II, Classe de Mollusques, Ordre des Céphalopodes, ser. 1*. Privately published, Praha. https://doi.org/10.5962/bhl.title.14776

Barrande J. 1868. *Système Silurien du centre de la Bohême, I.ère partie, Recherches Paléontologiques, vol. II, Classe de Mollusques, Ordre des Céphalopodes, ser. 8*. Privately published, Praha. https://doi.org/10.5962/bhl.title.14776

Barskov I.S. 1972. *Late Ordovician and Silurian Cephalopod Molluscs of Kazakhstan and Middle Asia*. Nauka, Izdatel'stvo Moskovskogo Universitate, Moskva.

Bassler R.S. 1915. Bibliographic index of American Ordovician and Silurian fossils. *Bulletin of the United States National Museum* 92: 1–1521. https://doi.org/10.5479/si.03629236.92

Bicknell R.D.C., Vargas-Parra E.E., Landman N.H. & Pärnaste H. 2024. Evidence for cryptic molting behavior in the trilobite *Toxochasmops vormsiensis* from the Upper Ordovician Katian Kõrgessaare Formation, Estonia. *Naturwissenschaften* 111 (3): 22. https://doi.org/10.1007/s00114-024-01906-8

Billings E. 1857. Report for the year 1856. *Geological Survey of Canada, Report of Progress for the Years 1853, 54, 55, 56*: 247–345.

Billings E. 1866. Catalogues of the Silurian fossils of the Island of Anticosti, with descriptions of some new genera and species. *Geological Survey of Canada* 93: 1–93. https://doi.org/10.4095/216072

Blake J.F.A. 1882. *Monograph of the British Fossil Cephalopoda, Part 1, Introduction and Silurian Species*. John Van Voorst, London. https://doi.org/10.5962/bhl.title.52044

Bolton T.E. 1977. *Catalogue of Type Invertebrate Fossils of the Geological Survey of Canada*. Geological Survey of Canada, Ottawa.

Calner M., Lehnert O. & Nılvak J. 2010. Palaeokarst evidence for widespread regression and subaerial exposure in the middle Katian (Upper Ordovician) of Baltoscandia: Significance for global climate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 296 (3–4): 235–247. https://doi.org/10.1016/j.palaeo.2009.11.028

Candela Y. 2015. Evolution of Laurentian brachiopod faunas during the Ordovician Phanerozoic sea level maximum. *Earth-Science Reviews* 141: 27–44. https://doi.org/10.1016/j.earscirev.2014.11.012

Chapman E.J. 1857. On the occurrence of the genus *Cryptoceras* in Silurian rocks. *Annals and Magazine of Natural History Series 2* 20: 114–117. https://doi.org/10.1080/00222935709487883

Clarke J.M. 1897. The Lower Silurian cephalopoda of Minnesota. *Minnesota Geology and Natural History Survey* 3 (2): 761–812.

Conrad T.A. 1842. Descriptions of new species of organic remains belonging to the Silurian, Devonian and Carboniferous systems of the United States. *Journal of the Academy of Sciences of Philadelphia* 8: 235–280. Available from https://www.biodiversitylibrary.org/page/24623233 [accessed 20 Jan. 2025].

Conrad T.A. 1843. Observations on the Lead Bearing Limestone of Wisconsin, and descriptions of a new genus of Trilobites and fifteen new Silurian fossils. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1: 329–335. Available from https://www.biodiversitylibrary.org/page/1779429 [accessed 20 Jan. 2025].

Cuvier G. 1797. *Tableau élémentaire de l'Histoire naturelle des Animaux*. No publisher recorded, Paris. https://doi.org/10.5962/bhl.title.11203

Dzik J. 1984. Phylogeny of the Nautiloidea. *Palaeontologia Polonica* 45: 1–203.

Dzik J. & Kiselev G.N. 1995. The Baltic nautiloids *Cyrtoceras ellipticum* Lossen 1860, *C. priscum* Eichwald 1861, and *Orthoceras damesi* Krause 1877. *Paläontologische Zeitschrift* 69 (1–2): 61–71. https://doi.org/10.1007/BF02985974

Eichwald E.D. von 1840. Über das silurische Schichtensystem in Esthland. *Zeitschrift für Naturwissenschaften und Heilkunde der Akademie St Petersburg* 8: 1–327. https://doi.org/10.5962/bhl.title.150763

Eichwald E.D. von 1842. *Die Urwelt Russlands durch Abbildungen erlaeutert. 2. Heft. Neuer Beitrag zur Geognosie Esthlands und Finlands*. Akademie der Wissenschaften, St Petersburg.

Eichwald E.D. von 1857. Beitrag zur geographischen Verbreitung der fossilen Thiere Russlands. Alte Periode. *Bulletin de la Societé impériale des Naturalistes de Moscou* 30: 192–212. Available from https://www.biodiversitylibrary.org/page/44192481 [accessed 20 Jan. 2025].

Eichwald E.D. von 1860. *Lethaea Rossica ou Paléontologie de la Russie. Première Section de l'ancienne Periode, contenant la Flore de l'ancienne Période et la Faune jusqu'aux Mollusques.* Schweizerbart, Stuttgart. https://doi.org/10.5962/bhl.title.52391

Einasto R. 2012. Saxby rannikupaljandis Vormsil. *Keskkonnatehnika* (6): 41–43.

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.

Finnegan S., Bergmann K., Eiler J.M., Jones D.S., Fike D.A., Eisenman I., Hughes N.C., Tripati A.K. & Fischer W.W. 2011. The magnitude and duration of Late Ordovician–Early Silurian glaciation. *Science* 331 (6019): 903–906. https://doi.org/10.1126/science.1200803

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 (5): 523–548.

Flower R.H. 1943a. Apsidoceras in the Trenton of Montreal. *Journal of Paleontology* 17 (3): 258–263.

Flower R.H. 1943b. Studies of paleozoic Nautiloidea. I: Tissue remnants in the phragmocone of *Rayonnoceras*. II. *Werneroceras* in the Devonian of New York. III. A *Ohioceras* from Virginia. IV. Investigations of actinosiphonate cephalopods. V. New Ordovician cephalopods from Indiana with notes on stratigraphic problems. VI. Annulated orthoceraconic genera of Paleozoic Nautiloids. *Bulletins of American Paleontology* 28 (109): 1–140.
Available from https://www.biodiversitylibrary.org/page/10679031 [accessed 20 Jan. 2025].

Flower R.H. 1946. Ordovician cephalopods from the Cincinnati region. Part 1. *Bulletins of American Paleontology* 29 (116): 3–547. Available from https://www.biodiversitylibrary.org/page/10650257 [accessed 20 Jan. 2025].

Flower R.H. 1957. Studies of the Actinoceratida, Part 1, The Ordovician development of the Actinocerida, with notes on actinoceroid morphology and Ordovician stratigraphy. *New Mexico Bureau of Mines and Mineral Resources, Memoir* 2: 1–73. https://doi.org/10.58799/M-2

Flower R.H. 1962. Part 1, Revision of *Buttsoceras*, Part 2, Notes on the Michelinoceratida. *State Bureau of Mines and Mineral Resources, New Mexico Institute of Mining and Technology, Memoir* 10: 1–58. https://doi.org/10.58799/M-10

Flower R.H. 1963. New Ordovician Ascoceratida. *Journal of Paleontology* 37 (1): 69–85.

Flower R.H. & Caster K.E. 1935. The cephalopod fauna of the Conewango Series of the Upper Devonian in New York and Pennsylvania. *Bulletins of American Paleontology* 22 (75): 197–270. Available from https://www.biodiversitylibrary.org/page/30374188 [accessed 20 Jan. 2025].

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

Flower R.H. & Teichert C. 1957. The cephalopod order Discosorida. *University of Kansas Paleontological Contributions* 6: 1–144.

Foerste A.F. 1924. Notes on American Paleozoic cephalopods. *Denison University Bulletin, Journal of the Scientific Laboratories* 20: 193–268.

Foerste A.F. 1925. Notes on cephalopod genera, chiefly coiled Silurian forms. *Journal of the Scientific Laboratories of Denison University* 21: 1–69.

Foerste A.F. 1926. Actinosiphonate, trochoceroid and other cephalopods. *Denison University Bulletin, Journal of the Scientific Laboratories* 21: 285–383.

Foerste A.F. 1928a. A restudy of American orthoconic Silurian cephalopods. *Denison University Bulletin, Journal of the Scientific Laboratories* 23: 236–320.

Foerste A.F. 1928b. American arctic and related cephalopods. *Denison University Bulletin, Journal of the Scientific Laboratories* 23: 1–110.

Foerste A.F. 1928c. Cephalopoda. *In*: Twenhofel W.H. (ed.) *The Geology of Anticosti*: 257–321. Department of Mines, Geological Survey, Ottawa.

Foerste A.F. 1928d. The cephalopods of Putnam Highland. *Contributions from the Museum of Geology University of Michigan* 3: 25–69.

Foerste A.F. 1929. The cephalopods of the Red River Formation of Southern Manitoba. *Denison University Bulletin, Journal of the Scientific Laboratories* 24: 129–235.

Foerste A.F. 1930a. The color patterns of fossil cephalopods and brachiopods, with notes on gastropods and pelecypods. *University of Michigan Contribution of the Museum of Paleontology* 3 (6): 109–150.

Foerste A.F. 1930b. Port Byron and other Silurian cephalopods. *Denison University Bulletin, Journal of the Scientific Laboratories* 23: 1–110.

Foerste A.F. 1932. Black River and other cephalopods from Minnesota, Wisconsin, Michigan, and Ontario (Part 1). *Journal of Scientific Laboratories of Denison University* 27: 47–136.

Foerste A.F. 1933. Black River and other cephalopods from Minnesota, Wisconsin, Michigan, and Ontario (Part 2). *Denison University Bulletin, Journal of the Scientific Laboratories* 28: 1–136.

Foerste A.F. 1935a. Big Horn and related cephalopods. *Denison University Bulletin, Journal of the Scientific Laboratories* 30: 1–96.

Foerste A.F. 1935b. The cephalopods of the Maquoketa shale of Iowa. *Denison University Bulletin, Journal of the Scientific Laboratories* 30 (5): 231–257.

Foerste A.F. 1936. Cephalopods from the Upper Ordovician of Percé, Quebec. *Journal of Paleontology* 10: 373–384.

Foerste A.F. & Teichert C. 1930. The actinoceroids of east-central North America *Denison University Bulletin, Journal of the Scientific Laboratories* 32: 201–296.

Foord A.H. 1891. *Catalogue of the Fossil Cephalopoda in the British Museum (Natural History) Part 2, Containing the Remainder of the Suborder Nautiloidea, Consisting of the Families Lituitidae, Trochoceratidae, and Nautilidae, with a Supplement*. British Museum, London. https://doi.org/10.5962/bhl.title.112429

Fortey R.A. & Cocks L.R.M. 2005. Late Ordovician global warming—The Boda event. *Geology* 33 (5): 405–408. https://doi.org/10.1130/G21180.1

Frey R.C. 1995. Middle and Upper Ordovician cephalopods of the Cincinnati Region of Kentucky, Indiana, and Ohio. *United States Geological Survey Professional Paper* 1066P: 1–119. https://doi.org/10.3133/pp1066P

Frye M.W. 1982. Upper Ordovician (Harjuan) nautiloid cephalopods from the Boda Limestone of Sweden. *Journal of Paleontology* 56: 1274–1292.

Frye M.W. 1987. Upper Ordovocian (Harjuan) oncoceratid nautiloids from Boda Limestone, Siljan District, Sweden. *Geologiska Föreningens i Stockholm Förhandlingar* 109: 83–99. https://doi.org/10.1080/11035898709454748

Furnish W.M. & Glenister B.F 1964. Nautiloidea-Tarphycerida. *In*: Teichert C. (ed.) *Treatise on Invertebrate Paleontology, Part K, Mollusca 3*: K343−K368. Geological Society of America and the University of Kansas Press, Boulder, CO.

Goldman D., Sadler P.M., Leslie S.A., Melchin M.J., Agterberg F.P. & Gradstein F.M. 2020. Chapter 20 – The Ordovician period geologic time scale 2020. *In*: Gradstein F.M., Ogg J.G., Schmitz M.D. & Ogg G.M. (eds.): 631–694. Elsevier. https://doi.org/10.1016/B978-0-12-824360-2.00020-6

Greenfield T. 2023. *Endoceras novamagnum* nom. nov., a replacement name for *Endoceras magnum* Stumbur, 1956 (Cephalopoda, Endocerida). *Munis Entomology & Zoology* 18 (2): 1790–1790.

Gu Z., Eils R. & Schlesner M. 2016. Complex heatmaps reveal patterns and correlations in multidimensional genomic data. *Bioinformatics* 32 (18): 2847–2849. https://doi.org/10.1093/bioinformatics/btw313

Guenser P., Ginot S., Escarguel G. & Goudemand N. 2022. When less is more and more is less: the impact of sampling effort on species delineation. *Palaeontology* 65 (3): e12598. https://doi.org/10.1111/pala.12598

Gul B., Ainsaar L. & Meidla T. 2021. Latest Ordovician–early Silurian palaeoenvironmental changes and palaeotemperature trends indicated by stable carbon and oxygen isotopes from northern Estonia. *Estonian Journal of Earth Sciences* 70 (4): 196–209. https://doi.org/10.3176/earth.2021.14

Hall J. 1847. *Natural History of New York, Paleontology, Volume 1, Containing Descriptions of the Organic Remains of the Lower Division of the New-York System (equivalent of the Lower Silurian Rocks of Europe)*. Van Benthuysen, Albany, NY. https://doi.org/10.5962/bhl.title.39838

Hall J. 1861. *Report of the Superintendent of the (Wisconsin) Geological Survey, Exhibiting the Progress of the Work, January 1, 1861 (Including the Descriptions of New Species of Fossils from the Investigations of the Survey*. E.A. Calkins and Co., Madison, WI. https://doi.org/10.5962/bhl.title.62903

Harper D.A.T., Rasmussen C.M.Ø., Liljeroth M., Blodgett R.B., Candela Y., Jin J., Percival I.G., Rong J.-Y., Villas E. & Zhan R.-B. 2013. Chapter 11 Biodiversity, biogeography and phylogeography of Ordovician rhynchonelliform brachiopods. *Geological Society, London, Memoirs* 38 (1): 127–144. https://doi.org/10.1144/M38.11

Hints L. & Meidla T. 1997a. Pirgu Stage. *In*: Raukas A. & Teedumäe A. (eds) *Geology and Mineral Resources of Estonia*: 82–85. Estonian Academy Publishers, Tallinn.

Hints L. & Meidla T. 1997b. Vormsi Stage. *In*: Raukas A. & Teedumäe A. (eds) *Geology and Mineral Resources of Estonia*: 81–82. Estonian Academy Publishers, Tallinn.

Hints L. & Rong J.-Y. 2024. Discovery of trimerellid brachiopod Gasconsia from the Ordovician of Estonia. *Estonian Journal of Earth Sciences* 73 (2): 124–133. https://doi.org/10.3176/earth.2024.12

Hints L., Oraspõld A. & Nõlvak J. 2005. The Pirgu Regional Stage (Upper Ordovician) in the East Baltic: lithostratigraphy, biozonation and correlation. *Proceedings of the Estonian Academy of Sciences, Geology* 54 (4): 225–259. https://doi.org/10.3176/geol.2005.4.02

Hints O., Delabroye A., Nõlvak J., Servais T., Uutela A. & Wallin Å. 2010. Biodiversity patterns of Ordovician marine microphytoplankton from Baltica: Comparison with other fossil groups and sea-level changes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 294 (3): 161–173. https://doi.org/10.1016/j.palaeo.2009.11.003

Hints O., Ainsaar L., Lepland A., Liiv M., Männik P., Meidla T., Nõlvak J. & Radzevičius S. 2023. Paired carbon isotope chemostratigraphy across the Ordovician–Silurian boundary in central East Baltic: Regional and global signatures. *Palaeogeography, Palaeoclimatology, Palaeoecology* 624: 111640. https://doi.org/10.1016/j.palaeo.2023.111640

Holland C.H. & Copper P. 2008. Ordovician and Silurian nautiloid cephalopods from Anticosti Island: traject across the O/S Mass extinction boundary. *Canadian Journal of Earth Sciences* 48: 1015–1038. https://doi.org/10.1139/E08-048

Horny R.J. 1956. On the genus *Dawsonoceras* Hyatt, 1884 (Nautiloidea) of Central Bohemia. *Sborník Ústředního Ústavu geologického, Oddíl paleontologický* 22: 425–452.

Hsieh T.C., Ma K.H. & Chao A. 2016. iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution* 7 (12): 1451–1456. https://doi.org/10.1111/2041-210X.12613

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

Hyatt A. 1884. Genera of fossil cephalopods. *Proceedings of the Boston Society of Natural History* 22: 253–338. Available from https://www.biodiversitylibrary.org/page/42025344 [accessed 20 Jan. 2025].

Hyatt A. 1894. Phylogeny of an acquired characteristic. *Proceedings of the American Philosophical Society* 32 (143): 349–647. https://doi.org/10.5962/bhl.title.59826

Hyatt A. 1900. Cephalopoda. *In*: Zittel K.A.V. (ed.) *Textbook of Paleontology, 1. Second Edition, Translated and Edited by C.R. Eastmann*: 502–592. Macmillan and Co, London.

Isakar M. & Sinicyna I. 1985. Redescription of E. Eichwald's Ordovician bivalve species. *Eesti NSV Teaduste Akadeemia Toimetised Geoloogia / Известия Академии наук Эстонской ССР Геология* 34 (2): 46–54. https://doi.org/10.3176/geol.1985.2.02

Jaanusson V. 1944. Übersicht über die Stratigraphie der Lyckholm-Komplexstufe. *Bulletin de la Commission géologique de Finlande* 16: 92–100.

Jeon J. & Toom U. 2024. First report of an aulaceratid stromatoporoid from the Ordovician of Baltica. *Estonian Journal of Earth Sciences* 73 (2): 71–80. https://doi.org/10.3176/earth.2024.07

Kaljo D., Hints L., Hints O., Männik P., Martma T. & Nõlvak J. 2011. Katian prelude to the Hirnantian (Late Ordovician) mass extinction: a Baltic perspective. *Geological Journal* 46 (5): 464–477. https://doi.org/10.1002/gj.1301

Karsten G. 1869. Die Versteinerungen des Uebergangsgebirges in den Geröllen der Herzogthümer Schleswig und Holstein. *Beiträge zur Landeskunde der Herzogthümer Schleswig und Holstein, Reihe 1* 1: 1–85.

Kiipli E., Kiipli T., Kallaste T. & Ainsaar L. 2010. Distribution of phosphorus in the Middle and Upper Ordovician Baltoscandian carbonate palaeobasin. *Estonian Journal of Earth Sciences* 59: 247–255. https://doi.org/10.3176/earth.2010.4.01

Kiselev G.N. 1990. Klass Cephalopoda. *In*: Kiselev G.N., Sinicyna I.N., Isakar M.A., Mironova M.G. & Saladzhius V.Y. (eds) *Atlas mollûskov verhnego ordovika i silura severo-zapada Vostočno-Evropejskoj platformy*: 33–65. Izdatielstvo Leningradskogo Universiteta, Leningrad.

Kiselev G.N. 1991. Revizia pozdneordovikskikh i siluriskikh tsefalopod Pribaltiki iz kollektsii E.I. Eichwalda. *Bulletin of the Moscow Society of Naturalists Geological series* 66 (4): 85–101.

Korn D. & Klug C. 2003. Morphological pathways in the evolution of Early and Middle Devonian ammonoids. *Paleobiology* 29: 329–348. https://doi.org/10.1666/0094-8373(2003)029<0329:MPITEO>2.0.CO;2

Kröger B. 2007. Concentrations of juvenile and small adult cephalopods in the Hirnantian cherts (Late Ordovician) of Porkuni, Estonia. *Acta Palaeontologica Polonica* 52: 591–608.

Kröger B. 2013. The cephalopods of the Boda Limestone, Late Ordovician, of Dalarna, Sweden. *European Journal of Taxonomy* 41: 1–110. https://doi.org/10.5852/ejt.2013.41

Kröger B. 2025. Additional data to "The Lyckholm acme of cephalopods – Review of the late Katian (Vormsi–Pirgu regional stages), Ordovician cephalopods of Estonia". Dataset. Zenodo. https://doi.org/10.5281/zenodo.14833042

Kröger B. & Aubrechtová M. 2017. Cephalopods from reef limestone of the Vasalemma Formation, northern Estonia (latest Sandbian, Upper Ordovician) and the establishment of a local warm-water fauna. *Journal of Systematic Palaeontology* 16 (10): 799–849. https://doi.org/10.1080/14772019.2017.1347212

Kröger B. & Aubrechtová M. 2019. The cephalopods of the Kullsberg Limestone Formation, Upper Ordovician, central Sweden and the effects of reef diversification on cephalopod diversity. *Journal of Systematic Palaeontology* 17 (12): 961–995. https://doi.org/10.1080/14772019.2018.1491899

Kröger B. & Ebbestad J.O.R. 2014. Palaeoecology and palaeogeography of Late Ordovician (Katian–Hirnantian) cephalopods of the Boda Limestone, Siljan district, Sweden. *Lethaia* 47 (1): 15–30. https://doi.org/10.1111/let.12034

Kröger B. & Isakar M. 2006. Revision of annulated orthoceridan cephalopods of the Baltoscandic Ordovician. *Fossil Record* 9 (1): 139–165. https://doi.org/10.1002/mmng.200600005

Kröger B. & Rasmussen J.A. 2014. Middle Ordovician cephalopod biofacies and palaeoenvironments of Baltoscandia. *Lethaia* 47 (2): 275–295. https://doi.org/10.1111/let.12057

Kröger B., Servais T. & Zhang Y. 2009a. The origin and initial rise of pelagic cephalopods in the Ordovician. *PLoS ONE* 4 (9): e7262. https://doi.org/10.1371/journal.pone.0007262

Kröger B., Zhang Y. & Isakar M. 2009b. Discosorids and oncocerids (Cephalopoda) of the Middle Ordovician Kunda and Aseri Regional Stages of Baltoscandia and the early evolution of these groups. *Geobios* 42: 273–293. https://doi.org/10.1016/j.geobios.2008.09.006

Kröger B., Ebbestad J.O.R., Högström A.E.S. & Frisk Å.M. 2011. Mass concentration of Hirnantian cephalopods from the Siljan District, Sweden; taxonomy, palaeoecology and palaeobiogeographic relationship. *Fossil Record* 14: 35–53. https://doi.org/10.1002/mmng.201000014

Kröger B., Hints L. & Lehnert O. 2016. Ordovician reef and mound evolution: The Baltoscandian picture. *Geological Magazine* 154 (4): 683–706. https://doi.org/10.1017/S0016756816000303

Kröger B., Penny A., Shen Y. & Munnecke A. 2019. Algae, calcitarchs and the Late Ordovician Baltic limestone facies of the Baltic Basin. *Facies* 66: 1. https://doi.org/10.1007/s10347-019-0585-0

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

Kuhn O. 1949. *Lehrbuch der Paläozoologie*. Schweitzerbart, Stuttgart.

Lehmann U. 1987. Cephalopodenreste aus dem Kaolinsand von Braderup auf Sylt. *In*: Hacht U.V. (ed.) *Fossilien von Sylt II*: 185–201. Inge-Marie von Hacht Verlag und Verlagsbuchhandlung, Hamburg.

Levendal T.C., Lehnert O., Sopher D., Erlström M. & Juhlin C. 2019. Ordovician carbonate mud mounds of the Baltoscandian Basin in time and space – A geophysical approach. *Palaeogeography, Palaeoclimatology, Palaeoecology* 535: 109345. https://doi.org/10.1016/j.palaeo.2019.109345

Linnaeus C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata*. *Tomus I*. Laurentii Salvii, Stockholm [Holmiae]. https://doi.org/10.5962/bhl.title.542

Lossen C. 1860. Über einige Lituiten. *Zeitschrift der deutschen geologischen Gesellschaft* 12: 15–28. Available from https://www.biodiversitylibrary.org/page/34776055 [accessed 20 Jan. 2025].

Manda Š. & Turek V. 2018. Silurian tarphycerid *Discoceras* (Cephalopoda, Nautiloidea): Systematics, embryonic development and paleoecology. *Journal of Paleontology* 92 (3): 412–431. https://doi.org/10.1017/jpa.2017.122

Männik P., Lehnert O., Nõlvak J. & Joachimski M.M. 2021. Climate changes in the pre-Hirnantian Late Ordovician based on $\delta^{18}O_{phos}$ studies from Estonia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 569: 110347. https://doi.org/10.1016/j.palaeo.2021.110347

M'Coy F. 1844. *Synopsis of the Characters of the Carboniferous Limestone Fossils of Ireland*. University Press, Dublin. https://doi.org/10.5962/bhl.title.11559

McLaughlin P.I., Vandenbroucke T.R.A., Esteves C.J.P., Bancroft A.M., Paton T.R., Williams M., Brett C.E., Farnam C. & Emsbo P. 2023. The late Katian Elkhorn event: Precursor to the Late Ordovician mass extinction. *Estonian Journal of Earth Sciences* 72 (1): 148. https://doi.org/10.3176/earth.2023.46

Meek F.B. & Worthen A.H. 1866. Contributions to the palaeontology of Illinois and other western states. *Proceedings of the Academy of Natural Sciences of Philadelphia* 18: 251–275. Available from https://www.biodiversitylibrary.org/page/1861711 [accessed 20 Jan. 2025].

Meidla T. 1983. Die Ostrakoden aus den Grenzschichten der Vormsi- und Pirgu-Stufen Westestlands. *Eesti NSV Teaduste Akadeemia Toimetised Geoloogia* / Известия Академии наук Эстонской ССР Геология 32 (2): 53–59. https://doi.org/10.3176/geol.1983.2.02

Meidla T., Ainsaar L., Hints O. & Radzevičius S. 2023. Ordovician of the Eastern Baltic palaeobasin and the Tornquist Sea margin of Baltica. *Geological Society, London, Special Publications* 532 (1): SP532–2022. https://doi.org/10.1144/SP532-2022-141

Melchin M.J., Mitchell C.E., Holmden C. & Štorch P. 2013. Environmental changes in the Late Ordovician–early Silurian: Review and new insights from black shales and nitrogen isotopes. *Geological Society of America Bulletin* 125 (11–12): 1635–1670. https://doi.org/10.1130/B30812.1

Miller A.K. 1932. The cephalopods of the Bighorn formation of the Wind River Mountains of Wyoming. *Transactions of the Connecticut Academy of Arts and Sciences* 31: 193–297.

Miller A.K. & Carrier J.B. 1942. Ordovician Cephalopods from the Bighorn Mountains of Wyoming. *Journal of Paleontology* 16 (5): 531–548.

Miller A.K. & Furnish W.M. 1937. Ordovician Cephalopods from the Black Hills, South Dakota. *Journal of Paleontology* 11 (7): 535–551.

Miller A.K. & Youngquist W. 1947. Ordovician cephalopods from the west-central shore of Hudson Bay. *Journal of Paleontology* 21 (5): 409–419.

Miller A.K. & Youngquist W. 1949. The Maquoketa Coquina of Cephalopods. *Journal of Paleontology* 23 (2): 199–204.

Miller S.A. 1877. *The American Palaeozoic Fossils: A Catalogue of the Genera and Species with Names of Authors, Dates, Places of Publication, Groups of Rocks in which Found, and the Etymology and Signification of the Words and an Introduction Devoted to the Stratigraphical Geology of the Palaeozoic Rocks*. Published privately, Cincinnati, OH. https://doi.org/10.5962/bhl.title.57489

Miller S.A. & Faber C.L. 1894. New species of fossils from the Hudson River Group and remarks upon others. *The Journal of the Cincinnati Society of Natural History* 17: 22–33.
Available from https://www.biodiversitylibrary.org/page/44085432 [accessed 20 Jan. 2025].

Moore R.C. 1964. *Treatise on Invertebrate Paleontology, Part K, Mollusca 3*. University of Kansas Press, Boulder, CO.

Mutvei H. 1957. On the relations of the principal muscles to the shell in *Nautilus* and some fossil nautiloids. *Arkiv för Mineralogi och Geologi* 2: 219–254.

Mutvei H. 2013. Characterization of nautiloid orders Ellesmerocerida, Oncocerida, Tarphycerida, Discosorida and Ascocerida: new superorder Multiceratoidea. *GFF* 135 (2): 171–183.
https://doi.org/10.1080/11035897.2013.801034

Neben W. & Krueger H.H. 1973. Fossilien ordovizischer und silurischer Geschiebe. *Staringia* 2: 51–109.

Nelson S.J. 1963. Ordovician paleontology of the northern Hudson Bay Lowland. *Geological Society of America Memoir* 90: 125–145. https://doi.org/10.1130/MEM90-p1

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

Nielsen A.T. 2011. A re-calibrated revised sea-level curve for the Ordovician of Baltoscandia. *Ordovician of the World: 11th International Symposium on the Ordovician System, Cuadernos del Museo Geominero* 14: 399–402.

Nielsen A.T., Ahlberg P., Ebbestad J.O.R., Hammer Ø., Harper D.A.T., Lindskog A., Rasmussen C.M.Ø. & Stouge S. 2023. The Ordovician of Scandinavia: a revised regional stage classification. *Geological Society, London, Special Publications* 532 (1): SP532–2022.
https://doi.org/10.1144/SP532-2022-157

Niko S. 2008. *Isorthoceras wahlenbergi*, a new Late Ordovician cephalopod from the Boda Limestone of Dalarna, Sweden. *Paleontological Research* 12: 195–198.

Oksanen J., Guillaume Blanchet F., Kindt R., Legendre P., Minchin P.R., O'Hara R.B., Simpson G.L., Peter S., Stevens H.H. & Wagner H. 2013. vegan: Community Ecology Package.

Penny A.M., Hints O. & Kröger B. 2022. Carbonate shelf development and early Paleozoic benthic diversity in Baltica: A hierarchical diversity partitioning approach using brachiopod data. *Paleobiology* 48 (1): 44–64. https://doi.org/10.1017/pab.2021.3

Pohle A., Kröger B., Warnock R.C.M., King A.H., Evans D.H., Aubrechtová M., Cichowolski M., Fang X. & Klug C. 2022. Early cephalopod evolution clarified through Bayesian phylogenetic inference. *BMC Biol* 20 (1): 88. https://doi.org/10.1186/s12915-022-01284-5

Pohle A., Jell P. & Klug C. 2024. Plectronoceratids (Cephalopoda) from the latest Cambrian at Black Mountain, Queensland, reveal complex three-dimensional siphuncle morphology, with major taxonomic implications. *PeerJ* 12: e17003. https://doi.org/10.7717/peerj.17003

Portlock J.E. 1843. *Report on the Geology of the County of Londonderry and of parts of Tyrone and Fermanagh*. Andrew Milliken, Dublin. https://doi.org/10.1515/9783112391341-021

Puura V. & Vaher R. 1997. Tectonics. *In*: Raukas A. & Teedumäe A. (eds) *Geology and Mineral Resources of Estonia*: 163–180. Estonian Academy Publishers, Tallinn.

Roemer C.F. 1861. *Die fossile Fauna der silurischen Diluvial-Geschiebe von Sadewitz bei Oels in Nieder-Schlesien*. Robert Nischkowsky, Breslau.

Roemer C.F. 1885. Lethaea erratica oder Aufzählung und Beschreibung der in der norddeutschen Ebene vorkommenden Diluvialgeschiebe nordischer Sedimentär-Gesteine. *Paläontologische Abhandlungen* 2: 248–420. Available from https://www.biodiversitylibrary.org/page/11307585 [accessed 20 Jan. 2025].

Rõõmusoks A. 1967. *Stratigraphy of the Viruan and Harjuan series (Ordovician) in Northern Estonia I*. Valgus, Tallinn.

Rüdiger H. 1889. *Ueber die Silur-Cephalopoden aus den Mecklenburgischen Diluvialgeschieben*. Rathsbuchdruckerei von C. Michaal & A. Schuster, Güstrow. https://doi.org/10.5962/bhl.title.14078

Saemann L. 1853. Über die Nautiliden. *Palaeontographica* 3: 121–167. Available from https://www.biodiversitylibrary.org/page/33098171 [accessed 20 Jan. 2025].

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

Sauramo M. 1929. Zur Kenntnis der Geologie von Worms und Nuckö, Estland. *Bulletin of the Geological Society of Finland* (2): 17–36.

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

Schmidt F. 1861. Nachträge und Berichtigungen zu den Untersuchungen über die Silurische Formation von Ehstland, Nord-Livland und Ösel. *Archiv für die Naturkunde Liv-, Ehst- und Kurlands, 1 Serie (Mineralogische Wissenschaften, nebst Chemie, Physik und Erdbeschreibung)* 2: 465–474.

Schröder, H. 1891. Untersuchungen über silurische Cephalopoden. *Palaeontologische Abhandlungen, Neue Folge* 1: 1–48. https://doi.org/10.5962/bhl.title.25535

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

Shimizu S. & Obata T. 1936. Study on the paleozoic cephalopods from Asia. Part I. *Journal of the Shanghai Science Institute Section II* 2: 85–146.

Sowerby J. 1816. *The Mineral Conchology of Great Britain; or Coloured Figures and Descriptions of those Remains of Testaceous Animals or Shells which have been Preserved at Various Times and Depths in the Earth*. Benjamin Meredith, London. https://doi.org/10.5962/bhl.title.14408

Stein B. 1937. Vohilaiu geoloogiast. *Eesti Loodus* 5 (5): 198–204.

Stigall A.L. 2023. A review of the Late Ordovician (Katian) Richmondian Invasion of eastern Laurentia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 618: 111520. https://doi.org/10.1016/j.palaeo.2023.111520

Stokes C. 1840. On some species of Orthocerata. *Transactions of the Geological Society of London, Series 2* 5: 705–714. https://doi.org/10.1144/transgslb.5.3.705

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

Stumbur H.A. 1956. O nautiloideâh Kohilaskogo ârusa (Verhnij Ordovik Pribaltiki). *Tartu Riikliku Ülikooli Toimetised* 42: 176–185.

Stumbur H.A. 1959. On the embryonic shells of some Ordovician Tarphyceratida. *Paleontologicheski Zhurnal* (2): 25–29.

Stumbur H.A. 1962. Rasprostranenie nautiloidei v ordovike Estonii (s opisaniem nekotorykh novykh rodov). *ENSV Teaduste Akadeemia Geoloogia Instituudi Uurimused* 10: 131–147.

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. 1959. Ordovician and Silurian Cyrtogomphoceratidae (Nautiloidea) from the Oslo Region, Norway. *Journal of Paleontology* 33 (1): 55–62. https://doi.org/10.2307/1300808

Sweet W.C. 1964a. Barrandeocerida. *In*: Moore R.C. (ed.) *Treatise on Invertebrate Paleontology, Part K, Mollusca 3*: K368–K382. University of Kansas Press, Boulder, CO.

Sweet W.C. 1964b. Oncocerida. *In*: Moore R.C. (ed.) *Treatise on Invertebrate Paleontology, Part K, Mollusca 3*: K277–K319. University of Kansas Press, Boulder, CO.

Sweet W.C. 1964c. Orthocerida. *In*: Moore R.C. (ed.) *Treatise on Invertebrate Paleontology, Part K, Mollusca 3*: K216–K261. University of Kansas Press, Boulder, CO.

Sweet W.C. & Miller A.K. 1957. Ordovician cephalopods from Cornwallis and Little Cornwallis Islands, district of Franklin, Northwest Territories. *Geological Survey of Canada, Bulletin* 38: 1–86. https://doi.org/10.4095/101537

Teichert C. 1930. Die Cephalopoden-Fauna der Lyckholm-Stufe des Ostbaltikums. *Paläontologische Zeitschrift* 12: 264–312. https://doi.org/10.1007/BF03044452

Teichert C. 1933. Der Bau der actinoceroiden Cephalopoden. *Palaeontographica, A* 77: 111–230.

Teichert C. 1939. Nautiloid Cephalopods from the Devonian of Western Australia. *Journal of the Royal Society of West Australia* 25: 103–121.

Teichert C. 1940. Contributions to nautiloid nomenclature. *Journal of Paleontology* 590–597.

Teichert C. 1964a. Actinoceratoidea. *In*: Moore R.C. (ed.) *Treatise on Invertebrate Paleontology, Part K, Mollusca 3*: K190–K216. Geological Society of America and the University of Kansas Press, Boulder, CO.

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

Teichert C. & Glenister B.F. 1953. Ordovician and Silurian cephalopods from Tasmania. *Bulletins of American Paleontology* 34 (144): 1–54.
Available from https://www.biodiversitylibrary.org/page/10672779 [accessed 20 Jan. 2025].

Teichert C. & Yochelson E.L. 1967. Major features of cephalopod evolution. *Essays in Paleontology & Stratigraphy RC Moore Commemorative Volume*: 162–210.

Thorslund P. 1936. Siljanområdets brännkalkstenar och kalkindustri. *Sveriges Geologiska Undersökning, Afhandlingar och Uppsater, C* 398: 1–57.

Troedsson G.T. 1926. On the Middle and Upper Ordovician faunas of northern Greenland. I. Cephalopods. *Meddeleser on Grønland* 71: 1–157.

Turek V. & Aubrechtová M. 2024. Micro-CT reveals 3D endosiphuncular structure in Late Ordovician actinoceratid cephalopod from the Prague Basin (Czech Republic). *Bulletin of Geoscience*s 99 (3): 1–21. https://doi.org/10.3140/bull.geosci.1901

Vinn O. & Mõtus M.-A. 2012. Diverse early endobiotic coral symbiont assemblage from the Katian (Late Ordovician) of Baltica. *Palaeogeography, Palaeoclimatology, Palaeoecology* 321: 137–141. https://doi.org/10.1016/j.palaeo.2012.01.028

Vinn O. & Wilson M.A. 2015. Symbiotic interactions in the Ordovician of Baltica. *Palaeogeography, Palaeoclimatology, Palaeoecology* 436: 58–63. https://doi.org/10.1016/j.palaeo.2015.06.044

Westermann G.E.G. 1998. Life habits of nautiloids. *In*: Savazzi E. (ed.) *Functional Morphology of the Invertebrate Skeleton*: 263–298. John Wiley & Sons, Chichester, NY.

Whiteaves J.F. 1890. Description of eight new species of fossils from the Cambro-Silurian rocks of Manitoba. *Transactions of the Royal Society of Canada, Series 2* 7 (4): 75–83. https://doi.org/10.1017/S0016756800189988

Whiteaves J.F. 1892. The Orthoceratidae of the Trenton limestone of the Winnipeg Basin. *Transactions of the Royal Society of Canada* 9 (4): 77–90. https://doi.org/10.1017/S0016756800146035

Wilson A.E. 1961. Cephalopoda of the Ottawa formation of the Ottawa–St. Lawrence Lowland. *Bulletin of the Geological Survey of Canada* 67: 1–106. https://doi.org/10.4095/100585

Young S.A., Edwards C.T., Ainsaar L., Lindskog A. & Saltzman M.R. 2023. Seawater signatures of Ordovician climate and environment. *Geological Society, London, Special Publications* 532 (1): 137–156. https://doi.org/10.1144/SP532-2022-258

Zou C., Qiu Z., Poulton S.W., Dong D., Wang H., Chen D., Lu B., Shi Z. & Tao H. 2018. Ocean euxinia and climate change "double whammy" drove the Late Ordovician mass extinction. *Geology* 46 (6): 535–538. https://doi.org/10.1130/G40121.1

Zhuravlyeva F.A. 1962. Otrâd Oncocerida. *In*: Orlov Û.A. (ed.) *Osnovy paleontologii. Spravočnik dlâ paleontologov i geologov SSSR. Mollûski – golovonogie. Nautiloidei, èndoceratoidei, aktinoceratoidei, baktritoidei, ammonoidei (agoniatidy, goniatidy, klimenii)*: 102–115. Izdatel'stvo Akademii Nauk.

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