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## M o n o g r a p h

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# Taxonomy and ontogeny of the Lituitida (Cephalopoda) from Orthoceratite Limestone erratics (Middle Ordovician)

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**Abstract.** Ordovician ectocoeliate cephalopods of the order Lituitida Starobogatov, 1983, mainly from erratics of the Orthoceratite Limestone embedded in Pleistocene glacio-fluvial sediments in Germany, Poland and the Kaliningrad Region of Russia are revised. In total, seven genera (*Rhynchorthoceras*, *Ancistroceras*, *Angelinoceras*, *Holmiceras*, *Lituites*, *Trilacinoceras*, *Cyclolitites*) and 28 species are identified. Eleven species are newly described: *Rhynchorthoceras kranepuhlense* sp. nov., *R. rugium* sp. nov., *Holmiceras havelense* sp. nov., *Lituites baculus* sp. nov., *L. bottkei* sp. nov., *L. clavis* sp. nov., *L. dewitzi* sp. nov., *L. kruegeri* sp. nov., *L. nebeni* sp. nov., *Trilacinoceras filix* sp. nov. and *T. knoeffleri* sp. nov. The concept of several taxa described in the 19<sup>th</sup> century, including the ambiguous species *L. lituus* de Montfort, 1808 and *L. perfectus* Wahlenberg, 1818, is refined. Neotypes are proposed for the latter two species.

**Keywords.** Lituitida, Orthoceratite Limestone, Middle Ordovician, ontogeny, intraspecific variation.

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## Introduction

### General aspects

Representatives of the Ordovician cephalopod order Lituitida Starobogatov, 1983 are among the iconic fossils of the Orthoceratite Limestone of Baltoscandia (Fig. 1). They were recognised already in the 18<sup>th</sup> century because of their conspicuous conch shape, which resembles the “*lituus*”, a curved Roman augur staff or war trumpet (Breyne 1732). Indeed, the conch of the genus *Lituites* Bertrand, 1763, and its type species *L. lituus* de Montfort, 1808, is coiled in its apical part, but only slightly curved or completely

straight in the apertural part (Fig. 2). Another typical character is the strongly modified aperture, which forms ventral and lateral sinuses and deep and pronounced ventrolateral, dorsolateral and dorsal lappets. The shell surface is covered by a distinctive ornament consisting of sinuous annuli and lirae. The coiled and uncoiled parts of the phragmocone contain thick internal cameral deposits that can extend into the siphuncle through openings in the connecting rings.

Since the first description of *L. lituus*, many other lituitids expressing a wide range of conch morphologies have been recognised, e.g., *Trilacinoceras* Sweet, 1958, with a simplified, three-lappeted mature aperture, *Angelinoceras* Hyatt, 1894, with conspicuously large coiled conch, *Cyclolituites* Remelé, 1886, with a conch lacking the uncoiled part, *Holmiceras* Hyatt, 1894, and *Ancistroceras* Boll, 1857, with a rapidly expanding straight part of the conch, as well as *Rynchorthoceras* Remelé, 1882, with a straight or only weakly cyrtoconic conch. The latter two genera comprise the stratigraphically oldest lituitids known to date (Fang *et al.* 2021).

Traditionally, the ancestry of the Lituitida has been sought among the coiled tarphyceratid or barrandeoceratid cephalopods (e.g., Flower 1955; Sweet 1958; Balashov 1962; Furnish & Glenister 1964), but the morphology and stratigraphic occurrence of the earliest lituitids led to assumptions of orthoceratidan relationships (e.g., Schindewolf 1942; Dzik 1984; King 1999; Mutvei 2002; Kröger 2006; Kröger *et al.* 2007). Recently, Fang *et al.* (2021) and Pohle *et al.* (in press) proved that phylogenetic analyses can be successfully applied to Palaeozoic non-ammonoid cephalopods including lituitids; their results supported orthoceratidan (or at least orthoceratoid) relationships of the lituitids. This view is also followed in the present paper; for a further discussion of the phylogenetic relationships of the Lituitida, see the summary provided by King & Evans (2019).

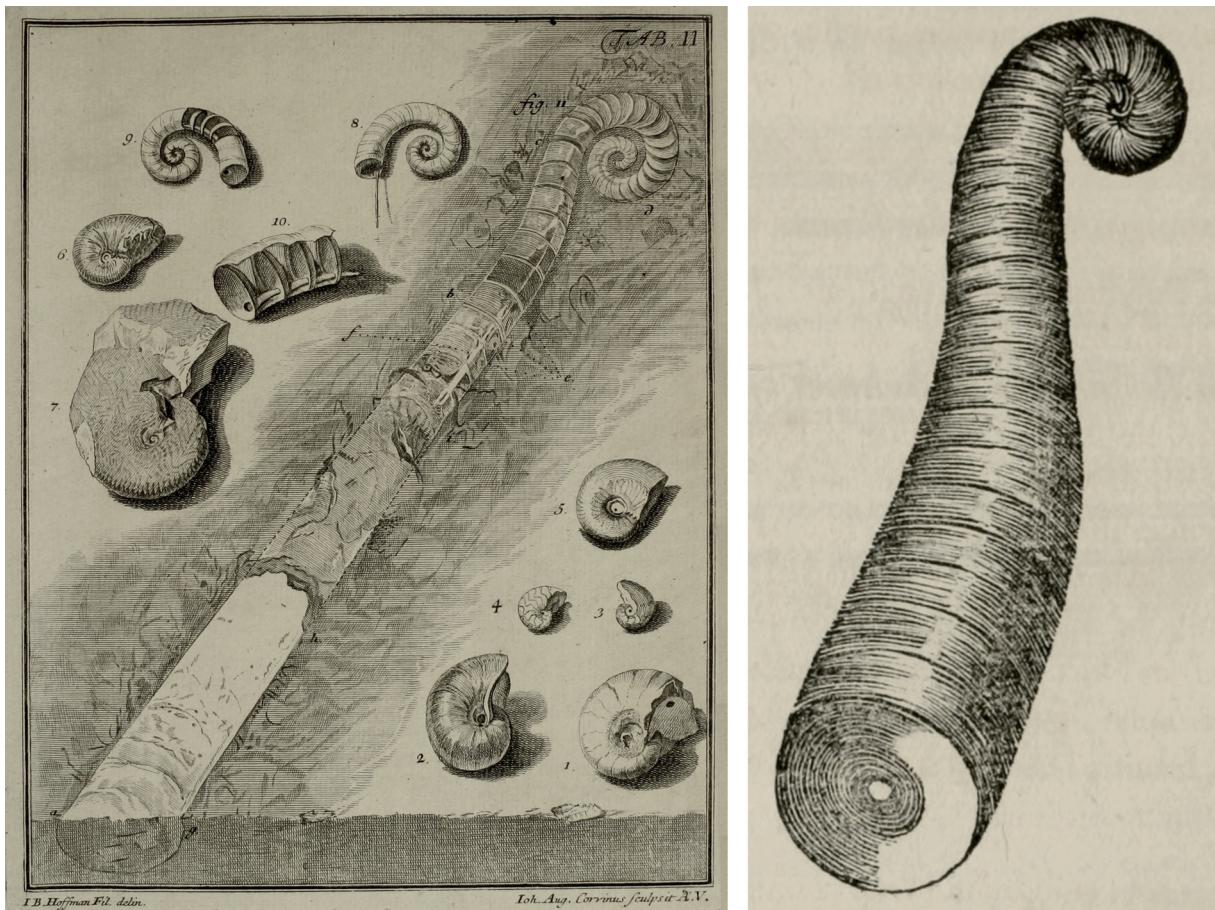
Although the Lituitida is a distinctive order of cephalopods with a good fossil record, the separation of individual species has always been problematic due to the existence of transitional morphologies and uncertainties about the taxonomic significance of individual characters. Moreover, it was further complicated by the incomplete preservation of nearly all of the specimens, which also includes the type material (discussion in Aubrechtová & Meidla 2020). Because of these problems, we use the full set of characters (see below) here for the taxonomic treatment of the material.



**Fig. 1.** Large slab of the Upper Grey Orthoceratite Limestone (late Darriwilian, Middle Ordovician) with scattered conchs of lituitid and orthoceratid cephalopods, sample MB.C.30490 from the Island of Öland (Sweden). Scale bar units = 10 mm.

Most species of Baltoscandian lituitids were described in the second half of the 19<sup>th</sup> century (e.g., Boll 1857; Angelin 1880; Dewitz 1880; Remelé 1880, 1882, 1890; Holm 1891; Hyatt 1894) and are often known only from unrevised type collections. Some detailed taxonomic works on Baltoscandian lituitids were published later (Foerste 1930; Balashov 1953; Sweet 1958; Furnish & Glenister 1964; Dzik 1984; Aubrechtová & Meidla 2020), while numerous lituitid taxa were described from other regions, especially China (e.g., Lai 1965, 1986; Qi 1980; Fang *et al.* 2017). In Baltoscandia and China, the lituitids have been used as low-resolution biostratigraphic indicators (e.g., Jaanusson & Mutvei 1953; Jaanusson 1960; Lai 1989; Xiao *et al.* 2006; Evans *et al.* 2014).

In the present study, we revise the Baltoscandian lituitids based on historical and more recent collections, mainly from the Middle Ordovician (Darriwilian) erratics in Pleistocene glacio-fluvial sediments in Germany and Poland, including type specimens of several species. The studied collection included also specimens from in-situ occurrences in Sweden (including the Island of Öland), Estonia and Norway. In addition to the material from Baltoscandia, one additional specimen was identified in the collections that originates from the brown limestone of the Datianba Formation (Middle or Late Ordovician) of the Songtao County (Guizhou, South China); this specimen was added to the study due to its exceptionally complete preservation. We further discuss the taxonomy and investigate the ontogenetic variation in some lituitid taxa.



**Fig. 2.** Historical illustrations of *Lituites* specimens of Breyne (1732) (left) and de Montfort (1808) (right).

### **Geological and stratigraphic outline**

The Middle and Late Ordovician Orthoceratite Limestone is a succession of thin-bedded, condensed, cool-water carbonate sedimentary rocks that were deposited in an epicontinental sea on the continental margin of Baltica (Schmitz *et al.* 1996; Lindskog & Eriksson 2017; Lindskog *et al.* 2020). Due to the gentle dipping of the marginal platform, the transport of weathering products was reduced; sedimentation was extremely slow, with recurring sedimentation breaks, development of hard-grounds and prolonged phases of erosion (e.g., Lindström 1971, 1979; Jaanusson 1973, 1982; Schmitz *et al.* 1996; Dronov & Holmer 1999; Ekdale & Bromley 2001; Lindskog *et al.* 2017). The character and distribution of the numerous facies of the Orthoceratite Limestone was strongly influenced by local bathymetric conditions, eustatic sea-level changes and the gradual drift of Baltica towards equatorial latitudes (Jaanusson 1973, 1982; Dronov & Holmer 1999; Cocks & Torsvik 2005; Dronov & Rozhnov 2007; Dronov *et al.* 2011; Bergström *et al.* 2013; Torsvik & Cocks 2017).

The Orthoceratite Limestone has a wide geographic distribution across Baltoscandia. It commonly occurs as erratic boulders within Pleistocene glacial and glacio-fluvial sediments in Western, Central and Eastern Europe. Research on erratic blocks in these regions has a long tradition and contributed substantially to the knowledge on the Orthoceratite Limestone in the source areas (Sendino & Bochmann 2021).

Parts of the Orthoceratite Limestone succession are well-known to yield abundant and well-preserved body fossils, for example brachiopods (e.g., Rasmussen *et al.* 2009), ostracods (Tinn & Meidla 2001; Tinn *et al.* 2006), molluscs (e.g., Lindskog *et al.* 2015; Sendino & Bochmann 2021) as well as trace fossils (Toom *et al.* 2019). The most important index macrofossils of the Orthoceratite Limestone are trilobites (Pärnaste & Bergström 2013; Pärnaste *et al.* 2013) and orthoconic cephalopods (King 1999; Kröger 2004b, 2006, 2012). The fossil content of the Orthoceratite Limestone, together with lithological features, enable the determination of the source areas and stratigraphic levels of erratic boulders (e.g., Remelé 1883; Hucke 1967; Neben & Krueger 1971; Dzik & Kiselev 1995; Malinky 2007; Maletz & Schöning 2017).

The variable facies characters of the Orthoceratite Limestone cause some difficulties in correlation between individual confacies belts (Jaanusson 1976); hence, separate stratigraphic scales for the in-situ Orthoceratite Limestone occurrences were used in the western, central and eastern areas of Baltoscandia (Dronov & Holmer 1999; Kröger 2004b; Ebbestad & Högström 2007; Malinky 2007; Pärnaste *et al.* 2013; Sendino & Bochmann 2021) and for the erratics (Hucke 1967; Neben & Krueger 1971). However, recent research has enabled the unification of the Baltoscandian stratigraphic scheme and correlation with the global chronostratigraphic standard (e.g., Nõlvak *et al.* 2006; Bergström *et al.* 2009). This has been achieved mainly by the application of chemostratigraphic methods (e.g., Ainsaar *et al.* 2007, 2010; Bergström *et al.* 2015), conodont and graptolite biostratigraphic data (e.g., Bergström 2007a, 2007b; Bergström & Löfgren 2008) and their integration (e.g., Wu *et al.* 2018).

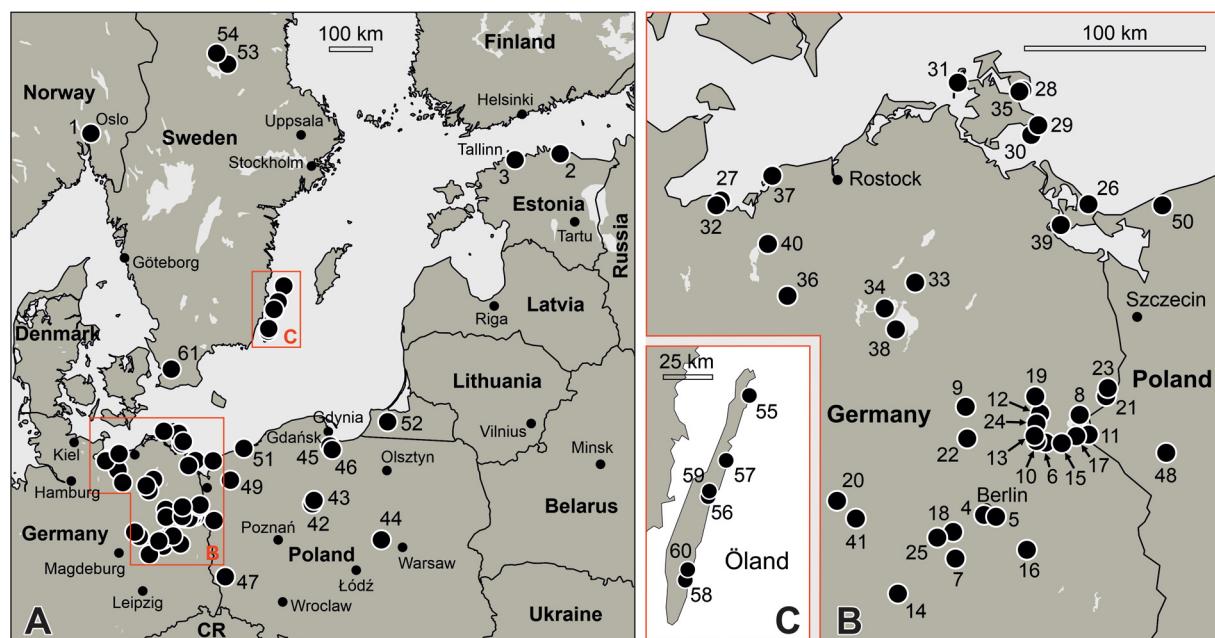
### **Material and methods**

#### **Studied material**

The present study is based on a total of 249 specimens of lituitid cephalopods (Supp. file 1, Supp. file 2) kept in the fossil invertebrate collection of the Museum für Naturkunde, Berlin (MB.C. prefix). The examined specimens were found in boulders of the Middle Ordovician Orthoceratite Limestone erratics embedded in Pleistocene glacio-fluvial sediments in northern Germany, Poland and the Kaliningrad Region of Russia. Twenty-three specimens come from in-situ limestones at localities in Sweden (including the Island of Öland), Estonia and Norway (Fig. 3). An additional specimen (MB.C.29655) from the brown limestone of the Datianba Formation (Middle or Late Ordovician) of the Songtao County

(Guizhou, South China) was included in the study, as well, because the preservation of the conch is exceptionally complete and enables direct comparisons with the Baltoscandian material.

Almost 50% of the specimens were collected at localities near Eberswalde (Brandenburg, Germany; Fig. 3B), where they came from erratic boulders of middle and/or late Darriwilian age. This leads to some collection and stratigraphy bias in the record, although the prevalence of specimens of the genera *Lituites* (42% of all specimens) and *Rhynchorthoceras* (30%) agrees with their general high abundance



**Fig. 3.** **A.** Map with localities from which the herein studied specimens originated. **B.** Localities in north-eastern Germany and western Poland. **C.** Localities in the Island of Öland (Sweden). Map prepared using the QGIS software (using the open-source World Map, OpenStreetMap and “WISE Large rivers and large lakes F1v1 geodatabase” of the European Environment Agency). Number coding of localities: **Norway:** 1 – Oslo (former Christiania); **Estonia:** 2 – Karula (Lääne-Viru County), 3 – Tallinn (former Reval, Harju County); **Germany, Berlin:** 4 – Schmargendorf, 5 – Tempelhofer Feld; **Germany, Brandenburg:** 6 – Eberswalde, 7 – Fresdorf, 8 – Gellmersdorf (Angermünde), 9 – Gransee (Ruppin), 10 – Heegermühle, 11 – Hohensaaten, 12 – Joachimsthal, 13 – Karlsröhre (Lichterfelde, Eberswalde), 14 – Kranepuhl, 15 – Niederfinow, 16 – Niederlehme, 17 – Oderberg, 18 – Potsdam, 19 – Ringenwalde, 20 – Schmetzdorf, 21 – Schwedt, 22 – Teschendorf (Löwenberg), 23 – Vierraden (Schwedt), 24 – Werbellinsee, 25 – Werder (Potsdam); **Germany, Mecklenburg-Vorpommern:** 26 – Bansin (Usedom), 27 – Boltenhagen (Gross Klütz Höved), 28 – Dwarsieden (Rügen), 29 – Göhren, 30 – Groß Zicker (Rügen), 31 – Hiddensee Island, 32 – Klütz Höved, 33 – Lansen (Malchin), 34 – Lebbin, 35 – Mukran (Sassnitz, Rügen), 36 – Neu-Ruthenbeck (Parchim), 37 – Rerik, 38 – Röbel, 39 – Usedom, 40 – Ventschow; **Germany, Saxony-Anhalt:** 41 – Schlangenthal; **Poland, Kujawi-Pomerania:** 42 – Bydgoszcz (former Bromberg), 43 – Osielsk (Bydgoszcz); **Poland, Masovia:** 44 – Czerwińsk; **Poland, Pomerania:** 45 – Juszkowo (former Gischkau), 46 – Skowarcz (former Schönwarling); **Poland, Silesia:** 47 – Żory (former Sorau); **Poland, West Pomerania:** 48 – Barnówko (former Berneuchen), 49 – Dewitz Castle (Dobra, former Dewitzburg bei Daber), 50 – Chrząszczewska Island (former Gristow), 51 – Ustronie Morskie (former Henkenhagen); **Russia:** 52 – Kaliningrad; **Sweden, Dalarna:** 53 – Fjecka (Boda), 54 – Skattungbyn; **Sweden, Öland:** 55 – Böda Hamn, 56 – Gärdslösa, 57 – Kårehamn, 58 – Skärlöv, 59 – Tjusby, 60 – Triberga; **Sweden, Skåne:** 61 – Södra Sandby.

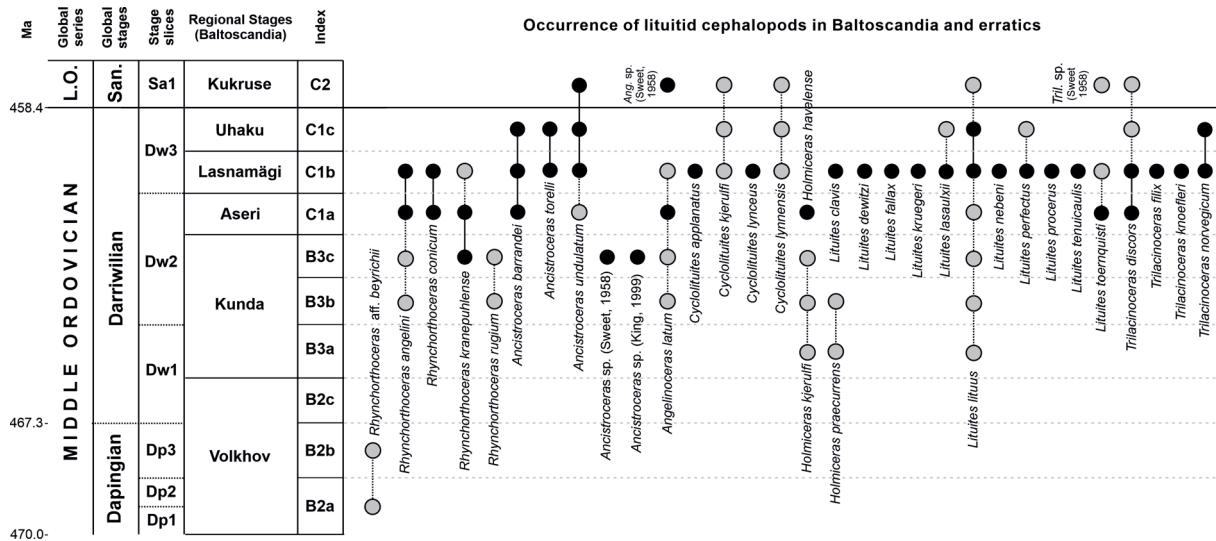
in Middle Ordovician strata of Baltoscandia and China. Other genera identified in the collection include *Ancistroceras* (ca 16% of all specimens), *Trilacinoceras* (5%), *Angelinoceras* (3%), *Cyclolituites* (2%) and *Holmiceras* (one single specimen).

A total of seven lituitid genera and 28 species were identified, eleven species are newly described below. Only four specimens could not be determined at the genus level, while 109 specimens (44%) of all investigated specimens were determined at genus level but not at species level. The highest proportion of unidentifiable specimens is in the genus *Ancistroceras* (68%), followed by *Lituites* (63% of all specimens) and *Rhynchorthoceras* (19%). The relatively high proportion of unidentifiable specimens in these genera is the result of fragmentary preservation, as diagnostic characters in many lituitid species are related to the coiled part of the conch.

The stratigraphic positions of the specimens were inferred from information on museum labels, as well as from the lithology and accompanying fossils (e.g., Jaanusson & Mutvei 1953; Jaanusson 1960, 1963; Hucke 1967; Neben & Krueger 1971, 1973; Ebbestad & Högström 2007). In most cases, it was possible to reliably assign the specimens to regional Baltoscandian and global stages (Supp. file 1, Fig. 4).

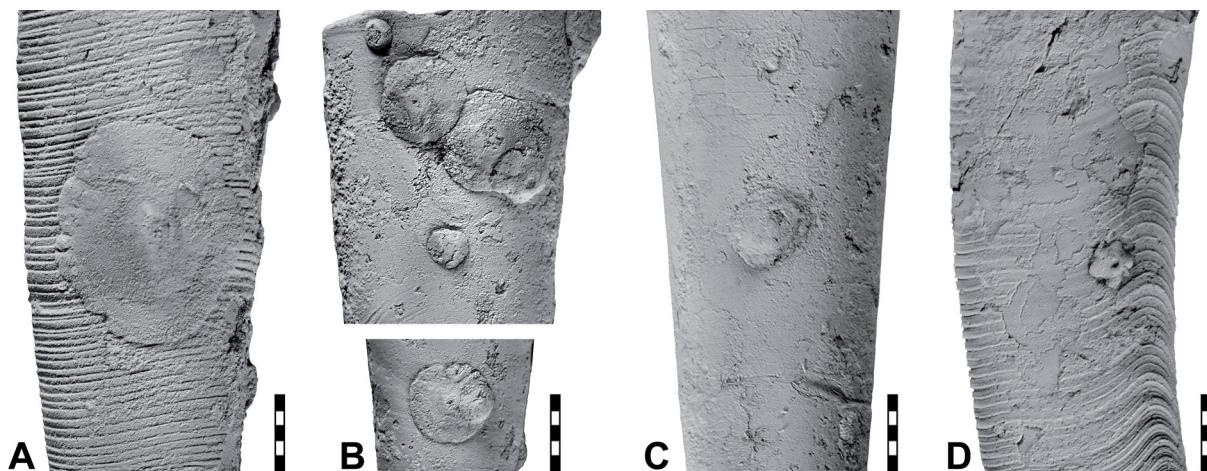
Most of the specimens are isolated fragments of coiled or uncoiled parts of the conchs. The specimens are not significantly deformed or corroded, but the initial and apertural parts of the conchs are usually broken off. The shell ornament is generally well preserved; in some cases, the shell surface bears shallow, irregular pits resembling structures described by Pohle *et al.* (2019); the authors listed local, post-mortem dissolution of the shell and the role of bacteria or fungi among the possible explanations for the origin of these pits.

Along with photographs, we have reproduced illustrations of some of the specimens described by Angelin (1880), Noetling (1882, 1884), Remelé (1890), Holm (1891) and Dzik (1984) because these are very accurate and show additional details of the conch morphology.

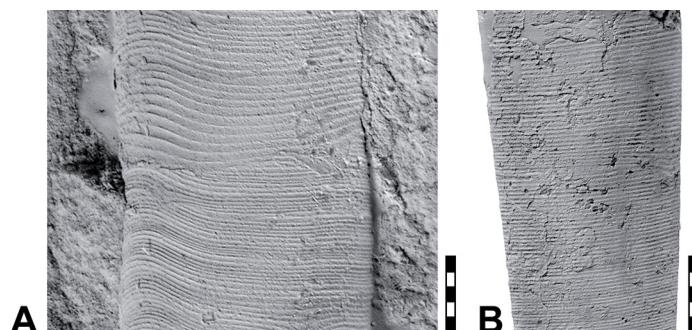


**Fig. 4.** Stratigraphic distribution of lituitid taxa in Ordovician strata of Baltoscandia and Ordovician erratics; black circles indicate unambiguous presence, grey circles indicate possible presence. Species with unknown stratigraphic occurrence are excluded from the scheme. Stratigraphic chart after Ebbestad & Högström (2007) and Meidla *et al.* (2014); stage slices after Bergström *et al.* (2009).

Macrofossils accompanying the lituitid specimens include endoceratid, orthoceratid and tarphyceratid cephalopods, asaphid, cheirurid, illaenid and lichid trilobites, gastropods of the genera *Clathrospira* Ulrich & Scofield, 1897 and *Lesueurilla* Koken, 1898, rhynchonellid brachiopods of the genus *Porambonites* Pander, 1830 and hyoliths. Holdfasts of stalked echinoderms are attached to the shell surfaces in sixteen cephalopod specimens (Fig. 5). Ichnofossils are represented in eight cephalopod specimens by small (ca 1 mm in diameter), circular borings (possibly *Trypanites* Mägdefrau, 1932), which are either scattered on the shell surface or located on the concave surface of septa, where they are concentrated around the septal foramen (MB.C.11700). The internal mould of specimen MB.C.11629 bears burrows attributable to the ichnogenus *Arachnostega* Bertling, 1992. The shells of eight cephalopod specimens bear healed injuries (Fig. 6); similar damages have been reported before and interpreted as likely caused by a predatory attack during the animal's life (Kröger 2004a; Klug 2007).



**Fig. 5.** Echinoderm holdfasts on shells of lituitid specimens. **A.** *Rhynchorthoceras angelini* (Boll, 1857), specimen MB.C.11727 (Schmidt Coll.) from near Berlin-Schmargendorf. **B.** *Rhynchorthoceras conicum* (Hisinger, 1837), specimen MB.C.30508 from Dewitz Castle, Dobra (former Dewitzburg bei Daber; West Pomerania, Poland). **C.** *Rhynchorthoceras rugium* sp. nov., holotype MB.C.11728 (Hoffmann & Gager 1972 Coll.) from Mönchgut (Island of Rügen). **D.** *Trilacinoceras knoeffleri* sp. nov., paratype MB.C.30559 (Krueger Coll.) from Mukran (Sassnitz, Island of Rügen) (Mecklenburg-Vorpommern). Scale bar units = 1 mm.



**Fig. 6.** Shell injuries of lituitid specimens (shown in the centre to the right in both A and B). **A.** *Lituites bottkei* sp. nov., holotype MB.C.29651 (Bottke Coll.) from Gårdslösa (Island of Öland, Sweden). **B.** *Rhynchorthoceras angelini* (Boll, 1857), specimen MB.C.29656 (Bottke Coll.) from Skärö (Island of Öland). Scale bar units = 1 mm.

## Morphological terminology

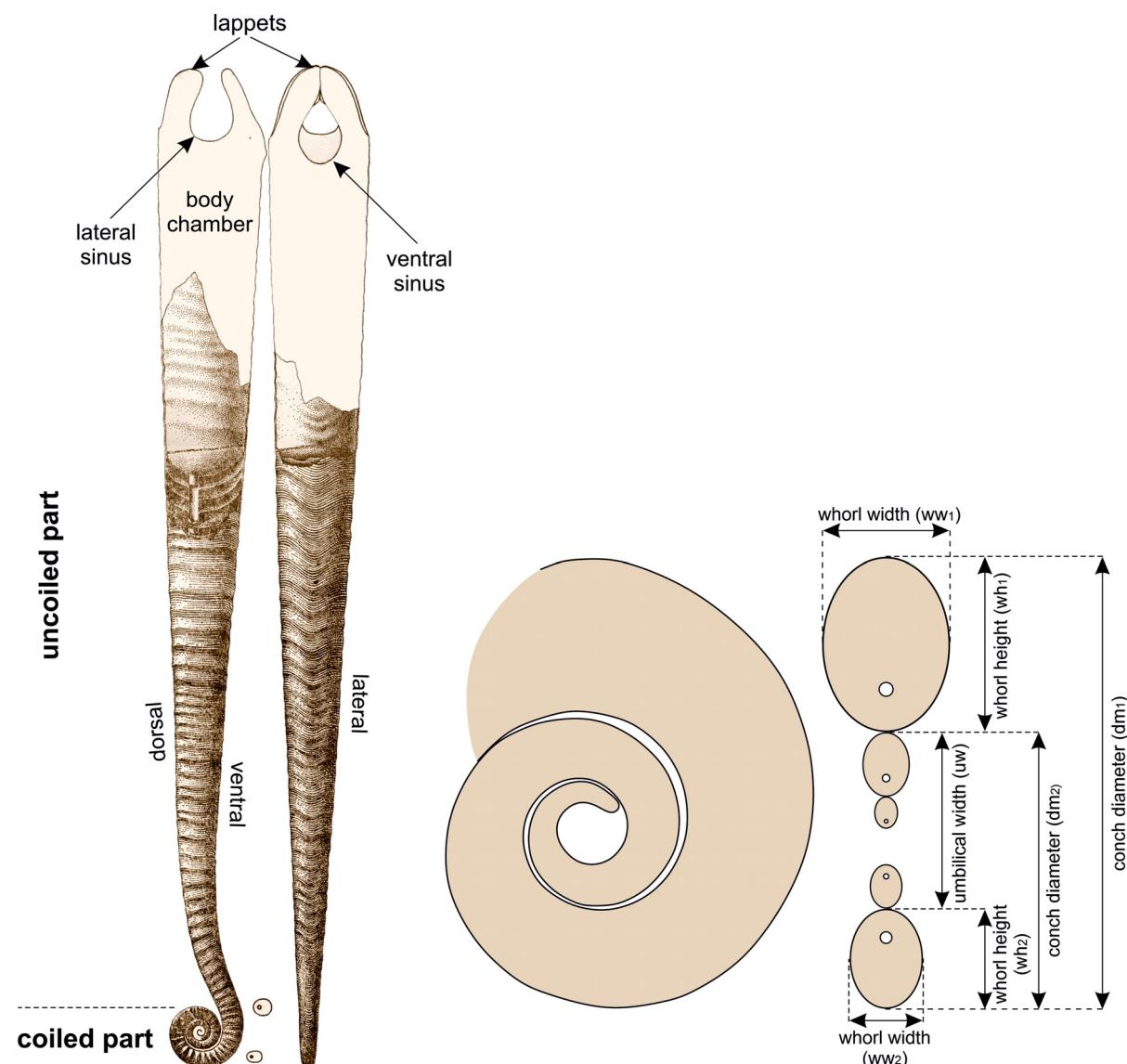
The terminology used here to describe lituitid conchs is based on the work of Furnish & Glenister (1964) and Flower (1964). The morphology of the coiled part of the conchs was quantified using parameters and ratios defined by Korn & Klug (2003) and Korn (2010) for ammonoids, while the terminology of shell ornament follows Kröger (2008) and Klug *et al.* (2015). The used terminology is summarised in Table 1 and Fig. 7.

Below follows a short explanation of the terms used:

### Conch shape

The lituitid conch is divided into three parts:

- coiled (juvenile) part – it consists of several, more or less tightly coiled, volutions (in the representatives of the family Sinoceratidae, the apical part of the conch is not coiled but cytro- or orthoconic);
- backcoiled (preadult) part – the conch shows inverted coiling direction;
- straight (adult) part – conch part without coiling.



**Fig. 7.** Morphological terminology used in this study to describe lituitid specimens; drawing from Dzik (1984).

**Table 1.** Terminology for the description of the specimens of lituitid cephalopods.

Parameter [unit]	Abbreviation	Calculation
conch diameter [mm]	dm	
whorl height [mm]	wh	
whorl width [mm]	ww	
umbilical width [mm]	uw	$dm_1 - wh_1 - wh_2$
apertural height [mm]	ah	
interspace width	iw	$(dm_1 - dm_2 - wh_1) / wh_1$
whorl expansion rate (outline)	WERdm	$(dm_1 / dm_2)^2$
whorl expansion rate apertural height)	WERah	$[dm_1 / (dm_1 - ah)]^2$
umbilical width index	UWI	$uw / dm$
whorl width index	WWI	$ww / wh$
angle of expansion [°]	EA	$2 * (\arctan((d_{max} - d_{min}) / h)) * 180 / \pi$ chamber length/wh
chamber length ratio	CLR	
siphuncule diameter [mm]	sd	
siphuncular diameter ratio	SDR	$sd / wh$
siphuncle distance [mm]	sp	
siphuncular position ratio	SPR	$sp / wh$

The backcoiled and straight parts are collectively referred to as “uncoiled part” when a particular character applies to both conch parts. In some representatives of the family Lituitidae Phillips, 1848, such as the genus *Ancistroceras*, a backcoiled part is lacking; in the species of the genus *Cyclolituites* of the family Lituitidae, the uncoiled part of the conch is not developed, and the conch remains coiled through ontogeny.

For the description of the general geometry of the uncoiled conch, the expansion rate of the conch is used:

$$EA = \text{expansion angle (in } ^\circ\text{)}$$

For the description of the whorl profile, the terms whorl height (wh), apertural height (ah, which is identical with the whorl height in openly coiled conchs) and whorl width (ww) are used for both the coiled and uncoiled parts of the conch (including in *Rhynchorthoceras*, which lacks the coiled part). The umbilical width (uw) refers to the coiled conchs. The size of the coiled conch is measured by its diameter (dm). In the descriptions, the following indexes are used:

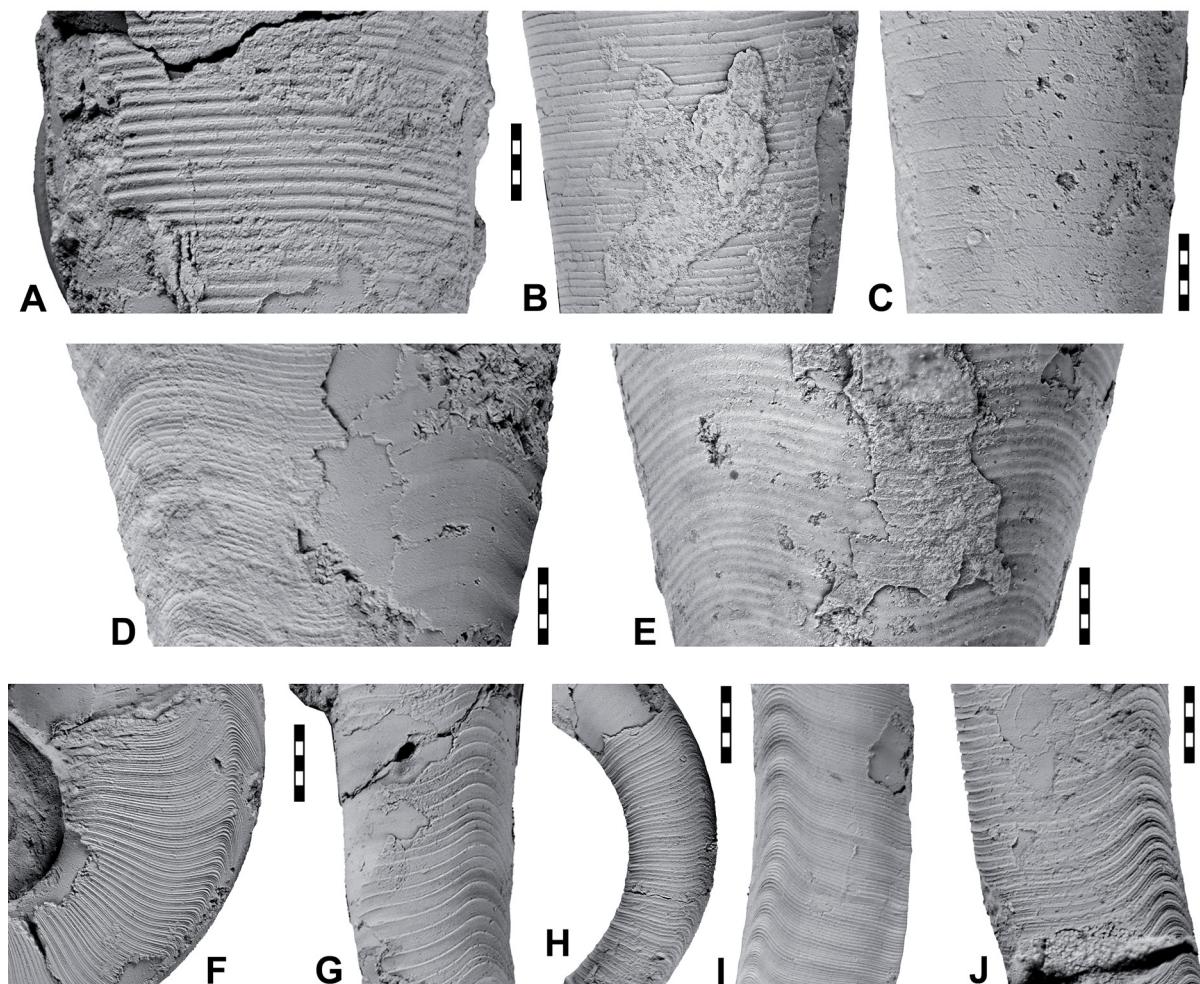
$$\begin{aligned} UWI &= \text{umbilical width index} = uw / dm \\ WWI &= \text{whorl width index} = ww / wh \end{aligned}$$

We used two measurements of the whorl expansion rate (WER) to distinguish between the mode of coiling and the actual expansion of the conch:

$WER_{dm} = \text{coiling rate calculated with the diameter of the conch} = (dm_1 / dm_2)^2$ ; this describes the opening rate of the whorls along the venter;

$WER_{ah}$  = coiling rate calculated with the apertural height (ah) of the conch =  $(dm_1/(dm_1 - ah_1))^2$ ; this describes the expansion rate of the whorl tube that accommodates the soft body. Note that in lituitid cephalopods the apertural height equals the whorl height.

For tightly coiled conchs, the distinction is unnecessary because both modes lead to the same result; then the whorl expansion rate WER is given without an index.



**Fig. 8.** Ornament details of lituitid specimens. **A.** Coarse lirae, symmetric crests; *Rhynchorthoceras angelini* (Boll, 1857), specimen MB.C.30495.1. **B.** Coarse lirae, asymmetric crests; *R. angelini* (Boll, 1857), specimen MB.C.11716. **C.** Faint, widestanding striae; *R. rugium* sp. nov., holotype MB.C.11728. **D.** Lirae and almost smooth internal shell; *Ancistroceras torelli* (Remelé, 1881), specimen MB.C.30519. **E.** Lirae and undulated internal shell; *A. undulatum* (Boll, 1857), specimen MB.C.11697. **F.** Narrow annuli, raised lirae and growth lines; *Cyclolituites appanatus* (Remelé, 1880), specimen MB.C.30560. **G.** Wide-standing, prorsiradiate lirae and very fine growth lines; *Lituites dewitzi* sp. nov., holotype MB.C.30538. **H.** Sharp lirae, straight on the flanks; *L. fallax* Remelé, 1890, holotype MB.C.11672.2. **I.** Sharp, prorsiradiate lirae and flat annuli; *L. kruegeri* sp. nov., holotype MB.C.30539. **J.** Wide-standing, sharp lirae and very flat annuli, straight on the flanks; *Trilacinoceras knoefleri* sp. nov., paratype MB.C.30559. Scale bar units = 1 mm.

### **Chambers**

The distance of the septa is expressed as the relative length of phragmocone chambers as the chamber length ratio: CLR = length of the phragmocone chamber divided by the whorl height of the chamber.

### **Siphuncle**

We refer to the relative size and position of the siphuncle using two ratios:

- SDR = siphuncular diameter ratio: dorso-ventral width of the septal foramen divided by the corresponding whorl height;
- SPR = siphuncular distance ratio: distance of the centre of the siphuncle from the dorsal shell wall divided by the corresponding whorl height.

### **Shell ornament**

We distinguish between the following elements to describe the shell ornament:

- growth lines – the finest ornament, formed by the discontinuous secretion of the shell at the aperture (Klug *et al.* 2015) (Fig. 8F–G);
- lirae – transverse raised lines, coarser than growth lines and sometimes formed by a dense amalgamation of growth lines; transverse profile of lirae may be symmetric (Fig. 8A, D–I) or asymmetric (Fig. 8B);
- ribs – coarse transverse ornament, which may be limited to certain part of the conch circumference, usually to the flanks;
- annuli – transverse rings around the whole conch circumference, formed either by shell wall thickening or shell wall undulation (Fig. 8F, I–J);
- striae – minute transverse grooves (Fig. 8C).

The direction of ornament elements is classified as:

- rursiradiate = general backward direction;
- rectiradiate = general radial direction;
- prorsiradiate = general forward direction.

The course of ornament elements is classified as:

- linear = with no remarkable projections and sinuses;
- convex = with only one wide lateral projection and a ventral sinus;
- concavo-convex = with a lateral sinus, ventrolateral projection and a ventral sinus;
- biconvex = with dorsolateral projection, a lateral sinus, a ventrolateral projection and a ventral sinus.

The measured parameters and ratios were plotted in diagrams to show changes of the characters through ontogeny. The logarithmic scale was used in the diagrams to account for the exponential conch size growth; the logarithmic scale was used also in the case of uncoiled conch parts and orthoconic conchs for consistency and to enable comparisons. In the illustrations of the growth lines, the arrow indicates the position of the middle of the venter, the double line the position of the middle of the dorsum.

## Results

Phylum Mollusca Linnaeus, 1758  
Class Cephalopoda Cuvier, 1797

Order **Lituitida** Starobogatov, 1983

### Diagnosis

Cephalopods with longiconic orthoconic or weakly cyrtoconic conchs, with cyrtoconic or coiled apical part. Siphuncle tubular, narrow (up to 0.20 of whorl height). Septal necks straight (orthochoanitic), rarely cyrtochoanitic in apical conch parts, and long (usually 0.25–0.30 of chamber length but over 0.50 in some taxa). Connecting rings often disaggregated and covered with cameral deposits that extend to cover the septal neck and inner parts of the connecting ring. Cameral deposits often consist of longitudinal lamellae or sheets that longitudinally divide chambers. Initial chamber small (length = 0.4 mm), subspherical, without cicatrix (after Kröger *et al.* 2007, emended).

Family **Sinoceratidae** Shimizu & Obata, 1935

### Diagnosis

Family of the order Lituitida with orthoconic or cyrtoconic apical part of the conch. Whorl profile elliptical to circular. Shell surface smooth or ornamented with growth lines and transverse lirae or striae; ventral sinus of ornament elements weakly developed. Siphuncle subcentral or central in position, septal necks orthochoanitic but sometimes cyrtochoanitic in the apical part (after Dzik 1984 and Kröger *et al.* 2007, emended).

### Genera included

*Rhynchorthoceras* Remelé, 1882; *Sinoceras* Shimizu & Obata, 1935; *Tyrioceras* Strand, 1934.

Genus **Rhynchorthoceras** Remelé, 1882

### Type species

*Lituites Breynii* Boll, 1857; subsequent designation by Furnish & Glenister (1964).

### Diagnosis

Genus of the family Sinoceratidae with orthoconic, longiconic conch, slightly curved in the apical part; expansion angle between 8° and 17°; whorl profile circular or compressed. Shell surface smooth or decorated with transverse lirae or striae. Siphuncle ca 15% of whorl height, central or subcentral in position, displaced towards the convex side of the conch; septal necks orthochoanitic, connecting rings tubular or slightly expanded within chambers. Cameral deposits with single vertical lamellae on the concave side of the conch (after Kröger *et al.* 2007, emended).

### Species included

*Lituites angelini* Boll, 1857; *Rhynchorthoceras Beyrichii* Remelé, 1882; *Lituites Breynii* Boll, 1857; *Rhynchorthoceras blackduckense* Stait, 1988; *Rhynchorthoceras concavum* Lai & Wang, 1986; *Orthceratites conicus* Hisinger, 1837; *Cyrtoceras damesi* Dewitz, 1879; *Rhynchorthoceras guanyinqiaense* Lai, 1986; *Rhynchorthoceras helgoeyense* Sweet, 1958; *Rhynchorthoceras jurongense* Zou, 1988; *Rhynchorthoceras kranepuhlense* sp. nov.; *Rhynchorthoceras lineatum* Lai, 1987; *Rhynchorthoceras lunshanense* Zou, 1988; *Rhynchorthoceras minor* Kröger *et al.*, 2007; *Rhynchorthoceras paucisinum* Lai, 1987; *Rhynchorthoceras rugium* sp. nov.; *Rhynchorthoceras*

*yizanense* Fang *et al.*, 2021; *Rhynchorthoceras Zaddachi* Remelé, 1882; *Rhynchorthoceras zhejiangense* Zou, 1987.

### Geographic and stratigraphic occurrence

Argentine Precordillera, Canada, Baltoscandia, Wales (?), northern Germany, Poland, the Kaliningrad Region of Russia, northern Poland, Bohemia and China; Middle to Late Ordovician.

### Remarks

*Rhynchorthoceras* includes the stratigraphically oldest, Dapingian, lituitid species (Kröger *et al.* 2007; Aubrechtová & Turek 2018; Fang *et al.* 2021).

Species of *Rhynchorthoceras* differ from the species of *Sinoceras* by a greater expansion angle and shorter septal necks, and from the species of *Tyrioceras* in shorter phragmocone chambers. Fang *et al.* (2021) suggested to synonymise *Tyrioceras* with *Rhynchorthoceras*, but the collection studied here is not sufficient to address this issue.

Species of *Ancistroceras* and *Holmiceras* of the family Lituitidae differ from the species of *Rhynchorthoceras* in the coiled juvenile conch. Also, the conchs in the species of *Ancistroceras* and *Holmiceras* usually expand more strongly and are more prominently ornamented (with annuli). However, some species of the three genera might be difficult to separate, if apical portions of the conchs are missing (Kröger *et al.* 2007; Aubrechtová & Meidla 2020; Fang *et al.* 2021).

#### *Rhynchorthoceras angelini* (Boll, 1857)

Figs 9–12, Tables 2–3

*Lituites Angelini* Boll, 1857: 89.

*Rhynchorthoceras Oelandicum* Remelé, 1882: 134–135, pl. 5 fig. 5.

*Rhynchorthoceras tenuistriatum* Remelé, 1882: 137–138.

*Rhynchorthoceras Angelini* var. *lineata* Remelé, 1882: 136.

*Rhynchorthoceras Angelini* var. *virgata* Remelé, 1882: 136.

*Orthoceras Angelini* – Boll 1857: pl. 4 fig. 11.

*Ancistroceras Angelini* – Remelé 1881: 195.

*Rhynchorthoceras Angelini* – Remelé 1882: 135; 1890: 19. — Rüdiger 1889: 37.

*Rhynchorthoceras Oelandicum* – Rüdiger 1889: 40.

*Rhynchorthoceras tenuistriatum* – Remelé 1890: 74, pl. 5 fig. 7.

*Rhynchorthoceras Angelini* var. *lineata* – Remelé 1890: pl. 5 fig. 6, pl. 6 fig. 6.

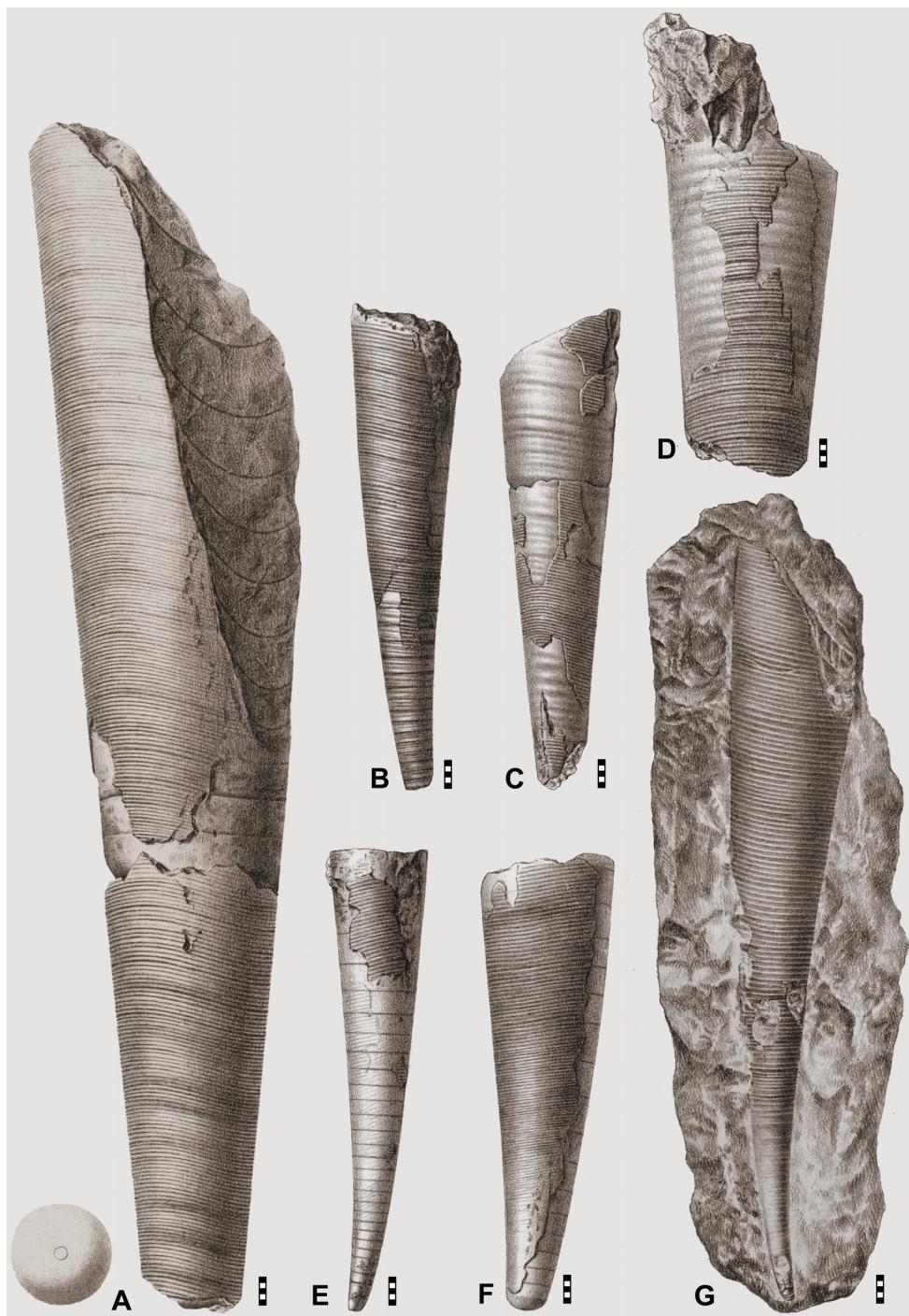
*Rhynchorthoceras Angelini* var. *virgata* – Remelé 1890: pl. 3 fig. 5, pl. 5 figs 3–5.

*Rhynchorthoceras angelini* var. *lineata* – Neben & Krueger 1971: pl. 21 figs 10–12.

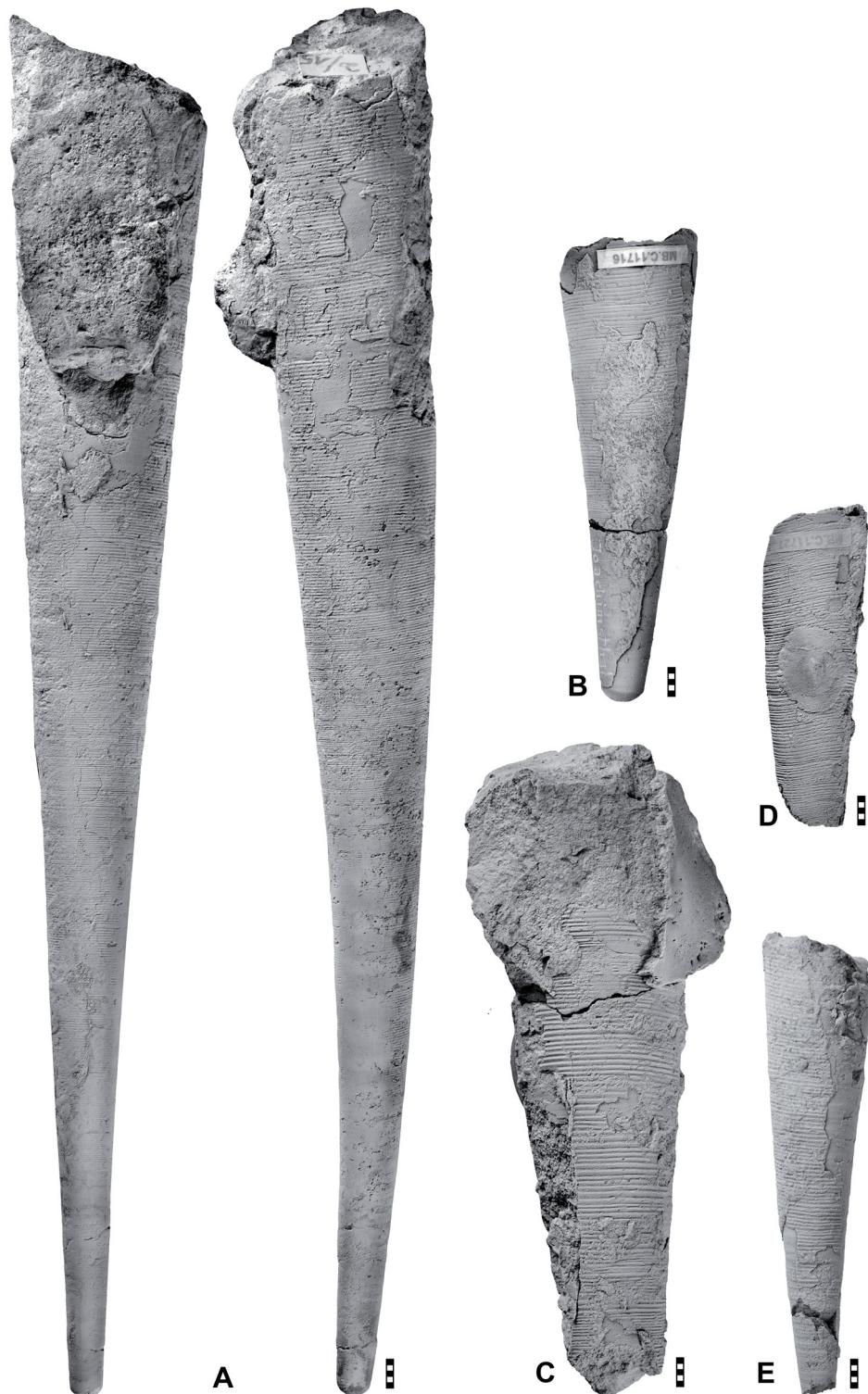
? *Rhynchorthoceras angelini* – Sweet 1958: 140.

### Diagnosis

Species of the genus *Rhynchorthoceras* with expansion angles between 8° and 13°; whorl profile circular, in the apical part of the conch sometimes slightly compressed and flattened on the dorsum. Shell surface consists of lirae with oblique and straight course across the flank, not oblique and straight ventrally, a low dorsal projection. Transverse profile of lirae either crested or flat, commonly asymmetric. Shell wall sometimes faintly undulated. Distance of lirae regular or slightly fluctuating, gradually decreases during ontogeny. Siphuncle 0.12–0.19 of whorl height, central or almost central in position.



**Fig. 9.** *Rhynchorthoceras angelini* (Boll, 1857); reproductions of illustrations by Remelé (1890). **A.** Specimen MB.C.11724 from Heegermühle (Brandenburg), illustrated by Remelé (1890: pl. 3 fig. 5). **B.** Specimen MB.C. 11725.1 from Heegermühle (Brandenburg), illustrated by Remelé (1890: pl. 5 fig. 3). **C.** Specimen from Heegermühle (Brandenburg), illustrated by Remelé (1890: pl. 5 fig. 4). **D.** Specimen MB.C.11732.2 from Heegermühle (Brandenburg), illustrated by Remelé (1890: pl. 5 fig. 5). **E.** Specimen MB.C.11726.1 from Heegermühle (Brandenburg), illustrated by Remelé (1890: pl. 5 fig. 6). **F.** Specimen MB.C.11716 from Joachimsthal (Brandenburg), illustrated by Remelé (1890: pl. 5 fig. 7). **G.** Specimen MB.C.22577 from Heegermühle, illustrated by Remelé (1890: pl. 6 fig. 6). Scale bar units = 1 mm.



**Fig. 10.** *Rhynchorthoceras angelini* (Boll, 1857) from the Upper Red Orthoceratite Limestone. A. Specimen MB.C.29656 (Bottke Coll.) from Skärlöv (Island of Öland); ventral and lateral views. B. Specimen MB.C.11716 (Hentig 1880 Coll.) from Joachimsthal (Brandenburg); lateral view. C. Specimen MB.C.30495.1 from Heegermühle (Brandenburg); dorsal? view. D. Specimen MB.C.11727 (Schmidt Coll.) from near Berlin-Schmargendorf; lateral view. E. Specimen MB.C.11725.1 (Remelé 1879 Coll.) from Heegermühle (Brandenburg); lateral view. Scale bar units = 1 mm.

### Type material

Not available for study; Boll (1857) did not specify a type but he had at least three specimens available, of which one was figured (Boll 1857: pl. 4 fig. 11).

### Material examined

GERMANY • 1 spec.; Berlin-Schmargendorf; Ordovician, Upper Red Orthoceratite Limestone; Schmidt Coll.; MB.C.11727 • 12 specs; Brandenburg, Heegermühle; Ordovician, Upper Red Orthoceratite Limestone; Kgl. Forstakademie Eberswalde Coll.; MB.C.11724, MB.C.11726.1 to MB.C.11726.7, MB.C.11729.2 to MB.C.11729.4, MB.C.11732.2 • 8 specs; Brandenburg, Heegermühle; Ordovician, Upper Red Orthoceratite Limestone; Remelé Coll.; MB.C.11725.1, MB.C.11725.2, MB.C.11731.1 to MB.C.11731.6 • 6 specs; Brandenburg, Heegermühle; Ordovician, Upper Red Orthoceratite Limestone; MB.C.22577, MB.C.30494, MB.C.30495.1, MB.C.30495.2, MB.C.30496, MB.C.30497 • 1 spec.; Brandenburg, Hohensaaten; Ordovician, Upper Red Orthoceratite Limestone; Neben and Krueger Coll.; MB.C.30498 • 1 spec.; Brandenburg, Joachimsthal (Uckermark); Ordovician, Upper Grey Orthoceratite Limestone; Hentig 1880 Coll.; MB.C.11716 • 1 spec.; Mecklenburg-Vorpommern, Neu-Ruthenbeck (Parchim); Ordovician, Upper Grey Orthoceratite Limestone; Helms 1974 Coll.; MB.C.11717.

SWEDEN • 1 spec.; Dalarna, Skattungbyn; Ordovician, Upper Red Orthoceratite Limestone; Dames 1890 Coll.; MB.C.11720.1 • 1 spec.; Island of Öland; Ordovician; MB.C.11723 • 2 specs; Island of Öland, Skäröv; Ordovician, Segerstad Limestone (upper part of the Upper Red Orthoceratite Limestone); Bottke Coll.; MB.C.29656, MB.C.29653.

COUNTRY UNKNOWN • 1 spec.; Ordovician; Otto Coll.; MB.C.11729.1.

### Description

All available specimens are fragments of faintly curved or orthoconic phragmocones (Figs 9–10) and represent various growth stages; the smallest preserved whorl height is 3 mm and the largest is 40 mm. Initial parts of the phragmocones and also mature body chambers are not preserved in any of the specimens. The expansion angles vary between 8° and 13° (median = 11°, n = 13; Fig. 13A). The relative chamber length is variable with a CLR between 0.25 and 0.50 (Fig. 11). The siphuncle has a central or almost central position, with diameters between 0.12 and 0.19 (median = 0.14, n = 13; Fig. 13B) of the whorl height.

The shell ornament consists of lirae, which are up to 1.3 mm apart in the largest specimens. The distance of lirae is more or less regular, fluctuates only slightly and gradually decreases during ontogeny (e.g., MB.C.11724, relative distance from ca 0.04 at wh 19 mm to ca 0.02 at wh 39 mm, Fig. 12B–C). The lirae extend straight across the venter; they are oblique and straight on the flanks and form a low projection on the dorsum (Fig. 12A, MB.C.11725.1). Their profile is crested and symmetric (MB.C.30495.1, MB.C.11724, MB.C.29656), crested and asymmetric (MB.C.11725.1) or flat and weakly asymmetric or symmetric (MB.C.11727, MB.C.22577).

### Remarks

*Rhynchorthoceras angelini* differs from *R. tenuistriatum* (from Middle Ordovician erratics of northern Germany) in the slightly lower expansion angle (8–12° vs 13°) and from *R. oelandicum* (from Middle Ordovician strata of Öland and erratics of northern Germany) in the central (vs slightly eccentric) position of the siphuncle in large growth stages. In all other characters, including the shell ornament, *R. angelini* is indistinguishable from *R. tenuistriatum* and *R. oelandicum*. Consequently, both *R. tenuistriatum* and *R. oelandicum* are synonymised with *R. angelini* herein.

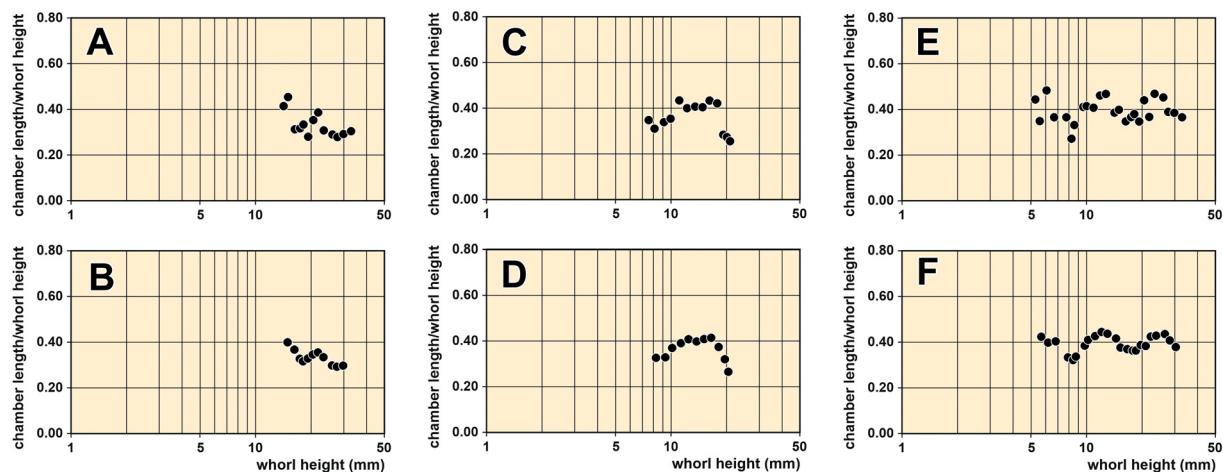
**Table 2** (continued on next page). Conch measurements (in mm), and expansion rates of specimens of *Rynchorthoceras* Remelé, 1882.

<b>taxon</b>	<b>catalogue nr</b>	<b>max. wh</b>	<b>max. ww</b>	<b>min. wh</b>	<b>min. ww</b>	<b>min WWI</b>	<b>fragm. length</b>	<b>EA (°)</b>
<i>R. rugium</i>	MB.C.11728	22.2	22.2	3.6	3.6	1.00	103.2	10.3
<i>R. kranepuhlense</i>	MB.C.11730	24.0	—	3.6	3.6	1.00	111.0	10.5
<i>R. kranepuhlense</i>	MB.C.30491	23.3	—	2.7	2.6	0.96	126.6	9.3
<i>R. kranepuhlense</i>	MB.C.30492	23.5	—	9.0	—	—	77.4	10.7
<i>R. kranepuhlense</i>	MB.C.30493	21.0	21.0	10.2	10.2	1.00	74.4	8.3
<i>R. angelini</i>	MB.C.11723b	—	30.0	—	13.0	—	82.2	11.8
<i>R. angelini</i>	MB.C.11729.4	17.8	—	13.4	—	—	25.1	10.0
<i>R. angelini</i>	MB.C.11727	—	20.6	—	11.8	—	48.8	10.3
<i>R. angelini</i>	MB.C.11726.1	17.0	16.5	4.0	4.0	1.00	67.5	11.0
<i>R. angelini</i>	MB.C.29656	—	33.0	5.7	5.6	0.98	209.0	7.5
<i>R. angelini</i>	MB.C.30495.1	29.3	29.3	18.0	18.0	1.00	52.0	12.4
<i>R. angelini</i>	MB.C.30495.2	38.0	—	23.0	—	—	—	—
<i>R. angelini</i>	MB.C.30497	—	26.0	11.4	11.4	1.00	75.8	11.0
<i>R. angelini</i>	MB.C.11724	39.0	—	18.5	18.3	0.99	143.0	8.2
<i>R. angelini</i>	MB.C.11725.1	19.0	19.0	6.3	6.2	0.98	63.6	11.4
<i>R. angelini</i>	MB.C.11732.2	29.7	—	22.7	—	—	36.7	10.9
<i>R. angelini</i>	MB.C.11720.1	39.5	—	11.4	11.0	0.96	—	—
<i>R. angelini</i>	MB.C.30498	29.0	—	15.4	15.4	1.00	74.0	10.5
<i>R. angelini</i>	MB.C.29653	35.3	—	3.3	3.0	0.91	166.1	11.0
<i>R. angelini</i>	MB.C.11716	23.0	22.5	7.6	7.5	0.99	69.7	12.6
<i>R. beyrichii</i>	MB.C.11718a,b	26.0	—	15.5	—	—	34.5	17.3
<i>R. conicum</i>	MB.C.30499	21.7	21.0	5.5	5.5	1.00	77.1	12.0
<i>R. conicum</i>	MB.C.11723a	21.0	19.3	10.5	10.3	0.98	60.0	10.0
<i>R. conicum</i>	MB.C.30507	21.0	20.1	7.2	7.1	0.99	78.1	10.1
<i>R. conicum</i>	MB.C.30508	16.5	16.5	8.3	8.0	0.96	39.3	11.9
<i>R. conicum</i>	MB.C.11702	46.0	—	6.0	—	—	178.3	12.8
<i>R. conicum</i>	MB.C.11703	38.0	—	8.0	—	—	174.9	9.8
<i>R. conicum</i>	MB.C.11719.1	36.0	—	8.3	8.2	0.99	150.7	10.5
<i>R. conicum</i>	MB.C.11719.2	15.3	15.1	8.0	7.7	0.96	44.4	9.4
<i>R. conicum</i>	MB.C.11721	19.0	—	8.6	8.8	1.02	66.1	9.0
<i>R. conicum</i>	MB.C.30505	27.0	—	7.6	7.4	0.97	116.7	9.5
<i>R. conicum</i>	MB.C.30501	18.0	—	2.8	—	—	84.3	10.3
<i>R. conicum</i>	MB.C.30506	17.3	17.3	3.0	—	—	78.6	10.4
<i>R. conicum</i>	MB.C.30502	40.0	—	4.4	—	—	172.2	11.8

**Table 2** (continued). Conch measurements (in mm), and expansion rates of specimens of *Rynchorthoceras* Remelé, 1882.

taxon	catalogue nr	max. wh	max. ww	min. wh	min. ww	min WWI	fragm. length	EA (°)
<i>R. conicum</i>	MB.C.30503	41.5	—	6.2	—	—	176.8	11.4
<i>R. conicum</i>	MB.C.11715	20.6	—	5.0	—	—	79.5	11.2
<i>R. sp.</i>	MB.C.11712	—	46.0	30.0	30.0	1.00	76.1	12.0
<i>R. sp.</i>	MB.C.11713	28.0	—	12.0	—	1.00	91.4	10.0
<i>R. sp.</i>	MB.C.29652	27.0	—	5.0	—	—	101.2	12.4
<i>R. sp.</i>	MB.C.30511	39.0	—	9.0	8.7	0.97	124.9	13.7
<i>R. sp.</i>	MB.C.30512	40.0	—	8.0	—	—	152.2	12.0
<i>R. sp.</i>	MB.C.30514	41.0	—	5.2	5.2	1.00	194.8	10.5
<i>R. sp.</i>	MB.C.30513	38.0	—	10.0	10.0	1.00	120.1	13.3
<i>R. sp.</i>	MB.C.11711	46.0	—	11.0	11.0	1.00	163.7	12.2

The intraspecific variation of *R. angelini* also concerns the shell ornament. Remelé (1882, 1890) recognised two varieties within the species: *R. angelini* var. *virgata* with more prominent lirae with acute, symmetric or asymmetric crests, while the lirae in *R. angelini* var. *lineata* are flat and only very slightly asymmetric. Remelé considered them as varieties of a single species because of common transitions between the two types of ornament. Furthermore, the specimens do not differ in any other morphological characters. Based on the study of original specimens of Remelé (1882, 1890) and subsequently collected material, the varieties are not distinguished here and only the name *R. angelini* is used.

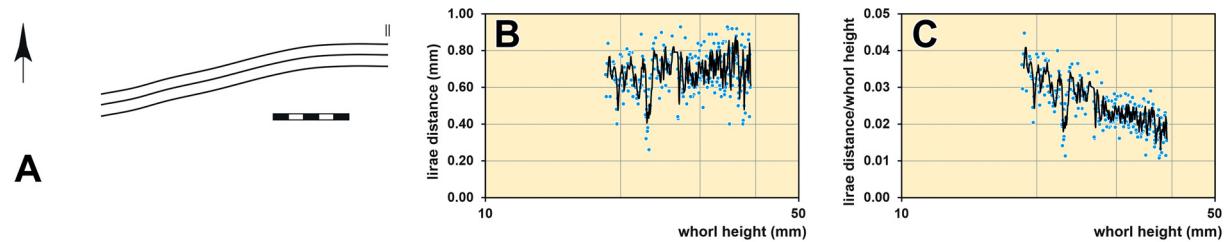


**Fig. 11.** Septum distances in *Rynchorthoceras angelini* (Boll, 1857) from the Upper Red Orthoceratite Limestone. Upper row = empirical data points; lower row = three data points averaged. **A–B.** Specimen MB.C.11725.1 (Remelé 1879 Coll.) from Heegermühle (Brandenburg). **C–D.** Specimen MB.C.11716 (Hentig 1880 Coll.) from Joachimsthal (Brandenburg). **E–F.** Specimen MB.C.29653 (Bottke Coll.) from Gårdslösa (Island of Öland, Sweden).

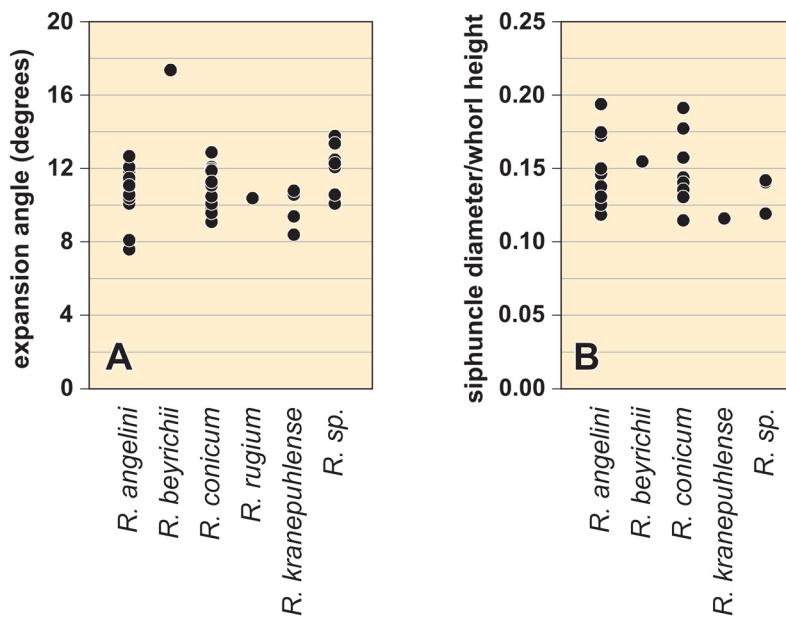
*Rhynchorthoceras angelini* is, together with *R. conicum*, by far the most abundant representative of *Rhynchorthoceras* in the Aserian and Lasnamägian (Middle Ordovician) strata of Baltoscandia and erratics in Germany and Poland. Most of the reported occurrences come from the Upper Red Orthoceratite Limestone, where *R. angelini* co-occurs with *Trilacinoceras discors* (Holm, 1891) and possibly other lituitids (e.g., Jaanusson 1960). The species is palaeogeographically widespread and stratigraphically long-ranging compared to other species of the genus; it probably occurs already in the latest Dapingian (early Middle Ordovician) rocks of central Bohemia (Marek 1999; Manda 2008; Aubrechtová & Turek 2018).

### Geographic and stratigraphic occurrence

Norway (?), Sweden (in situ) and northern Germany (in erratics within Pleistocene gravels), central Bohemia (?); middle Volkov (?) Kunda to Lasnamägi regional stages (latest Dapingian (?) to late Darriwilian, Middle Ordovician).



**Fig. 12.** *Rhynchorthoceras angelini* (Boll, 1857) from the Upper Red Orthoceratite Limestone. A. Lirae of specimen MB.C.11725.1 (Remelé 1879 Coll.) from Heegermühle (Brandenburg), at wh = 14 mm. B–C. Ontogenetic development of lirae distance (in mm) and lirae distance/whorl height of specimen MB.C.11724 (Kgl. Forstakademie Eberswalde Coll.) from Heegermühle (Brandenburg). Blue dots = individual measurements, black lines = three data point averaged values. Scale bar units = 1 mm.



**Fig. 13.** Conch expansion rates (A) and siphuncle diameter rates (B) in species of *Rhynchorthoceras* Remelé, 1882.

***Rhynchorthoceras conicum* (Hisinger, 1837)**  
Fig. 14A–C, Tables 2–3

*Orthoceratites conicus* Hisinger, 1837: 29, pl. 9 fig. 5.

*Orthoceras conicum* – Boll 1857: 72, pl. 4 fig. 12. — Angelin 1880: 5, pl. 9 figs 2–3. — Rüdiger 1889: 18, pl. 1 fig. 4.

? *Orthoceras conicum* – Angelin 1880: pl. 9 fig. 1

*Conorthoceras conicus* – Troedsson 1931: 24

*Rhynchorthoceras angelini* – Hardt 1953: 44, text-fig. 9.

*Rhynchorthoceras conicum* – Dzik 1984: 133, pl. 38 figs 3–4, text-fig. 50d–e. — Kröger 2004b: 65. — Kröger et al. 2007: 1280.

Sinoceratidae, gen et sp. nov. cf. “*Conorthoceras*” *conicum* – King 1999: fig. 6a–b.

non *Orthoceras conicum* – Woodward 1856: 379, pl. 6 fig. 2.

non *Nevadaceras conicum* – Flower 1968: 43.

### Diagnosis

Species of the genus *Rhynchorthoceras* with expansion angle of 9–13°; whorl profile circular. Shell surface smooth or decorated with extremely fine transverse and/or longitudinal lines. Siphuncle diameter 0.11–0.19 of whorl height, central or nearly central in position.

### Type material

Not available for study; Hisinger (1837: pl. 9 fig. 5) did not specify a type but he figured one specimen that was re-figured by Boll (1857: pl. 4 fig. 12).

### Material examined

GERMANY • 1 spec.; Brandenburg, Gellmersdorf (Angermünde); Ordovician; Schröter 1979 Coll.; MB.C.11715 • 2 specs; Brandenburg, Heegermühle; Ordovician, Upper Red Orthoceratite Limestone; MB.C.30499, MB.C.30500 • 3 specs; Brandenburg, Niederfinow; Ordovician, Upper Red Orthoceratite Limestone; Neben and Krueger Coll.; MB.C.30501 to MB.C.30503 • 1 spec.; Brandenburg, Niederfinow; Ordovician, Upper Red Orthoceratite Limestone; Neben and Krueger Coll.; MB.C.30504 • 1 spec.; Brandenburg, Niederlehme; Ordovician; Siegert 1914 Coll.; MB.C.11703 • 2 specs; Brandenburg, Oderberg; Ordovician, Upper Red Orthoceratite Limestone; Neben and Krueger Coll.; MB.C.30505, MB.C.30506 • 1 spec.; Brandenburg, Oderberg; Ordovician, Upper Red Orthoceratite Limestone; Remelé Coll.; MB.C.30507.

POLAND • 1 spec.; West Pomerania, Dewitz Castle, Dobra (former Dewitzburg bei Daber); Ordovician, Upper Red Orthoceratite Limestone; MB.C.30508 • 1 spec.; West Pomerania, Skowarcz (former Schönwarling), Gdańsk County; Ordovician, Upper Red Orthoceratite Limestone; Hoyers 1912 Coll.; MB.C.30509.

SWEDEN • 1 spec.; Dalarna; Ordovician; Coll.; MB.C.11721 • 2 specs; Island of Öland; Ordovician; Coll.; MB.C.11702, MB.C.11723 • 1 spec.; Island of Öland, Triberga; Ordovician, Upper Red Orthoceratite Limestone; Dames 1881 Coll.; MB.C.11722.

COUNTRY UNKNOWN • 2 specs; Ordovician; Otto Coll.; MB.C.11719.1, MB.C.11719.2.

## Description

All specimens are fragments of faintly curved or orthoconic phragmocones (Fig. 14A–C) and represent various growth stages of the conch, with the smallest preserved whorl height of 3 mm and the largest of 40 mm. None of the specimens has initial parts of the phragmocone or a mature body chamber preserved. The expansion angles vary between 9° and 13° (median = 11°, n = 15; Fig. 13A). The relative chamber length is variable, the CLR is between 0.18 and 0.32. The siphuncle is central or almost central in position and its diameter is between 0.11 and 0.19 (median = 0.14, n = 9; Fig. 13B) of the whorl height. The shell surface is nearly smooth; only some specimens (MB.C. 11723a, MB.C.11721, MB.C.30501) possess delicate longitudinal and/or transverse lines or impressions.

## Remarks

Troedsson (1931) stated that *Orthoceratites conicus* is the type species of a new genus *Conorthoceras*. However, Troedsson did not formally describe the genus, nor did he provide any diagnosis, descriptions or figures. The validity of the name *Conorthoceras* was disputed by Jaanusson & Mutvei (1953) and Teichert (1964), but Sweet (1958) considered the name as valid. The systematic position of *O. conicus* remained unclear, until Dzik (1984) assigned the species to *Rhynchorthoceras*, thereby acknowledging its lituitid affinities. King (1990, 1999) agreed that *O. conicus* represented a lituitid but suggested that the smooth shell surface would justify a separate genus. Later authors (e.g., Kröger 2004b; Kröger *et al.* 2007) retained the species in *Rhynchorthoceras*, which is also the approach followed herein.

*Rhynchorthoceras conicum* must not be confused with *Nevadaceras conicum* Flower, 1968. The latter is known from a single, fragmentary specimen, which has oblique sutures, compressed whorl profile and a wider siphuncle (0.25 of whorl height) located between the centre and venter. Thus, *N. conicum* can neither be synonymised with *R. conicum*, nor assigned to the order Lituitida.

*Rhynchorthoceras conicum* is almost identical, in conch proportions and internal conch morphology, to *R. angelini*, *R. kranepuhlense* sp. nov. and *R. rugium* sp. nov. (all described herein), but it can be readily distinguished by the smooth surface of its shell.

## Geographic and stratigraphic occurrence

Sweden (in situ) and northern Germany and Poland (in erratics within Pleistocene gravels); Aseri to Lasnamägi regional stages (middle to late Darriwilian, Middle Ordovician).

***Rhynchorthoceras beyrichii* Remelé, 1882**  
Fig. 14D, Tables 2–3

*Rhynchorthoceras Beyrichii* Remelé, 1882: 128, pl. 5 fig. 3a–b.

*Orthoceratites* – Breyn 1732: 33, pl. 4 figs 1–3.

*Ancistroceras Breynii* – Remelé 1881: 194.

*Rhynchorthoceras beyrichi* – Foerste 1930: 277, pl. 42 fig. 2a–c. — Balashov 1962: pl. 7 fig. 3.

## Diagnosis

Species of the genus *Rhynchorthoceras* with an expansion angle of 15–17°. Shell surface with pronounced lirae, straight in the apical part but faintly sinuous later in ontogeny. Distance of lirae increasing up to 1.5 mm during ontogeny; distance and thickness of lirae might be irregular. Siphuncle eccentric in position (after Remelé 1882).

**Table 3.** Siphuncular diameter ratio (SDR) and siphuncular distance ratio (SPR) at their corresponding whorl height in specimens of *Rhynchorthoceras* Remelé, 1882.

<b>taxon</b>	<b>catalogue nr</b>	<b>wh</b>	<b>SDR</b>	<b>wh</b>	<b>SPR</b>
<i>R. kranepuhlense</i>	MB.C.11730	20.0	0.12	—	—
<i>R. angelini</i>	MB.C.11729.4	17.8	0.13	—	—
<i>R. angelini</i>	MB.C.11727	20.6	0.15	—	—
<i>R. angelini</i>	MB.C.11726.1	17.0	0.12	17.0	0.47
<i>R. angelini</i>	MB.C.29656	5.7	0.19	—	—
<i>R. angelini</i>	MB.C.30495.1	28.0	0.17	—	—
<i>R. angelini</i>	MB.C.11724	18.5	0.12	18.5	0.49
<i>R. angelini</i>	MB.C.11725.1	19.0	0.14	19.0	0.47
<i>R. angelini</i>	MB.C.11720.1	11.4	0.15	—	—
<i>R. angelini</i>	MB.C.30498	15.4	0.13	—	0.50
<i>R. angelini</i>	MB.C.11716	23.0	0.17	23.0	0.48
<i>R. beyrichii</i>	MB.C.11718a, b	26.0	0.15	26.0	0.42
<i>R. conicum</i>	MB.C.30499	21.0	0.14	—	—
<i>R. conicum</i>	MB.C.11723a	10.5	0.19	10.5	0.44
<i>R. conicum</i>	MB.C.30507	7.2	0.14	7.2	0.50
<i>R. conicum</i>	MB.C.30508	16.5	0.14	16.5	0.50
<i>R. conicum</i>	MB.C.11702	26.0	0.13	—	—
<i>R. conicum</i>	MB.C.11719.1	8.3	0.16	—	—
<i>R. conicum</i>	MB.C.11719.2	15.3	0.18	—	—
<i>R. conicum</i>	MB.C.30505	27.0	0.13	—	—
<i>R. conicum</i>	MB.C.30502	4.4	0.11	—	—
<i>R. sp.</i>	MB.C.11713	26.5	0.14	26.5	0.49
<i>R. sp.</i>	MB.C.30511	39.0	0.14	39.0	0.46
<i>R. sp.</i>	MB.C.30514	—	—	—	0.50
<i>R. sp.</i>	MB.C.11711	11.0	0.12	11.0	0.48

**Type material**

Not available for study; Remelé (1882: pl. 5 fig. 3a–b) did not specify a type, but he mentioned and illustrated only one specimen from Szczecin (formerly Stettin; West Pomerania, Poland), found in Upper Grey Orthoceratite Limestone erratics in Pleistocene gravel (late Darriwilian, Middle Ordovician).

**Material examined**

POLAND • 1 spec.; Osselsk; Ordovician; Henke 1901 Coll.; MB.C.11718.

**Description**

Specimen MB.C.11718 (Fig. 14D) is a 50 mm long fragment of an orthoconic phragmocone; it is sectioned along the median plane (a thin section was also produced by a previous researcher). The conch expands with an expansion angle of 17°. The ornament consists of flat, asymmetric lirae (the steeper side facing the aperture), which form a shallow lateral sinus and a low dorsal projection. The shell wall



**Fig. 14.** Species of *Rhynchorthoceras* Remelé, 1882 from the Upper Red Orthoceratite Limestone. **A.** *Rhynchorthoceras conicum* (Hisinger, 1837), specimen MB.C.30503 (Neben & Krueger Coll.) from Niederfinow (Brandenburg); lateral view. **B.** *Rhynchorthoceras conicum* (Hisinger, 1837), specimen MB.C.11719.1 (Otto Coll.) from an unknown locality; dorsal? view. **C.** *Rhynchorthoceras conicum* (Hisinger, 1837), specimen MB.C.30508 from Dewitz Castle, Dobra (former Dewitzburg bei Daber; West Pomerania, Poland); lateral? view. **D.** *Rhynchorthoceras beyrichii* Remelé, 1882, specimen MB.C.11718 (Henke 1901 Coll.) from Osselsk (Poland); previously figured by Foerste (1930: pl. 42 fig. 2); lateral view and polished median section. Scale bar units = 1 mm.

is not preserved on the ventral side. During ontogeny, the siphuncle shifts slightly in position (from 0.40–0.45); it has a diameter of 0.15 of the whorl height. The connecting rings are slightly expanded in their first half. The chamber length is stable ( $CLR = 0.25$ –0.27).

### Remarks

*Rhynchorthoceras beyrichii* is distinguished from the other species of the genus by the moderately high expansion angle ( $15^\circ$ – $17^\circ$ ) and an ornament with sinuous lirae. The lirae are much less sinuous and narrower than in the otherwise similar *R. breynii* (from Middle Ordovician erratics of northern Germany) and *R. zaddachi* (Remelé, 1882) (from Darriwilian erratics of the Kaliningrad Region, Russia).

*Rhynchorthoceras beyrichii* is a rare species that is unequivocally known only from two specimens figured by Remelé (1882) and Foerste (1930); the latter specimen was available for study herein. Dzik (1984) figured a specimen of *Rhynchorthoceras* from Volkhanian (early Middle Ordovician) strata of Poland that he assigned to *R. aff. beyrichii*.

### Geographic and stratigraphic occurrence

Poland (in erratics within Pleistocene gravels); Upper Grey Orthoceratite Limestone, late Lasnamägi Regional Stage (late Darriwilian, Middle Ordovician).

### *Rhynchorthoceras rugium* sp. nov.

urn:lsid:zoobank.org:act:3285F969-0E64-45B9-87BA-52BECCB14B9E

Fig. 15A, Table 2

### Diagnosis

Species of the genus *Rhynchorthoceras* with an expansion angle of  $10^\circ$ ; whorl profile circular. Shell surface with transverse striae, which are arranged conspicuously far apart from each other (up to 4 mm at  $wh = 22$  mm), distance increasing more or less regularly during ontogeny. Striae oblique but straight laterally, directly transverse and straight ventrally, with a low projection dorsally.

### Etymology

From Rugia, the Latin name of the Island of Rügen, from which the holotype originates.

### Type material

#### Holotype

GERMANY • Mecklenburg-Vorpommern, Mönchgut Peninsula (Island of Rügen); Ordovician, Upper Red Orthoceratite Limestone (Kunda Regional Stage, middle Darriwilian); Hoffmann 1972 Coll.; MB.C.11728 (illustrated in Fig. 15A).

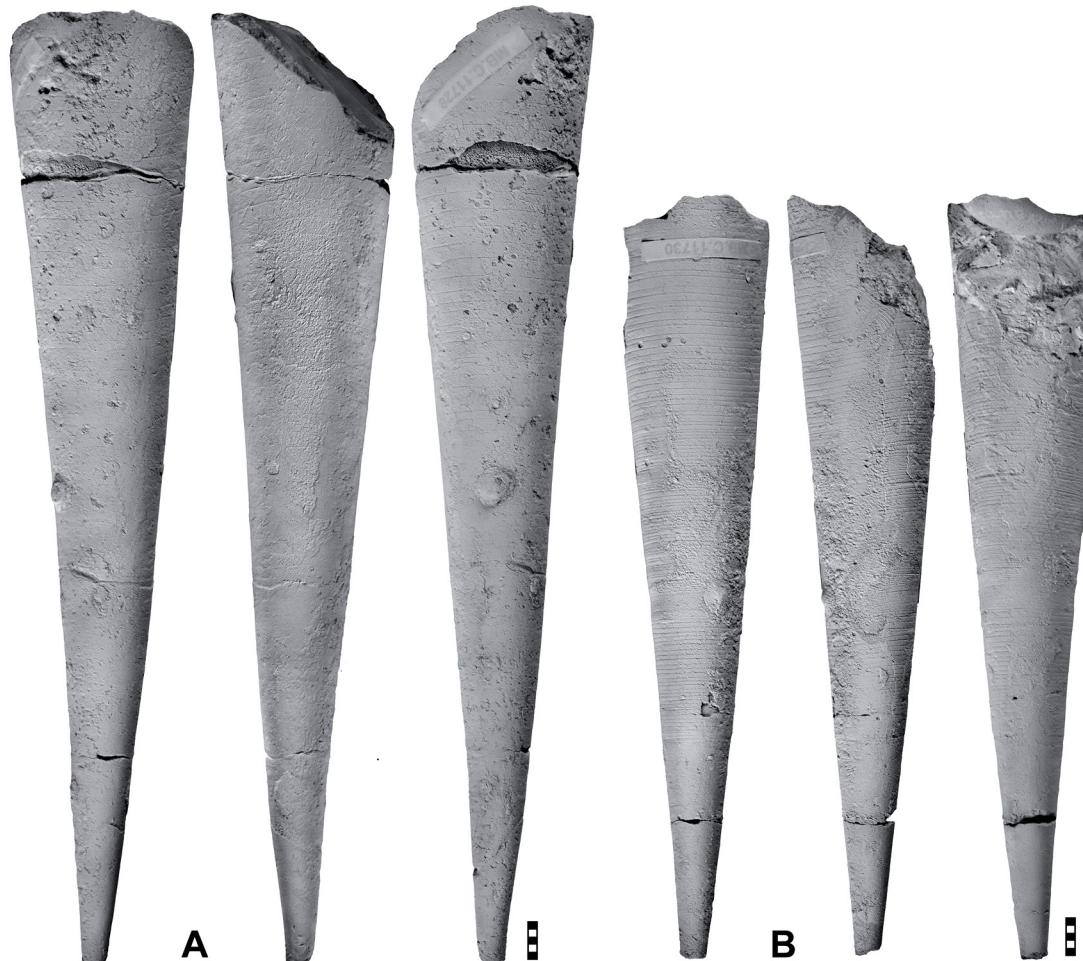
### Description

Holotype MB.C.11728 (Fig. 15A) is an orthoconic but apically weakly curved phragmocone of 125 mm length. At its maximum whorl height of 22 mm, the conch has a circular cross section; the expansion angle is  $10^\circ$ . The shell ornament is preserved in more than half of the specimen and consists of transverse striae. The distances of these increase gradually along the conch and stand conspicuously far apart (up to 4 mm). Only at a whorl height of 18 mm, the striae stand closer together. They extend in oblique direction with straight course across the flanks and are straight on the venter; on the dorsum they form a low projection.

### Remarks

Rüdiger (1889) was the first to recognise striated forms of *Rhynchorthoceras* and considered them as representing a separate species. Patrunky (1926) named these forms *R. ruedigeri* but did not provide any further description or figures. The name *Rhynchorthoceras ruedigeri* is thus a nomen nudum and two striated species of *Rhynchorthoceras* are newly defined here (see also the text below).

*Rhynchorthoceras rugium* sp. nov. might be confused with *R. angelini* (described above), if lirae in the latter are very flat or poorly preserved. However, the ornament elements are apparently more widely spaced in *R. rugium* sp. nov. The other striated species, *R. kranepuhlense* sp. nov. (described below), differs from *R. rugium* sp. nov. in its finer, more irregularly spaced striae; furthermore, the conch is locally slightly constricted in *R. kranepuhlense* sp. nov.



**Fig. 15.** Species of *Rhynchorthoceras* from the Upper Red Orthoceratite Limestone. **A.** *Rhynchorthoceras rugium* sp. nov., holotype MB.C.11728 (Hoffmann & Gager 1972 Coll.) from Mönchgut (Island of Rügen); lateral, dorsal and ventral views. **B.** *Rhynchorthoceras kranepuhlense* sp. nov., holotype MB.C.11730 (Kummerow Coll.) from Kranepuhl (Brandenburg); ventral, lateral and dorsal views. Scale bar units = 1 mm.

*Rhynchorthoceras kranepuhlense* sp. nov.

urn:lsid:zoobank.org:act:C6275788-FF3A-4730-9E8B-237DC086E929

Figs 15B, 16, Tables 2–3

**Diagnosis**

Species of the genus *Rhynchorthoceras* with expansion angles between 8° and 11°; whorl profile circular. Shell surface with transverse striae, up to 1 mm apart (at wh = 21 mm) and spaced irregularly. Conch slightly constricted, where the striae are finest. The striae extend oblique but straight laterally and directly transverse and straight ventrally, with a low projection dorsally. Siphuncle ca 0.12 in diameter, central or almost central in position.

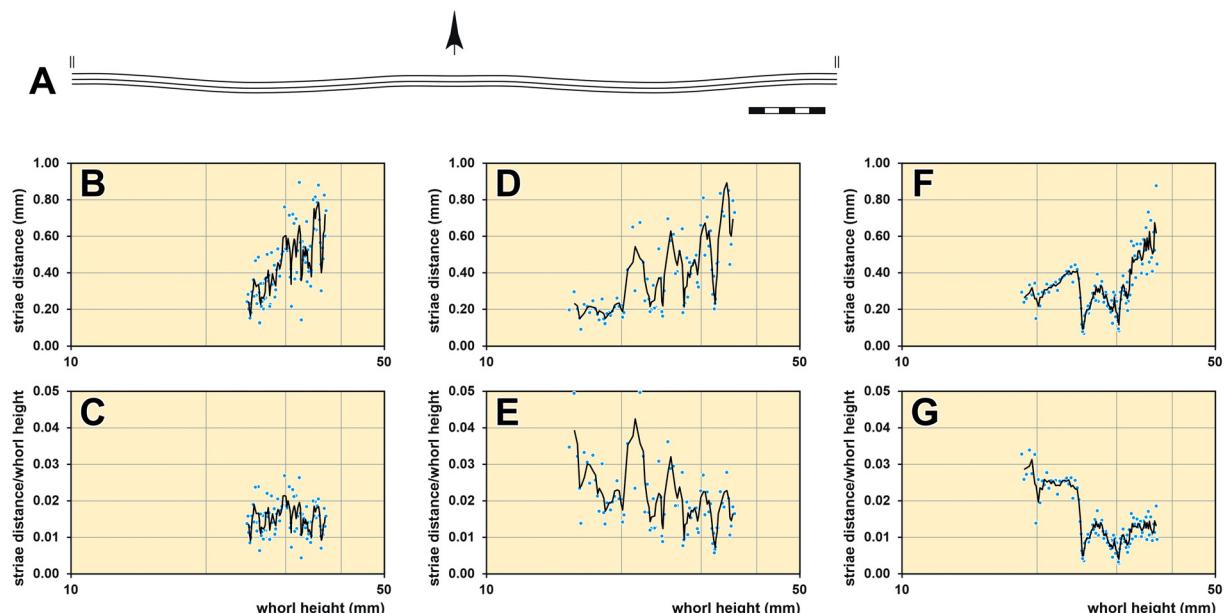
**Etymology**

From the type locality Kranepuhl.

**Type material**

**Holotype**

GERMANY • Brandenburg, Kranepuhl; Ordovician, Upper Red Orthoceratite Limestone (Aseri Regional Stage, middle Darriwilian); Kummerow Coll.; MB.C.11730 (illustrated in Fig. 15B).



**Fig. 16.** *Rhynchorthoceras kranepuhlense* sp. nov. from the Upper Red Orthoceratite Limestone. **A.** Striae of holotype MB.C.11730 (Kummerow Coll.) from Kranepuhl (Brandenburg), at wh = 16 mm. **B–C.** Ontogenetic development of striae distance (in mm) and striae distance/whorl height of specimen MB.C.30492 (Neben & Krueger Coll.) from Oderberg (Brandenburg). **D–E.** Ontogenetic development of striae distance (in mm) and striae distance/whorl height of specimen MB.C.30491 (Neben & Krueger Coll.) from Niederfinow (Brandenburg). **F–G.** Ontogenetic development of striae distance (in mm) and striae distance/whorl height of holotype MB.C.11730 (Kummerow Coll.) from Kranepuhl (Brandenburg). Blue dots = individual measurements, black lines = three data point averaged values. Scale bar units = 1 mm.

### Paratypes

GERMANY • 1 spec.; Brandenburg, Niederfinow; Ordovician, Upper Red Orthoceratite Limestone; Neben and Krueger Coll.; MB.C.30491 • 1 spec.; Brandenburg, Oderberg; Ordovician, Upper Red Orthoceratite Limestone; Neben and Krueger Coll.; MB.C.30492.

POLAND • 1 spec.; West Pomerania, Dewitz Castle, Dobra (former Dewitzburg bei Daber); Ordovician, Upper Red Orthoceratite Limestone; MB.C.30493.

### Description

Holotype MB.C.11730 (Fig. 15B) is a fragment of an orthoconic phragmocone with 100 mm length. The conch has a circular whorl profile and expands with an angle of 11°. The shell ornament is preserved along the whole length of the specimen. It consists of transverse striae, which are up to 1.5 mm apart (at the maximum whorl height of 24 mm). The distance of the striae changes irregularly during ontogeny (Fig. 16F–G); at about 10 mm whorl height, the striae become extremely fine and the conch is slightly constricted at this position (Fig. 15B). The shell wall is slightly undulated in the second half of the specimen. The striae are oblique but straight on the flanks, completely transverse and straight on the venter; they possess a low projection on the dorsum (Fig. 16A). The siphuncle is seen at the latest preserved septum; it is narrow (0.12 of whorl height) and central in position.

### Remarks

*Rhynchorthoceras kranepuhlense* sp. nov. is morphologically closest to *R. rugium* sp. nov. (described above) because of its striated shell surface. However, the striae in *R. kranepuhlense* sp. nov. stand much closer together and their distance is much more irregular. Also, at places where the distance of the striae is decreased, shallow conch constrictions (Fig. 15B) appear around the conch circumference.

### Geographic and stratigraphic occurrence

Northern Germany and Poland (in erratics within Pleistocene gravels); late Kunda to early Lasnamägi regional stages (middle to late Darriwilian, Middle Ordovician).

### *Rhynchorthoceras* sp.

### Material examined

GERMANY • 1 spec.; Brandenburg, Eberswalde; Ordovician, Upper Grey Orthoceratite Limestone; MB.C.30510 • 1 spec.; Brandenburg, Gransee (Ruppin); Ordovician, Upper Grey Orthoceratite Limestone; Kirchner Coll.; MB.C.11689 • 2 specs; Brandenburg, Hohensaaten; Ordovician, Upper Grey Orthoceratite Limestone; Neben and Krueger Coll.; MB.C.30511, MB.C.30512 • 2 specs; Brandenburg, Niederfinow; Ordovician, Upper Grey Orthoceratite Limestone; MB.C.30513, MB.C.30514 • 1 spec.; Mecklenburg-Vorpommern, Dwasieden (Island of Rügen); Ordovician, Upper Grey Orthoceratite Limestone; MfN excursion 1964 Coll.; MB.C.11711 • 1 spec.; Mecklenburg-Vorpommern, Lebbin; Ordovician; Böhm 1906 Coll.; MB.C.11713 • 2 specs; Mark?; Ordovician; MB.C.11705.1, MB.C.11705.2.

POLAND • 1 spec.; Silesia, Kunzendorf; Ordovician; MB.C.11712 • 1 spec.; West Pomerania, Island of Chrząszczewska (former Gristow); Ordovician; MB.C.11710.

SWEDEN • 1 spec.; Island of Öland, Gärdslösa; Ordovician; Bottke Coll.; MB.C.29652.

### Remarks

In the collection under study, there are several specimens of orthoconic or weakly cyrtoconic lituitids, which have expansion angles between 10–14° (Fig. 13A, Table 2), a circular whorl profile and a

centrally located siphuncle with SDR between 0.12 and 0.14 (Fig. 13B, Table 3). Thus, the specimens are assigned here to the genus *Rhynchorthoceras*. Since the shell surface in the above specimens is covered by conspicuously sinuous and asymmetric lirae, which form deep sinuses on the flanks and the venter, they should be assigned either to *R. breynii* from the Middle Ordovician erratics of northern Germany, or the other European species of *Rhynchorthoceras* with sinuous lirae, i.e., *R. beyrichii* (from late Darriwilian erratics of Poland), *R. helgoeyense* Sweet, 1958 (from the late Middle or early Late Ordovician of Norway) and *R. zaddachi* (from the Darriwilian erratics of the Kaliningrad Region, Russia). Unfortunately, these species are rare and unequivocally known only from the type material, which has not been revised since the species descriptions and was not available for study herein. In addition, the ornament in the specimens in discussion is often incompletely or poorly preserved. Any species-level assignment of these specimens is thus avoided herein.

#### Family **Lituitidae** Phillips, 1848

##### **Diagnosis**

Family of the order Lituitida with coiled apical part of the conch; whorls detached or weakly impressed dorsally. Whorl profile elliptic in the coiled stage, elliptic or circular in the uncoiled stage. Shell surface with growth lines, transverse lirae and/or annuli; ornament elements variable in outline but typically with conspicuous lateral and ventral sinus. Terminal aperture characterised by two to five lappets and deep ventral and lateral sinuses. Siphuncle ventral in the earliest phragmocone chambers, subdorsal in the following part of the coiled stage and subcentral or central in the uncoiled stage (after Furnish & Glenister 1964).

##### **Genera included**

*Ancistroceras* Boll, 1857; *Angelinoceras* Hyatt, 1894; *Cyclolitites* Remelé, 1886; *Holmiceras* Hyatt, 1894; *Jingshanlingoceras* Zou, 1987; *Lituites* Bertrand, 1763; *Pseudoancistroceras* Xu & Lai, 1987; *Sinoceroides* Xu & Lai, 1987; *Tapinolitites* Gao, 1982; *Trilacinoceras* Sweet, 1958; *Yangjiapingoceras* Xu, 1977.

#### Genus ***Ancistroceras*** Boll, 1857

##### **Type species**

*Lituites undulatus* Boll, 1857; by monotypy.

##### **Diagnosis**

Genus of the family Lituitidae with 1.5–2 tightly coiled or only slightly separated early volutions; long, rapidly expanding straight part; umbilical window small. Whorl profile elliptic or circular in the coiled stage, circular in the uncoiled stage. Uncoiled part expands with an angle of 18–35° and is straight in longitudinal profile. Shell surface with sinuous growth bands and annulations, which form five projections in the coiled part, three and finally two in the straight part. Aperture of mature conch with broad dorsal and ventral projections and shallow lateral sinus (after Aubrechtová & Meidla 2020).

##### **Species included**

*Ancistroceras Barrandei* Dewitz, 1880; *Ancistroceras Bollii* Remelé, 1882; *Ancistroceras clinotum* Xu & Lai, 1987; *Ancistroceras densum* Qi, 1980; *Sinoceras fengxiangense* Chang, 1964; *Ancistroceras magnum* Flower, 1975; *Ancistroceras ristnensis* Aubrechtová & Meidla, 2020; *Ancistroceras subcurvatum* Qi, 1980; *Strombolitites Torelli* Remelé, 1881; *Lituites undulatus* Boll, 1857; *Ancistroceras vahikuelaensis* Aubrechtová & Meidla, 2020.

## Remarks

The authorship of *Ancistroceras* is a confusing matter. Boll (1857: 87) stated in the description of his new species *Lituites undulatus* that he originally planned to define a new genus *Ancistroceras* for this species, but then changed his mind. However, Boll (1857: 3, fig. 25) presented the species as *Ancistroceras undulatum*. Dewitz (1880: 387) restored the genus name and designated *L. undulatus* as the type species. Boll (1857) was then accepted throughout the literature as the author of the genus *Ancistroceras*. This view is also followed here.

In contrast to *Rhynchorthoceras*, species of the genus *Ancistroceras* are characterised by a coiled early juvenile conch, a greater expansion angle, a larger chamber length ratio and a strongly annulated shell surface. Representatives of the genus *Holmiceras* are similar to species of *Ancistroceras*, but the former are distinguished by an openly coiled juvenile conch part and a sigmoidally shaped backcoiled part with a smaller expansion angle.

## Geographic and stratigraphic occurrence

North America, Wales (?), Baltoscandia, northern Germany, the Kaliningrad Region of Russia, northern Poland and China; Middle to Late Ordovician. The stratigraphically oldest species of *Ancistroceras* were described from early Dapingian strata of China and hence belong to the earliest lituitids known to date (Kröger *et al.* 2007; Fang *et al.* 2021).

*Ancistroceras undulatum* (Boll, 1857)  
Figs 17–18, Tables 5–6

*Lituites undulatus* Boll, 1857: 87.

*Ancistroceras undulatum* – Boll 1857: pl. 8 fig. 25a. — Dewitz 1880: 387, pl. 17 fig. 5. — Holm 1885: 21, pl. 3 fig. 2, pl. 4 figs 1, 3–20. — Patrunky 1926: 120. — Foerste 1930: 272, pl. 41 figs 1a–b, 3a–b, 4a–c, pl. 42 figs 3–4. — Balashov 1953: 236, pl. 14 figs 5a–b, 8. — Sweet 1958: 129, pl. 13 figs 2–3, 5, pl. 18 fig. 1. — Zhuravleva 1961: pl. 12 figs 2–3. — Aubrechtová & Meidla, 2020: 272, text-figs 5–6.

*Strombolitites undulatus* – Remelé 1881: 191, text-fig. 1; 1882: 11, pl. 5 fig. 1.

*Ancistroceras* cf. *undulatum* – Schindewolf 1942: 348, text-fig. 4c.

non *Ancistroceras undulatum* – Noetling 1884: pl. 18 fig. 6–6a. — Rüdiger 1889: 44. — Balashov 1953: pl. 14 figs 6–7. — Neben & Krueger 1971: pl. 17 fig. 1. — Qi 1980: 254, pl. 2 fig. 6, text-fig. 5.  
non *Ancistroceras* cf. *undulatum* – Chen 1987: 178, pl. 6 fig. 18, text-fig. 38.

## Diagnosis

Species of the genus *Ancistroceras* with a moderately curved end of the coiled part of the conch; uncoiled part conical with an expansion angle of 25–27°. Whorl profile circular throughout ontogeny. Relative chamber length ca 0.35. Ornament with wide and low annuli (spaced at 2 mm distance after uncoiling and 4 mm distance in later growth stages) and lirae (0.5 mm in distance after uncoiling and 0.5–1 mm in distance in later growth stages); crests of annuli commonly with raised pairs of lirae. Course of the lirae with ventral sinus and lateral sinus; dorsal projection roof-shaped and flanked by shallow dorsolateral sinuses. Position of the siphuncle slightly more dorsad in the juvenile part of the conch and gradually relocated to central or almost central position. Connecting rings thin, slightly expanded, siphuncular segments thus slightly constricted at the septal necks (after Aubrechtová & Meidla 2020, emended).

**Table 4.** Conch measurements (in mm), ratios and rates of coiled conch parts of *Ancistroceras* Boll, 1857.

<b>taxon</b>	<b>catalogue nr</b>	<b>dm</b>	<b>wh</b>	<b>uw</b>	<b>WERdm</b>	<b>WERah</b>	<b>UWI</b>
<i>A. barrandei</i>	MB.C.11991a	17.6	8.9	4.6	4.19	4.09	0.26
<i>A. torelli</i>	MB.C.22575	20.6	11.4	4.7	5.01	>3.00	0.23
<i>A. torelli</i>	MB.C.30519	19.6	11.0	—	5.19	5.00	—
<i>A. sp.</i>	MB.C.1860	23.4	13.0	5.6	4.53	5.06	0.24

#### Type material

Holotype not available for study; Boll (1857: pl. 8 fig. 25) figured one specimen from Usadel near Neubrandenburg (Mecklenburg-Vorpommern, Germany), found in erratics from Pleistocene gravel (Uhaku Regional Stage, late Darriwilian, Middle Ordovician).

#### Material examined

GERMANY • 1 spec.; Brandenburg, Niederfinow; Ordovician, Upper Grey Orthoceratite Limestone; Neben 1936 Coll.; MB.C.11696 • 2 specs; Brandenburg, Oderberg; Ordovician, Upper Grey Orthoceratite Limestone; Neben and Krueger Coll.; MB.C.30520, MB.C.30521.

POLAND • 1 spec.; West Pomerania, Juszkowo (former Gischkau); Ordovician, Upper Grey Orthoceratite Limestone; Neben and Krueger Coll.; MB.C.30522 • 1 spec.; West Pomerania, Skowarcz (former Schönwarling), Gdańsk County; Ordovician; Hoyers 1912 Coll.; MB.C.11697.



**Fig. 17.** *Ancistroceras undulatum* (Boll, 1857) from the Upper Grey Orthoceratite Limestone; specimen MB.C.11697a (Hoyers 1912 Coll.) from Skowarcz (former Schönwarling); previously figured by Foerste (1930: pl. 41 fig. 1); dorsal, lateral and ventral views. Note imprints of the vascular system near the apex visible in the photograph on the left. Scale bar units = 1 mm.

## Description

The five specimens are fragments of the uncoiled parts of conchs (only the very end of the coiled parts are preserved). The conchs expand with angles of 25–27° (Fig. 19A). The largest specimen is MB.C.30520, which attains 57 mm whorl height; at this size, the whorl profile is circular with centrally located siphuncle and an SDR of 0.13 (Fig. 19B). The shell ornament is preserved in all specimens. It consists of annuli (up to 3.5 mm apart), which bear raised pairs of lirae (up to 1 mm apart) on their crests. The ornament elements form a ventral sinus, lateral sinuses and a dorsal projection that is roof-shaped and flanked by low dorsolateral sinuses (Figs 17–18).

## Remarks

*Ancistroceras undulatum* is very similar to *A. barrandei* (described below), from which it differs chiefly in the weaker curvature at the end of the coiled part of the conch (Aubrechtová & Meidla 2020). However, the present material reveals further differences in the shell ornament: the dorsal projection is roof-shaped, flanked by low dorsolateral sinuses in *A. undulatum*. By contrast, the dorsal projection in *A. barrandei* is continuously rounded and lacks dorsolateral sinuses.

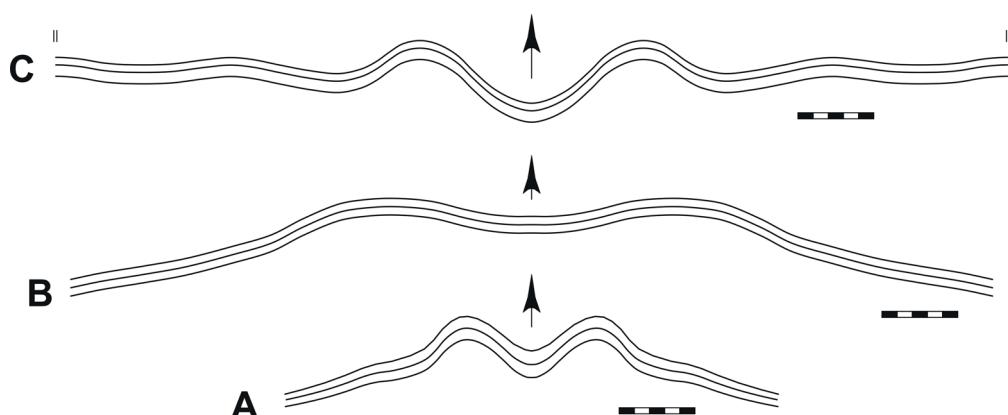
Specimen MB.C.11687 is the largest *Ancistroceras* in the collection with the length of 226 mm and maximum whorl height of 49 mm. The conch is, however, incompletely preserved and the specimen is thus assigned to *A. cf. undulatum*.

A regular network of radial lines and impressions is preserved in the posterior surface of cameral deposits in the specimen MB.C.11696. These were interpreted as remains of a vascular system by Aubrechtová & Meidla (2020: fig. 5f–g). The same structures are found also in the specimen MB.C.11697a (Fig. 17).

## Geographic and stratigraphic occurrence

Norway, Sweden, Estonia (in situ) and northern Germany, northern Poland and the Kaliningrad Region (Russia) (in erratics within Pleistocene gravels); Lasnamägi, Uhaku and early Kukruse regional stages (Darriwilian to early Sandbian, Middle to early Late Ordovician).

*Ancistroceras undulatum* is a stratigraphically significant species in Baltoscandia indicating the Uhakuan age (e.g., Jaanusson 1960; Evans *et al.* 2014).



**Fig. 18.** *Ancistroceras undulatum* (Boll, 1857), lirae course in selected specimens. **A.** Specimen MB.C.30522 (Neben & Krueger Coll.) from Juszko (former Gischkau), Gdańsk County (Pomerania, Poland), at wh = 10 mm. **B.** The same specimen, at wh = 27 mm. **C.** Specimen MB.C.30521 (Neben & Krueger Coll.) from Oderberg (Brandenburg), at wh = 18 mm. Scale bar units = 1 mm.

**Table 5.** Conch measurements (in mm), and expansion rates of uncoiled conch parts of *Ancistroceras* Boll, 1857.

taxon	catalogue nr	max. wh	max. ww	min. wh	min. ww	fragm. length	EA (°)
<i>A. barrandei</i>	MB.C.11700	—	38.0	—	17.5	48.2	24.0
<i>A. barrandei</i>	MB.C.11991a	27.1	—	11.4	10.4	53.5	16.7
<i>A. barrandei</i>	MB.C.30516	40.0	—	9.6	8.5	84.5	20.4
<i>A. barrandei</i>	MB.C.30517	35.7	35.4	7.0	—	71.2	22.8
<i>A. barrandei</i>	MB.C.30518	45.0	46.0	13.0	13.3	99.3	18.3
<i>A. torelli</i>	MB.C.22575	32.0	—	17.5	16.0	25.3	32.0
<i>A. torelli</i>	MB.C.30519	30.7	32.5	17.0	18.0	26.5	29.0
<i>A. undulatum</i>	MB.C.11696	29.0	—	8.0	8.0	47.4	25.0
<i>A. undulatum</i>	MB.C.11697a	32.0	—	10.0	—	47.8	25.9
<i>A. undulatum</i>	MB.C.30521	39.0	39.0	15.2	15.2	49.6	27.0
<i>A. undulatum</i>	MB.C.30520	57.0	57.0	16.0	—	87.7	26.3
<i>A. undulatum</i>	MB.C.30522	36.0	—	14.0	—	—	—
<i>A. cf. barrandei</i>	MB.C.11692.1, 3	39.1	—	21.1	—	36.1	28.0
<i>A. cf. undulatum</i>	MB.C.11687	49.0	—	14.4	—	72.0	27.0
<i>A. cf. undulatum</i>	MB.C.11692.2, 4	28.8	—	14.6	—	24.8	32.0
<i>A. cf. undulatum</i>	MB.C.30565	38.0	40.0	14.0	15.3	54.1	25.0
<i>A. cf. undulatum</i>	MB.C.30564	45.0	46.0	10.5	11.0	81.5	23.9
<i>A. sp.</i>	MB.C.30566	54.0	—	11.0	11.0	89.5	27.0

***Ancistroceras barrandei* Dewitz, 1880**

Figs 20–22, 23A–C, Tables 4–6

*Ancistroceras Barrandei* Dewitz, 1880: 389, pl. 17 fig. 6–6a.

*Strombolitites Barrandei* – Remelé 1881: 192.

*Ancistroceras Barrandei* – Noetling 1884: 128. — Patrunky 1926: 120.

*Ancistroceras undulatum* – Noetling 1884: pl. 18 fig. 6–6a. — Rüdiger 1889: 44. — Qi 1980: 254, pl. 2 fig. 6, text-fig. 5. — Neben & Krueger 1971: pl. 17 fig. 1

*Endoceras barrandei* – Foerste 1930: 300.

*Ancistroceras barrandei* – Neben & Krueger 1971: pl. 21 fig. 9.

### Diagnosis

Species of the genus *Ancistroceras* with strongly curved end of the coiled part of the conch, expansion angle of straight part 17–21°. Tubular connecting rings. Dorsal projection of ornament elements continuously rounded, without dorsolateral sinuses (after Aubrechtová & Meidla 2020, emended).

### Type material

Not available for study; Dewitz (1880) mentioned three specimens, one of them was figured (Dewitz 1880: pl. 17 fig. 6), from Mayakovskoye (former Nemmersdorf; Kaliningrad Region, Russia), Middle Ordovician erratics from Pleistocene gravel.

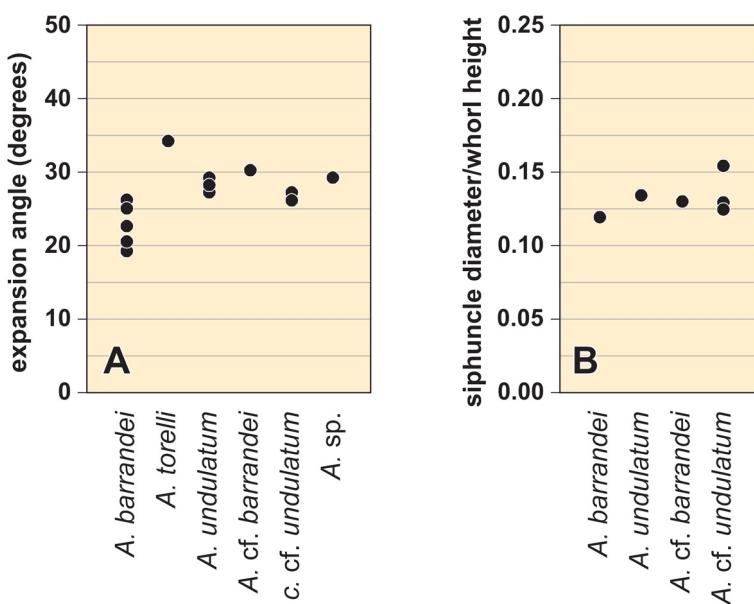
### Material examined

GERMANY • 1 spec.; Brandenburg, Heegermühle; Ordovician; MB.C.11700 • 1 spec.; Brandenburg, Niederfinow; Ordovician, Upper Grey Orthoceratite Limestone; Neben and Krueger Coll.; MB.C.30515 • 1 spec.; Mecklenburg-Vorpommern, Groß Zicker (Island of Rügen); Ordovician, Upper Grey Orthoceratite Limestone; Helms 1966 Coll.; MB.C.11991a • 2 specs; Mecklenburg-Vorpommern, Rerik (Ostsee); Ordovician, Upper Grey Orthoceratite Limestone; MB.C.30516, MB.C.30517 • 1 spec.; Mecklenburg-Vorpommern, Rerik (Ostsee); Ordovician, Upper Grey Orthoceratite Limestone; Neben and Krueger 1971 Coll.; MB.C.30518.

### Description

Specimen MB.C.30518 (Figs 21A, 23A) consists of the coiled part ( $dm = 12$  mm; inner whorls not preserved, last quarter of the last whorl detached from preceding whorl) and a part of the straight uncoiled part of the conch (length = 140 mm;  $wh = 45$  mm; EA  $\sim 18^\circ$ ). The shell ornament in the coiled and beginning of the uncoiled part consists of annuli (1 mm apart) that bear raised pairs of lirae (0.3–0.5 mm apart) on their crests. In the remaining part of the uncoiled conch, the annuli are wide and flat and the lirae are standing up to 1.3 mm apart. The dorsal projection of ornament elements is low and continuously rounded, i.e., not flanked by dorsolateral sinuses. The length of the phragmocone chambers can be measured only in the middle part of the straight part (CLR = 0.34 at  $wh = 40.5$  mm).

Specimen MB.C.11991 (Figs 21C, 23C) consists of the almost complete coiled part ( $dm = 15$  mm; coiling tight, only the last part of the last volution is detached; WER = 4.20) and a part of the weakly sigmoid uncoiled part (length = 90 mm;  $wh = 27$  mm; EA  $\sim 17^\circ$ ). The shell ornament consists of narrow annuli (up to 1.4 mm in distance) and lirae (up to 0.3 mm in distance) in the coiled part and beginning of the uncoiled part; the annuli become wider and applanate in the remaining uncoiled part; the distance of lirae increases up to 1 mm. The ventral sinus is deep but becomes shallower during ontogeny. On the flanks, the ornament elements extend transversely with a lateral sinus that develops at a whorl height of ca 17 mm. The dorsal projection is low, continuously rounded and is not flanked by any dorsolateral sinuses. The chamber length increases during ontogeny (CLR = 0.32–0.42).



**Fig. 19.** Conch expansion rates (A) and siphuncle diameter rates (B) in species of *Ancistroceras* Boll, 1857.

Specimen MB.C.30516 (Figs 21B, 23B) consists of the almost complete coiled part (inner whorls are tightly coiled and the last whorl widely detaches from preceding whorls; dm = 10 mm) and a part of the straight uncoiled part (length = 115 mm; wh = 40 mm; EA ~ 20°) of the conch. The shell ornament in the coiled part of the specimen and after uncoiling consists of indistinct annuli and raised pairs of lirae (up to 0.5 mm apart). In the larger half of the specimen, the annuli are very wide and flat, and the shell surface is ornamented by slightly irregularly developed lirae (up to 0.7 mm apart). The ornament elements form deep sinuses on the venter and flanks of the conch; the dorsal projection is low and continuously rounded. The chamber length is variable (CLR = 0.16–0.33) and decreases towards the aperture (Fig. 22).



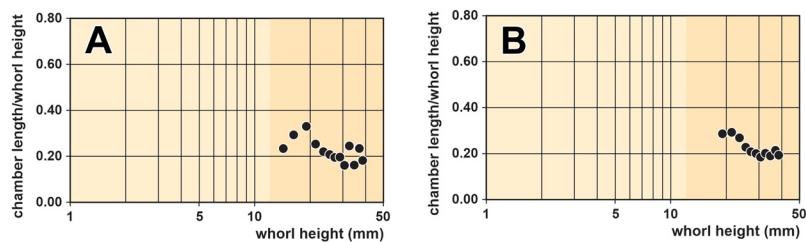
**Fig. 20.** *Ancistroceras barrandei* Dewitz, 1880, reproduction of the figure provided by Noetling (1884: pl. 16 Fig. 6–6a). Scale bar units = 1 mm.

**Remarks**

*Ancistroceras barrandei* is very similar to *A. undulatum* (described above), from which it differs in the stronger curvature at the end of the coiled part of the conch (Aubrechtová & Meidla 2020). The specimens studied here also show that the dorsal projection of the ornament is continuously rounded



**Fig. 21.** *Ancistroceras barrandei* Dewitz, 1880 from the Upper Grey Orthoceratite Limestone. **A.** Specimen MB.C.30518 (Neben & Krueger Coll.) from Rerik (Ostsee); previously figured by Neben & Krueger (1971: pl. 17 fig. 1). **B.** Specimen MB.C.30516 (Neben & Krueger Coll.) from Rerik (Ostsee). **C.** Specimen MB.C.11991 (Helms 1966 Coll.) from Groß Zicker (Island of Rügen). Scale bar units = 1 mm.



**Fig. 22.** *Ancistroceras barrandei* Dewitz, 1880, chamber length/whorl height of specimen MB.C.30516 (Neben & Krueger Coll.) from Rerik (Ostsee). Left = empirical data, right = three data point averaged.

without dorsolateral sinuses in *A. barrandei*, while the dorsal projection is roof-shaped with shallow adjacent dorsolateral sinuses in *A. undulatum*.

In *A. barrandei*, the coiled conch is so far known only from a single specimen (Noetling 1884: pl. 18 fig. 6) (Fig. 20). Here, we describe additional specimens with preserved coiled parts. Their morphology is variable in the degree to which the last whorl loses contact with the preceding whorl (Fig. 23). In other characters, the specimens are similar to each other.

Specimen MB.C.11991 has a weakly sigmoid uncoiled part of the conch and a rather low expansion angle ( $17^\circ$ ), which might suggest it should be assigned to *Holmiceras*. However, the specimen has a tightly, not loosely coiled apical part of the conch and at the conch length of 90 mm, it does not reach the mature growth stage.

#### Geographic and stratigraphic occurrence

Estonia (in situ) and northern Germany, northern Poland and the Kaliningrad Region (Russia) (in erratics within Pleistocene gravels); Aseri to Uhaku regional stages, Middle Ordovician. According to Dewitz (1880), the type material of *A. barrandei* comes from the “lower Silurian” of Königsberg (= Kaliningrad), where it was found in co-occurrence with *Ancistroceras undulatum*. The co-occurrence of the two species suggests a late Darriwilian age.

*Ancistroceras torelli* (Remelé, 1881)  
Figs 23D–E, 24–25, Tables 4–5

*Strombolituites Torelli* Remelé, 1881: 192, text-fig. 2.

*Ancistroceras Torelli* – Noetling 1884: pl. 18 fig. 7. — Holm 1885: pl. 4 fig. 2. — Remelé 1890: pl. 4 fig. 1.

*Ancistroceras torelli* – Balashov 1962: pl. 9 fig. 8. — Neben & Krueger 1971: pl. 17 figs 2, 7.

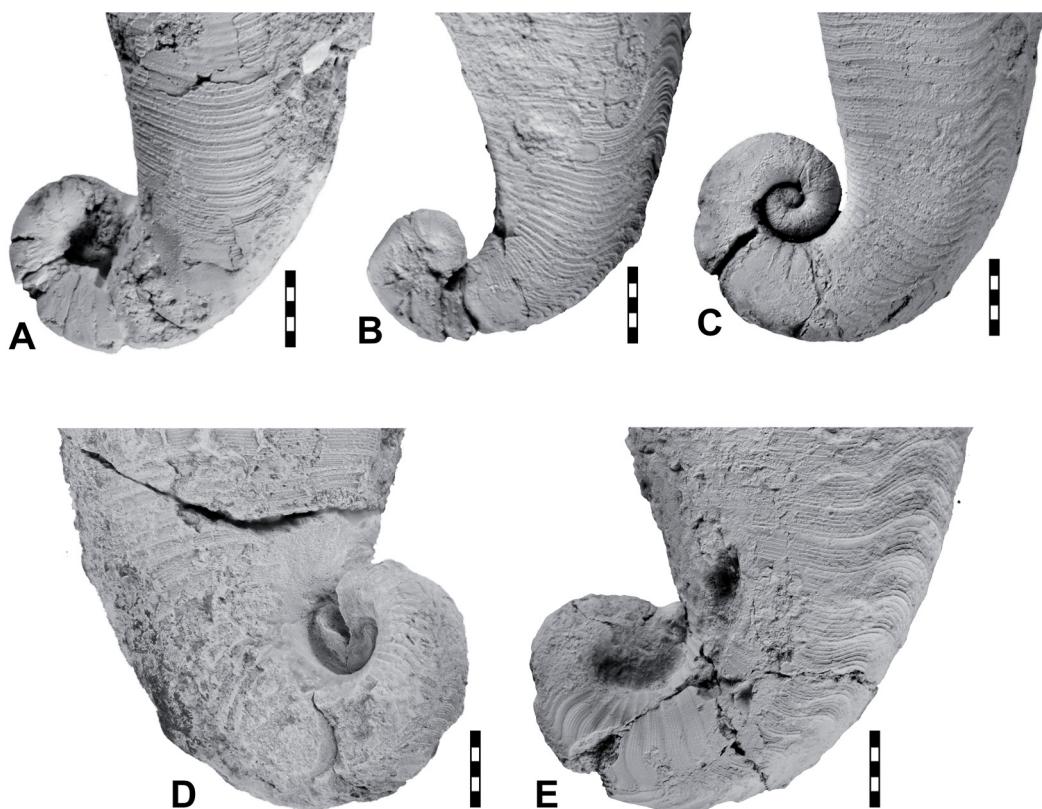
? *Ancistroceras torelli* – Foerste 1930: pl. 41 fig. 2a–b. — Dzik 1984: pl. 39 figs 8–9, pl. 40 figs 1–2.

#### Diagnosis

Species of the genus *Ancistroceras* with strongly curved end of the coiled part of the conch; uncoiled part of the conch straight; expansion angle ca  $30^\circ$ . Whorl profile slightly depressed in the coiled part and circular in the uncoiled part of the conch. Ornament with distinct, narrow annuli and lirae, well-developed even in the coiled part of the conch. Ornament with shallow lateral sinus, low dorsal projection and ventral sinus; the latter deep at the coiled part and flattened out in the uncoiled part of the conch.

**Table 6.** Siphuncular diameter ratio (SDR) and siphuncular distance ratio (SPR) at their corresponding whorl height in specimens of *Ancistroceras* Boll, 1857.

<b>taxon</b>	<b>catalogue nr</b>	<b>wh</b>	<b>SDR</b>	<b>wh</b>	<b>SPR</b>
<i>A. barrandei</i>	MB.C.11700	38.0	0.12	38.0	0.41
<i>A. undulatum</i>	MB.C.30521	—	—	41.0	0.56
<i>A. undulatum</i>	MB.C.30520	57.0	0.13	57.0	0.49
<i>A. cf. barrandei</i>	MB.C.11692.1, 3	32.5	0.13	32.5	0.50
<i>A. cf. undulatum</i>	MB.C.11692.2, 4	21.5	0.15	21.5	0.52
<i>A. cf. undulatum</i>	MB.C.30565	14.0	0.13	14.0	0.41
<i>A. cf. undulatum</i>	MB.C.30564	10.5	0.12	10.5	0.48



**Fig. 23.** Comparison of the coiled parts of species of *Ancistroceras* Boll, 1857 from the Upper Grey Orthoceratite Limestone. **A.** *Ancistroceras barrandei* Dewitz, 1880, specimen MB.C.30518 (Neben & Krueger Coll.) from Rerik (Ostsee). **B.** *Ancistroceras barrandei* Dewitz, 1880, specimen MB.C.30516 (Neben & Krueger Coll.) from Rerik (Ostsee). **C.** *Ancistroceras barrandei* Dewitz, 1880, specimen MB.C.11991 (Helms 1966 Coll.) from Groß Zicker (Island of Rügen). **D.** *Ancistroceras torelli* (Remelé, 1881), lectotype MB.C.22575 from Heegermühle (Brandenburg). **E.** *Ancistroceras torelli* (Remelé, 1881), specimen MB.C.30519 (Neben & Krueger Coll.) from Schmetzdorf (Brandenburg). Scale bar units = 1 mm.

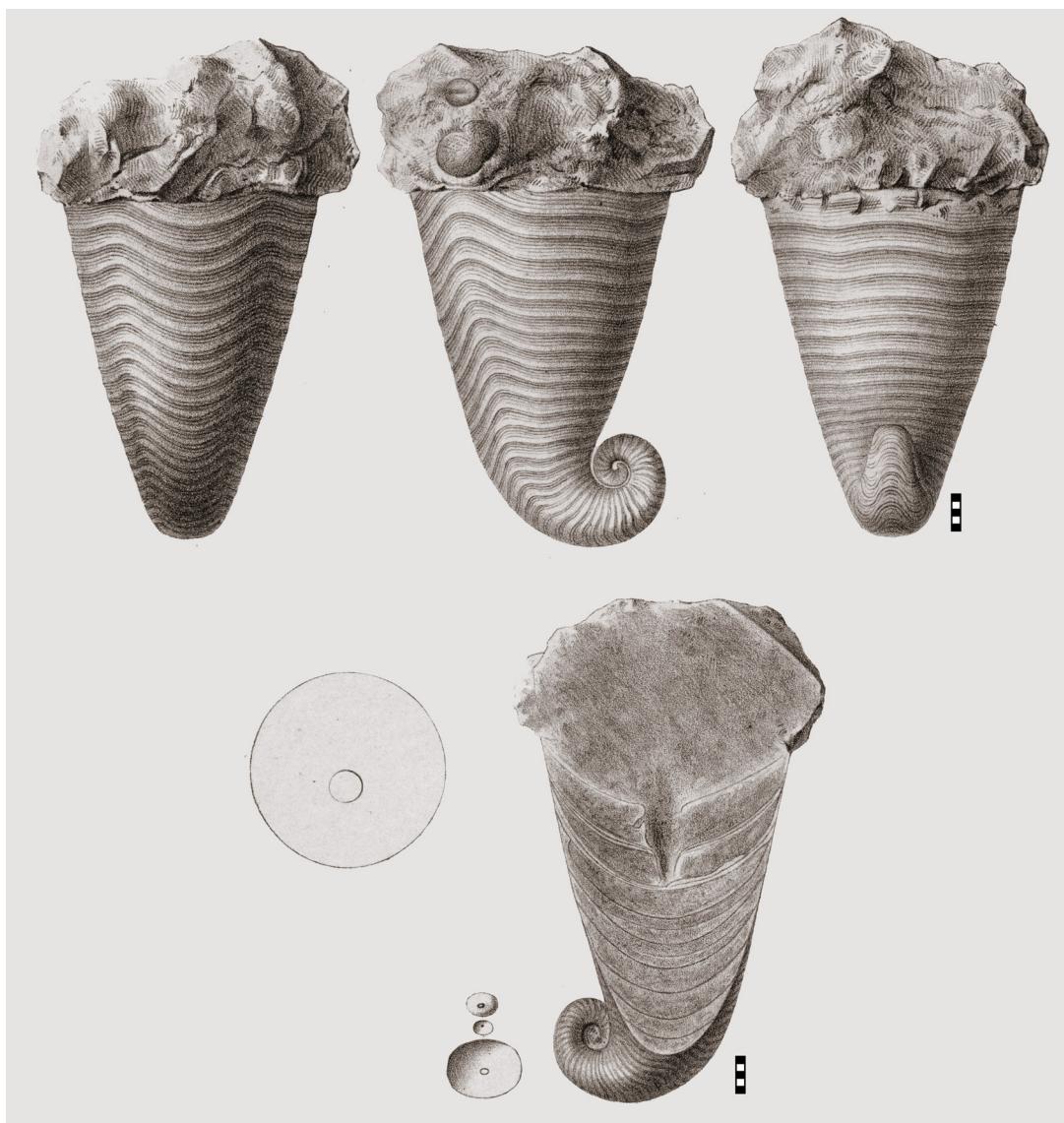
Type material

Lectotype (designated here)

GERMANY • Brandenburg, Heegermühle; erratics in Pleistocene gravel, Ordovician, Upper Grey Orthoceratite Limestone; illustrated by Remelé (1881: text-fig. 2; 1890: pl. 4 fig. 1) and Neben & Krueger (1971: pl. 17 fig. 7); re-illustrated here in Fig. 23D, 24, 25A; MB.C.22575.

Paralectotype

GERMANY • Brandenburg, Schmetzdorf; Ordovician, Upper Grey Orthoceratite Limestone; Neben and Krueger Coll.; MB.C.30519.



**Fig. 24.** *Ancistroceras torelli* (Remelé, 1881) from the Upper Grey Orthoceratite Limestone. Reproduction of the illustration of lectotype MB.C.22575 from Heegermühle (Brandenburg) from Remelé (1890: pl. 4 fig. 1). Scale bar units = 1 mm.

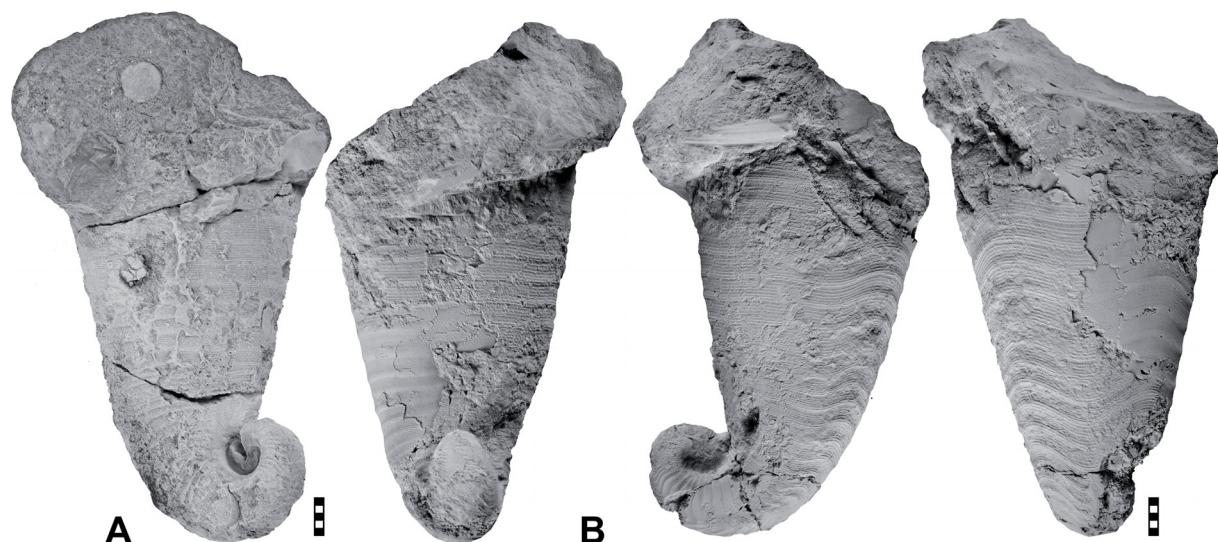
### Description

Lectotype MB.C.22575 (Figs 23D, 24, 25A) is undeformed but some measurements are difficult to obtain because of an imprecise, oblique section that was ground by a previous researcher. The conch consists of the coiled part ( $dm = 20.5$  mm; tightly coiled; WER  $> 3$ ) and the straight uncoiled part (length = 33 mm long; wh  $\sim 32$  mm; EA  $\sim 32^\circ$ ). The shell ornament consists of raised lines in the coiled part of the conch, but towards the uncoiled part of the conch, these lines grade into narrow but clearly marked annuli (2.5 mm apart) with lirae 0.5 mm apart. The chamber length can be measured precisely only at the end of the uncoiled part of the specimen (CLR = 0.18 at wh = 28 mm). The siphuncle has a central position and measures ca 0.12 of the whorl height.

Paralectotype MB.C.30519 (Figs 23E, 25B) is similar in size to the lectotype. The conch consists of the coiled part ( $dm = 19.7$  mm; tightly coiled; WER  $\sim 5$ ) and the straight uncoiled part (length = 41 mm; wh = 31 mm; EA  $\sim 29^\circ$ ). The shell ornament consists of narrow annuli that are clearly visible along the whole extension of the conch including the coiled part. Their distances increase gradually from 0.7 mm to 2.5 mm. The annuli are accompanied by lirae (0.5 mm apart). The ornament elements form a low dorsal projection, a shallow lateral sinus and a ventral sinus, which is deep in the coiled part and flattens out in the uncoiled part.

### Remarks

Unlike the other species of the genus, *Ancistroceras torelli* has distinctly developed annuli even in the coiled part of the conch. Additionally, the species differs from the above described *A. undulatum* in the stronger curvature at the end of the coiled part and from *A. barrandei* in a much larger expansion angle (ca  $30^\circ$ ). *Ancistroceras bollii* (Remelé, 1882) from the Darriwilian erratics of northern Germany has a more bulbous conch than *A. torelli* and it is generally smaller, ventrally curved and retains the circular whorl profile during ontogeny.



**Fig. 25.** *Ancistroceras torelli* (Remelé, 1881) from the Upper Grey Orthoceratite Limestone. **A.** Lectotype MB.C.22575 from Heegermühle (Brandenburg); dorso-lateral view. **B.** Specimen MB.C.30519 (Neben & Krueger Coll.) from Schmetzdorf (Brandenburg); dorsal, lateral and ventral views. Scale bar units = 1 mm.

### Geographic and stratigraphic occurrence

Northern Germany and northern Poland (in erratics within Pleistocene gravels); late Darriwilian, Middle Ordovician.

According to Remelé (1881), the lectotype originated from the “light grey orthoceratite limestone”, where it co-occurs with *Lituites perfectus* and the trilobites *Asaphus* sp., *Illaneus* sp. and *Hoplolichas tricuspidatus* Beyrich, 1846. This co-occurrence suggests a late Darriwilian (probably Lasnamägian) age of the lectotype.

Genus *Angelinoceras* Hyatt, 1894

#### Type species

*Lituites latus* Angelin, 1880; subsequent designation by Sweet (1958).

#### Diagnosis

Genus of the family Lituitidae with loosely coiled apical part of the conch, 30 to over 50 mm in diameter, and moderately expanded (ca 8°) sigmoidal backcoiled part. Whorl profile compressed throughout (WWI ~ 0.90 at the last whorl). Whorl expansion rate based on whorl height decreases during ontogeny from 3.00 to 2.00. Ornament with regularly spaced narrow annuli/raised lirae and finer lirae in between; annuli with deep ventral sinus, prominent ventrolateral projections, broad and asymmetric lateral sinuses, low dorsolateral projections, and a broad, nearly straight dorsal sinus subdivided, at least in the early stages, by a mid-dorsal projection. Ventral band with ventrolateral ridges may be present (after Sweet 1958; Furnish & Glenister 1964).

#### Species included

Only the type species.

#### Remarks

Fang *et al.* (2021) proposed, among others, to synonymise *Angelinoceras* with *Lituites*. The species of the two genera are indeed similar, essentially differing only in the conch size (coiled conch diameters in *Angelinoceras* may exceed 50 mm). The herein studied material is, however, too incomplete in preservation to make a proper decision on this matter.

The genus *Angelinoceras* consists only of the type species *A. latum*. This species is known from the middle Darriwilian strata of mainland Sweden and the Island of Öland, and also from erratics in Germany that derived from Darriwilian rocks of Baltoscandia. With its narrow stratigraphic range, *A. latum* is a stratigraphically significant taxon in Baltoscandia (e.g., Jaanusson & Mutvei 1953; Evans *et al.* 2014).

Sweet (1958) described a probable second, stratigraphically younger species from the *Ampyx* Limestone of the Oslo-Asker district (Sandbian, early Late Ordovician). However, because of its fragmentary preservation, he assigned this specimen as *Angelinoceras* sp. Aceñolaza *et al.* (1977) reported *Angelinoceras* sp. from the San Juan Formation (Middle Ordovician) of the Argentine Precordillera, but that specimen differs in the geometry of the coiled conch part and has a lower expansion rate than characteristic representatives of *Angelinoceras*. In fact, based on the photograph provided by Aceñolaza *et al.* (1977: pl. 1g), it seems the specimen might actually belong to the family Estonioceratidae (order Tarphyceratida Flower, 1950), rather than the lituitids.

**Geographic and stratigraphic occurrence**

Norway and Sweden (in situ) and northern Germany and northern Poland (in erratics within Pleistocene gravels); Kunda to early Kukruse regional stages (Middle to early Late Ordovician).

*Angelinoceras latum* (Angelin, 1880)

Figs 26–28, Table 7

*Lituites latus* Angelin, 1880: 9, pl. 11 figs 1–4.

*Lituites Hageni* Remelé, 1880: 228, pl. 1 figs 4–5, pl. 3 fig. 3.

*Lituites Hageni* – Remelé 1890: 19, pl. 1 figs 4–5, pl. 3 fig. 3.

*Lituites latus* – Jaanusson & Mutvei 1953: 18, fig. 3b.



**Fig. 26.** *Angelinoceras latum* (Angelin, 1880); reproduction of illustrations by Angelin (1880: pl. 3 fig. 5). Scale bar units = 1 mm.

**Table 7.** Conch measurements (in mm), ratios and rates of coiled conch parts of *Angelinoceras* Hyatt, 1894.

taxon	catalogue nr	dm	wh	uw	ww	WERdm	WERah	UWI	WWI
<i>A. latum</i>	MB.C.11681	—	19.7	21.0	—	—	—	—	—
<i>A. latum</i>	MB.C.11682	52.2	—	18.6	21.9	—	2.63	2.41	0.42
<i>A. latum</i>	MB.C.11683	53.6	16.0	18.2	24.7	47.2	—	2.29	0.46
<i>A. latum</i>	MB.C.30525	41.5	15.0	16.0	15.8	39.0	3.15	2.65	0.38
<i>A. sp.</i>	MB.C.29658	32.9	—	11.0	—	21.7	2.20	2.26	—

*Angelinoceras latum* – Sweet 1958: 132. — Balashov 1962: pl. 7 fig. 2.

*Lituites hageni* – Neben & Krueger 1971: pl. 21 figs 4–5.

*Lituites cf. hageni* – Neben & Krueger 1971: pl. 21 fig. 6.

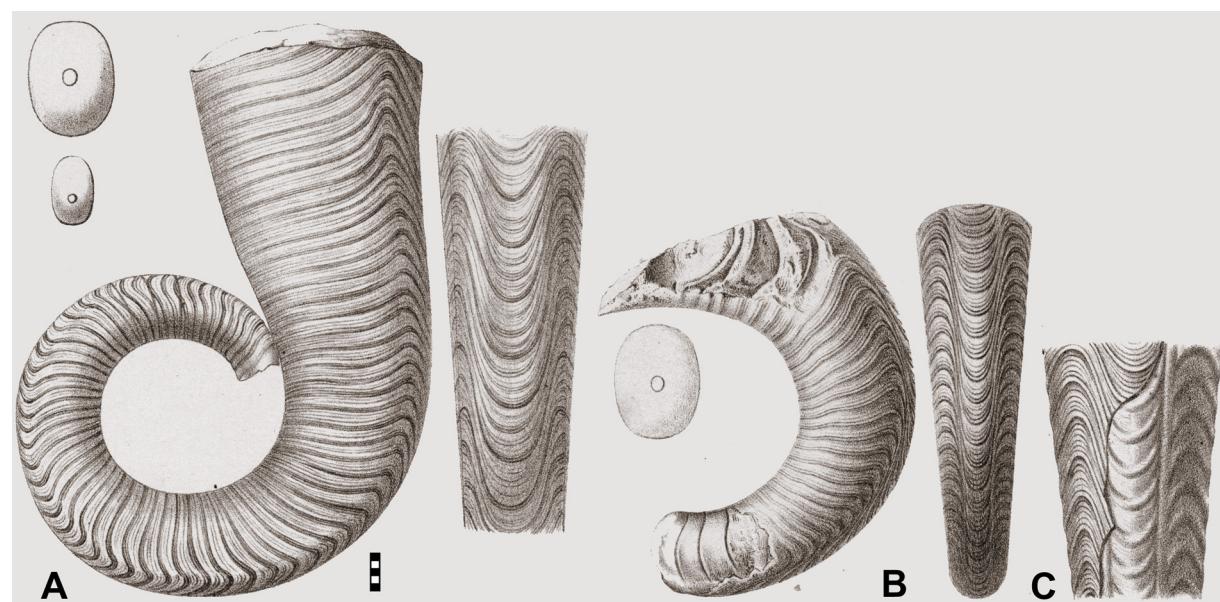
### Diagnosis

As for the genus.

### Type material

#### Lectotype

Not re-studied; the specimen figured by Angelin (1880: pl. 11 figs 1–4; illustration reproduced here in Fig. 26), from Vikarbyn (Dalarna, Sweden) and was found in the lower part of the Segerstad Limestone (Upper Red Orthoceratite Limestone, Aseri Regional Stage, middle Darriwilian, Middle Ordovician; designated and re-illustrated by Jaanusson & Mutvei (1953: 18, fig. 3b).



**Fig. 27.** *Angelinoceras latum* (Angelin, 1880); reproductions of illustrations of Remelé (1890). **A.** Specimen MB.C.11682 from Eberswalde (Brandenburg), illustrated by Remelé (1890: pl. 1 fig. 4). **B.** Specimen MB.C.11683 from Heegermühle (Brandenburg), illustrated by Remelé (1890: pl. 3 fig. 3). **C.** Specimen MB.C.11681 from Eberswalde (Brandenburg), illustrated by Remelé (1890: pl. 1 fig. 5). Scale bar units = 1 mm.

### Material examined

GERMANY • 1 spec.; Brandenburg, Vierraden (Schwedt); Ordovician, Upper Grey Orthoceratite Limestone; Krueger 1974 Coll.; MB.C.11687 • 1 spec.; Brandenburg, Eberswalde; Ordovician; MB.C.11681 • 1 spec.; Brandenburg, Eberswalde railway station; Ordovician, Upper Red Orthoceratite Limestone; Remelé 1878 Coll.; MB.C.11682 • 1 spec.; Brandenburg, Heegermühle; Ordovician, Upper Red Orthoceratite Limestone; Kgl. Forstakademie Eberswalde Coll.; MB.C.11683 • 2 specs; Brandenburg, Niederfinow; Ordovician, Upper Red Orthoceratite Limestone; MB.C.30523, MB.C.30524 • 1 spec.; Brandenburg, Oderberg; Ordovician, Upper Red Orthoceratite Limestone; Neben Coll.; MB.C.30525.

POLAND • 1 spec.; Silesia, probably Żory (former Sorau); Ordovician, Upper Red Orthoceratite Limestone; Kirchner Coll.; MB.C.11684.

### Description

The seven specimens are fragments of the last whorl of the coiled part (coiling tight at least in the last whorl; 42–54 mm in diameter; WWI = 0.88–0.94; WER<sub>ah</sub> = 2.30–2.60; WER<sub>dm</sub> = 2.60–3.10). Only the specimen MB.C.11682 (Fig. 28A) has a short part of the uncoiled part (27 mm long; 29 mm whorl height) of the conch. The shell ornament consists of narrow annuli (up to 2 mm apart) and fine lirae in between (up to 1 mm apart); a ventral band flanked by ventrolateral ridges is formed on the venter (Fig. 27). Annuli may have pairs of raised lirae on their crests.

### Remarks

Three of the seven specimens (MB.C.11681–MB.C.11683; Fig. 27) studied here are syntypes of *Lituites hageni* from Darriwilian erratics of northern Germany. Rüdiger (1889) and Dzik (1984) suggested that *L. hageni* is a junior synonym of *Angelinoceras latum*. This view is followed and supported here because the syntypes of *L. hageni* differ from the lectotype of *A. latum* (Fig. 26) only in the larger diameter of their coiled parts. Moreover, the additional specimen MB.C.30525, figured by Neben & Krueger (1971: pl. 21 fig. 6), is even smaller than the lectotype, while closely resembling all other investigated specimens.

### Geographic and stratigraphic occurrence

Sweden (in situ) and northern Germany and northern Poland (in erratics within Pleistocene gravels); upper Kunda to Aseri (possibly up to lower Lasnamägi) regional stages (middle to late Darriwilian, Middle Ordovician).

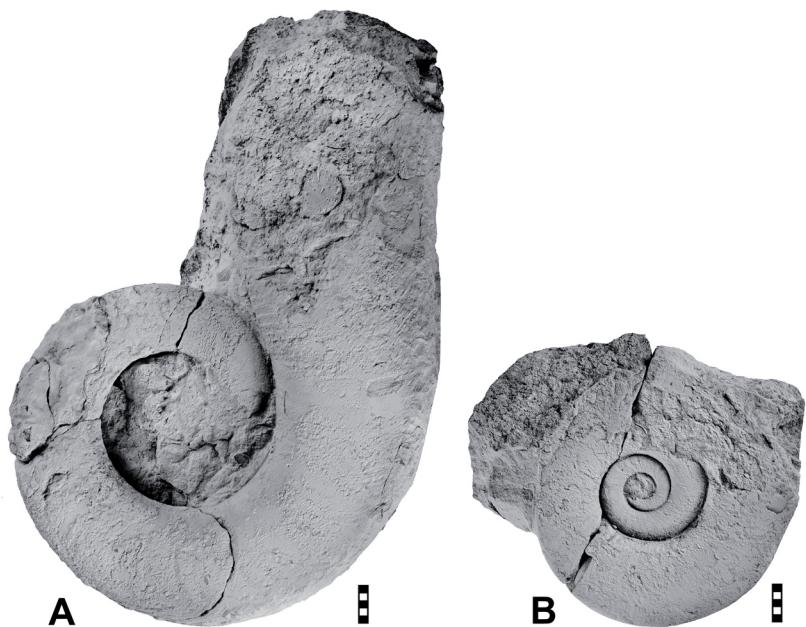
*Angelinoceras* sp.  
Fig. 28B, Table 7

### Material examined

GERMANY • 1 spec.; Brandenburg, Oderberg; Ordovician, Upper Red Orthoceratite Limestone; Krueger Coll.; MB.C.29658.

### Description

Specimen MB.C.29658 (Fig. 28B) consists of the coiled part (coiling tight; 33 mm diameter; WWI = 0.66; WER<sub>dm</sub> = 2.20 and WER<sub>ah</sub> = 2.30) of a conch. The shell surface is only locally and indistinctly preserved. Narrow annuli are separated by very thin lirae and both form a deep ventral sinus, which is delineated by paired longitudinal grooves.



**Fig. 28.** *Angelinoceras* Hyatt, 1894 from the Upper Red Orthoceratite Limestone. **A.** *Angelinoceras latum* (Angelin, 1880), specimen MB.C.11682 (Remelé 1878 Coll.) from Eberswalde (Brandenburg); lateral view. **B.** *Angelinoceras* sp., specimen MB.C.29658 (Krueger Coll.) from Oderberg (Brandenburg). Scale bar units = 1 mm.

#### Remarks

The specimen represents an *Angelinoceras* as indicated by its conch ratios and type of ornament. The specimen differs from *A. latum* in the smaller, tightly coiled conch with a slightly lower whorl expansion rate. The incomplete preservation of the last whorl and of the early uncoiled part makes it difficult to decide whether the specimen should be assigned to a new species or whether it only reflects morphological variation within *A. latum*.

#### Genus *Holmiceras* Hyatt, 1894

##### Type species

*Lituites praecurrentis* Holm, 1891; subsequent designation by Sweet (1958).

##### Diagnosis

Genus of the family Lituitidae with 1 to 1.5 loosely coiled volutions of the coiled conch; uncoiled part short, sigmoidal, with expansion angles of 7°–20°. Whorl profile either slightly compressed or somewhat depressed. Chamber length between 0.20 and 0.30 of the whorl height. Shell surface with annuli and/or lirae; lateral and dorsal sinuses and ventrolateral and dorsolateral projections in the apical parts of the conch, but adorally, the ventral and dorsal sinuses disappear so, that on the mature body chamber, the venter and dorsum are occupied by broad projections (after Sweet 1958).

### Species included

*Holmiceras benneti* Flower, 1975; *Orthoceras coreanicum* Kobayashi, 1928; *Lituites Kjerulfi* Brøgger, 1882; *Lituites praecurrents* Holm, 1891; *Holmiceras sichuanense* Lai, 1986; *Holmiceras havelense* sp. nov.

### Remarks

The species of *Holmiceras* are morphologically closely similar to species of *Ancistroceras*, which have a smaller and tightly coiled juvenile conch and attain greater expansion angles (usually between 20 and 30°). The conch shapes in the species of *Holmiceras* are also somewhat similar to those in *Angelinoceras* because the uncoiled conch in both genera expands rapidly. The species of *Angelinoceras* have much larger general dimensions, though, with coiled conch diameters of 30–50 mm. The species of the genus *Lituites* generally have lower expansion angles (Fig. 30), larger overall conch sizes and mature aperture with five projections and deep sinuses on the ventral and lateral sides of the conch. Sweet (1958), Dzik (1984) and Fang *et al.* (2021) discussed the phylogenetic relationships of *Holmiceras* in greater detail.

### Geographic and stratigraphic occurrence

Canada, Norway, Sweden, northern Germany, Korea and China; Middle to Late Ordovician.

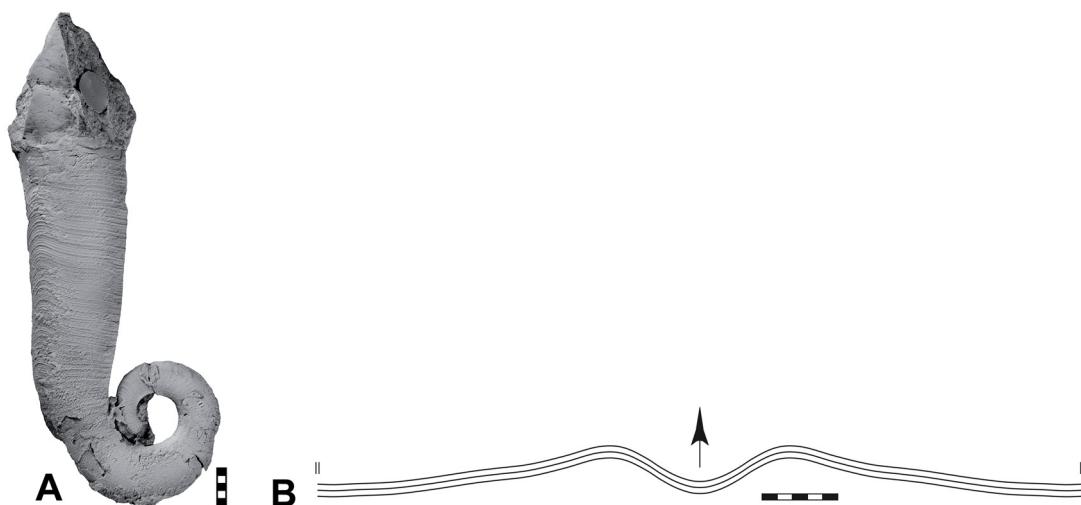
The type species *H. praecurrents* is a stratigraphically significant species in the Orthoceratite Limestone of Baltoscandia, indicating a Kundan age (Evans *et al.* 2014).

#### *Holmiceras havelense* sp. nov.

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Fig. 29, Table 8

*Lituites* aff. *praecurrents* – Neben & Krueger 1971: pl. 21 figs 2–3.



**Fig. 29.** *Holmiceras havelense* sp. nov. from the Upper Red Orthoceratite Limestone. **A.** Holotype MB.C.30526 (Neben & Krueger Coll.) from Werder (Brandenburg); previously figured by Neben & Krueger (1971: pl. 21 figs 2–3). **B.** Lirae of holotype MB.C.30526 at wh = 14 mm. Scale bar units = 1 mm.

**Table 8.** Conch measurements (in mm), ratios and rates of coiled conch parts of *Holmiceras* Hyatt, 1894.

taxon	catalogue nr	dm	wh	uw	ww	WERdm	WERah	UWI	WWI
<i>H. havelense</i>	MB.C.30526	20.6	7.8	7.8	—	2.85	2.59	0.38	—

### Diagnosis

Species of the genus *Holmiceras* with coiled part 21 mm in diameter; uncoiled part nearly straight; expansion angle 7°. Shell surface with growth lines and fine, irregularly spaced lirae.

### Etymology

From the river Havel, which flows through the type region.

### Type material

#### Holotype

GERMANY • Brandenburg, Werder (Potsdam); Ordovician, Upper Red Orthoceratite Limestone; Neben and Krueger Coll.; previously illustrated by Neben & Krueger (1971: pl. 21 figs 2–3), re-illustrated here in Fig. 29A; MB.C.30526.

### Description

Holotype MB.C.30526 (Fig. 29A) consists of the coiled part (dm = 21 mm; coiling probably loose, the end of the last volution nearly in contact with the preceding whorl;  $WER_{ah} = 2.60$ ;  $WER_{dm} = 2.90$ ) and a short part of the almost straight uncoiled part (length = 29 mm; wh = 14 mm; EA ~ 7°). The delicate shell ornament consists of growth lines and thin lirae, some of which are more raised than others; any prominent annulation is absent. The lirae are laterally oblique, sloping towards the dorsal side; the ventral sinus is deep and rounded and the dorsal projection is flat (Fig. 29B). The CLR is between 0.20 and 0.25.

### Remarks

Specimen MB.C.30526 fits in the diagnosis of *Holmiceras* but differs from all species of this genus in the more delicate ornament and a much smaller expansion angle of the uncoiled conch part (7° in the new species but 20° in the others).

### Geographic and stratigraphic occurrence

The holotype is from Werder (Brandenburg, Germany) and comes from erratics (Aseri Regional Stage, middle Darriwilian, Middle Ordovician) in Pleistocene gravel.

Genus *Lituites* Bertrand, 1763

### Type species

*Lituites lituus* de Montfort, 1808; by original designation.

### Diagnosis

Genus of the family Lituitidae with tightly or loosely coiled apical part of the conch; uncoiled part straight or variably curved; expansion angle up to ca 8°. Whorl profile compressed in the coiled and backcoiled part and circular in the straight part of the conch. Shell surface with sinuous annuli and/or lirae. Siphuncle position changes from subdorsal to subcentral during ontogeny. Fully mature aperture

with a pair of pronounced ventrolateral lappets, similar but shorter dorsolateral lappets and a low dorsal projection (after Furnish & Glenister 1964, emended).

### Species included

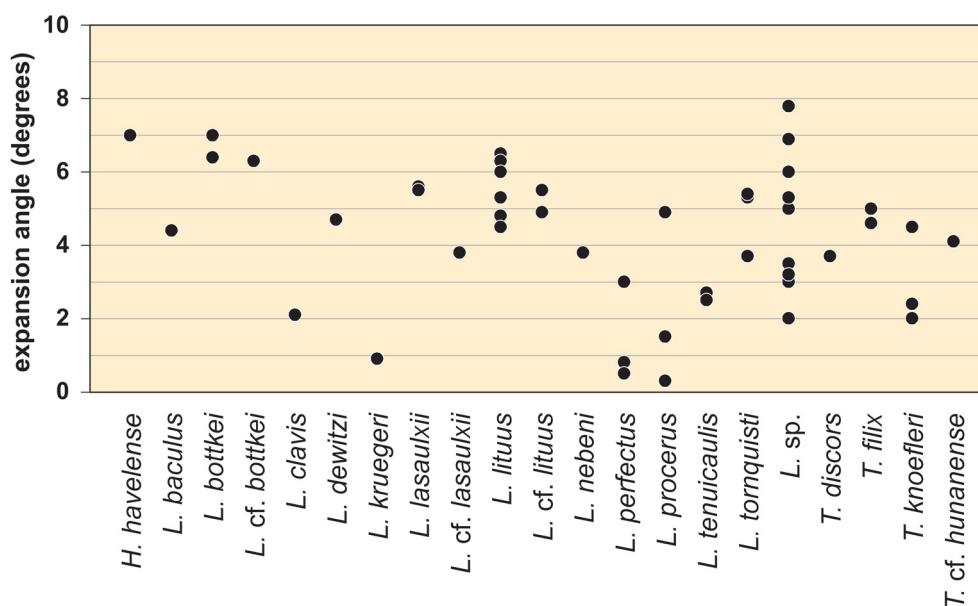
*Lituites anginus* Angelin, 1880; *Lituites anhuiense* Qi, 1980; *Lituites baculus* sp. nov.; *Lituites bottkei* sp. nov.; *Lituites clavis* sp. nov.; *Lituites dewitzi* sp. nov.; *Lituites evolutus* Fang, Chen & Zhang in Fang et al., 2017; *Lituites fallax* Remelé, 1890; *Lituites hengshanensis* Qi, 1980; *Lituites kruegeri* sp. nov.; *Lituites lii* Yü, 1930; *Lituites Lasaulxii* Remelé, 1890; *Lituites lituus* de Montfort, 1808; *Lituites nebeni* sp. nov., *Lituites ningkiangense* Lai, 1965; *Lituites perfectus* Wahlenberg, 1818; *Lituites procerus* Remelé, 1890; *Lituites tenuicaulis* Remelé, 1890; *Lituites Törnquisti* Holm, 1891; *Lituites wuweiense* Qi, 1980 (synonym of *L. ningkiangense* Lai, 1965); *Lituites xizangense* Lai, 1982.

### Remarks

Most species of the genus *Lituites* known from Baltoscandia and erratics in north central and eastern Europe were described already in the 19<sup>th</sup> century. Differences between the species concern mainly the mode of coiling, the shape of the whorl profile, the degree of curvature of the backcoiled part, the expansion angle and the shell ornament (Aubrechtová & Meidla 2020: 278, table 2). However, the apparently high intraspecific variation and common morphological transitions between the species make it often difficult to distinguish between them. An additional problem is that the species were originally defined based on the coiled and backcoiled parts of the conch. The straight part and mature aperture are not known in most of the species, which makes it impossible to taxonomically determine specimens consisting only of the uncoiled part (Holm 1891).

### Geographic and stratigraphic occurrence

Argentina, Baltoscandia, northern Germany, northern Poland, Kaliningrad Region of Russia, Bohemia, Lhasa Terrane (North Tibet), North and South China; Middle to Late Ordovician.



**Fig. 30.** Conch expansion rates in species of the Lituitidae Phillips, 1848.

***Lituites lituus*** de Montfort, 1808  
Figs 31–32, 33A–B, 34–35, Tables 9–10

*Lituites lituus* de Montfort, 1808: 278, text–fig. on p. 278.

*Lituites lituus* – Lossen 1860: 15, pl. 1a–d. — Remelé 1880: 432; 1890: 7, pl. 1 fig. 1. — Angelin 1880: 8, pl. 9 fig. 8. — Noetling 1882: 156, pl. 11 fig. 1. — Holm 1891: 20, pl. 3 figs 1–2. — Sweet 1958: 141, pl. 14 fig. 5, pl. 15 fig. 4. — Neben & Krueger 1971: pl. 31 fig. 1. — Dzik 1984: 137, pl. 41 fig. 1. — Aubrechtová & Meidla 2020: 279, text–figs 9, 10f, h–i, k.

*Lituites procerus* – Balashov 1953: 233, pl 14 fig. 2; 1962: pl. 7 fig. 9.

### Diagnosis

Species of the genus *Lituites* with coiled conch ca 25–30 mm in diameter; coiling tight or whorls slightly detached. Backcoiled part of the conch moderately to strongly curved, expansion angle ca 5°. Straight part of the conch orthoconic or slightly cyrtoconic with expansion angle ca 8°. Shell ornament with coarse annuli, clearly developed along the whole length of the conch including the coiled part and terminal body chamber; growth lines and lirae present in between the annuli. Ornament elements rectiradiate or weakly prorsiradiate (backcoiled part); ventral sinus moderately deep, lateral sinus comparatively wider and shallower, dorsolateral sinus shallow, dorsal projection low.

### Type material

#### Neotype

GERMANY • Brandenburg, Oderberg (Bralitz); Ordovician (late Lasnamägi Regional Stage, late Darriwilian), Upper Grey Orthoceratite Limestone; Neben and Krueger Coll.; previously illustrated by Neben & Krueger (1971: pl. 31 fig. 1), re-illustrated here in Fig. 33A; MB.C.30527.

### Additional material

GERMANY • 1 spec.; near Berlin; Ordovician; MB.C.11639 • 1 spec.; Mecklenburg-Vorpommern, Bansin (Gothensee, Usedom); Ordovician; v. Mensebach Coll.; MB.C.11657 • 2 specs; Mecklenburg-Vorpommern, Groß Zicker (Island of Rügen); Ordovician, Upper Grey Orthoceratite Limestone; Krueger 1966 Coll.; MB.C.2497, MB.C.11990.

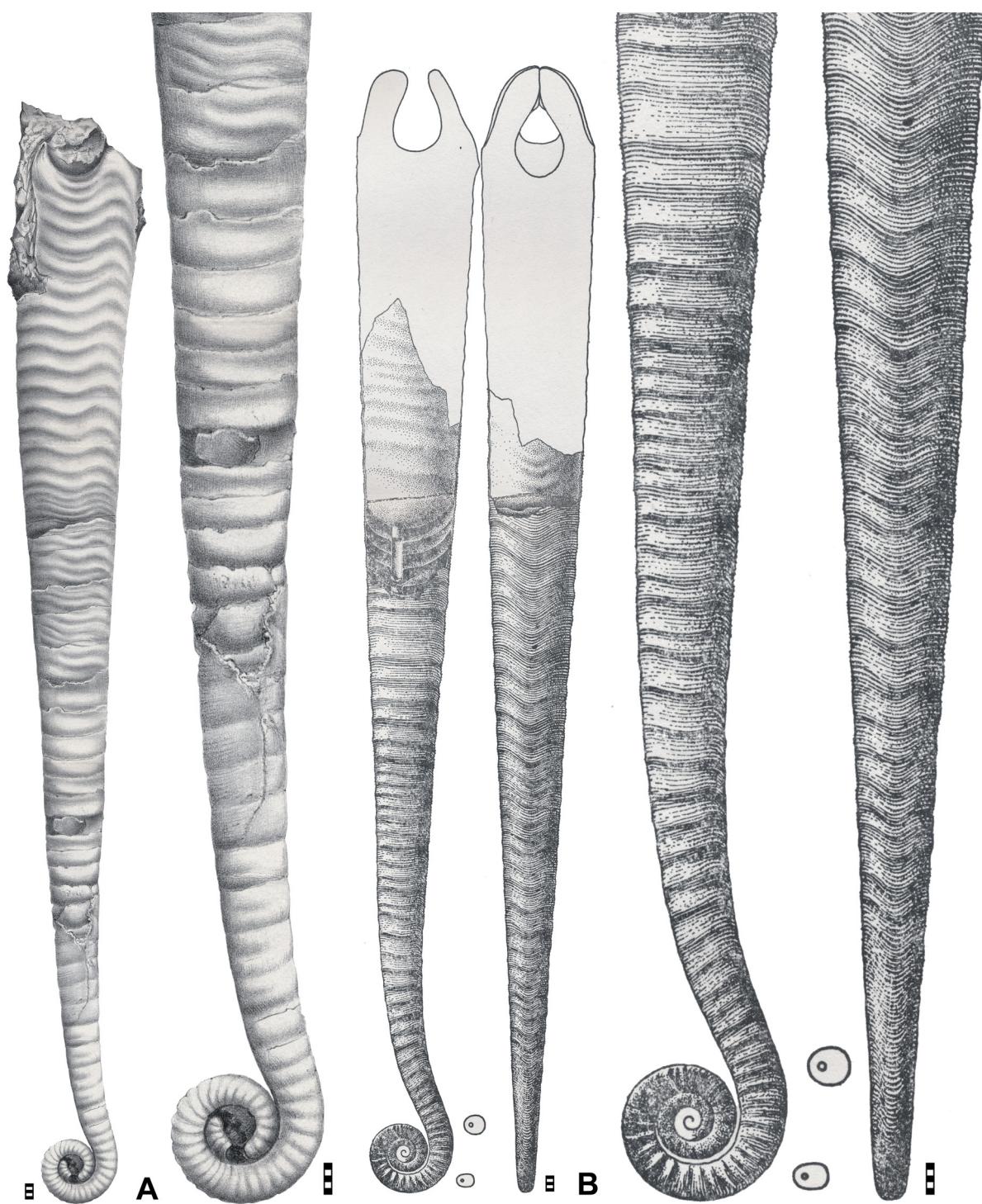
SWEDEN • 1 spec.; Södra Sandby, Skåne; Ordovician, Seby Limestone (transition between the Upper Red and Upper Grey Orthoceratite Limestone); Bottke Coll.; MB.C.29650.

ESTONIA • 1 spec.; Karula, Lääne-Viru County; Ordovician, Upper Grey Orthoceratite Limestone; Dames 1876 Coll.; MB.C.9714.

COUNTRY UNKNOWN • 1 spec.; “West Prussia”; Ordovician, *Echinospaerites* Limestone; Kiesow 1901 Coll.; MB.C.30528 • 1 spec.; Ordovician; MB.C.11640.

### Description

Neotype MB.C.30527 (Figs 33A, 34A–E) consists of the coiled part (2.5 tightly coiled volutions; dm = 29 mm; WER<sub>dm</sub> = 2.17, WER<sub>ah</sub> = 2.14; WWI = 0.86 at wh = 9 mm) and the moderately curved uncoiled part (length = 220 mm; EA ~ 6°). The terminal aperture is not preserved. The shell ornament in the penultimate whorl consists of shallow annuli standing 1.6 mm apart. These annuli bear five sharp growth lines, while the interspaces between the annuli are either smooth or occupied by very delicate growth lines. The annuli weaken on the last whorl and are only barely visible at the beginning of the backcoiled part. In the middle of the backcoiled part, about 50 mm apart from the beginning, the shell ornament shows raised lirae in distances of 0.8–1.1 mm; between them there are four or five delicate growth



**Fig. 31.** *Lituites lituus* de Montfort, 1808; reproductions from the literature. **A.** Reproduction of the illustration by Noetling (1882: pl. 11 fig. 1). **B.** Reproduction of the illustration by Dzik (1984: pl. 41 fig. 1). Scale bar units = 1 mm.

lines. The lirae are imprinted on the internal mould and appear as shallow undulation. They extend with shallow ventral sinus, low and symmetric ventrolateral projection, wide and very shallow lateral sinus and low dorsal projection. In the backcoiled part of the conch, narrow annuli appear again (up to 4 mm apart) and are covered by lirae (up to 0.7 mm apart); ventral sinus is deep but rounded. The phragmocone chambers are variable in length but the CLR generally decreases towards the aperture from 0.56–0.42.

Specimens MB.C.11990 (Fig. 32) and MB.C.2497 (Fig. 33B) are rather well-preserved conchs which consist of the coiled parts (2.25–2.5 tightly coiled volutions; dm = 30 mm; Fig. 34) and the moderately curved uncoiled parts (length more than 200 mm; EA ~ 5°). The whorl expansion rate is between 2.10 and 2.20 (Fig. 34F–O). Terminal apertures are not preserved. In specimen MB.C.2497, the coiled part has regularly spaced annuli standing 1.5 mm apart. Sharp growth lines occur on the annuli and also in

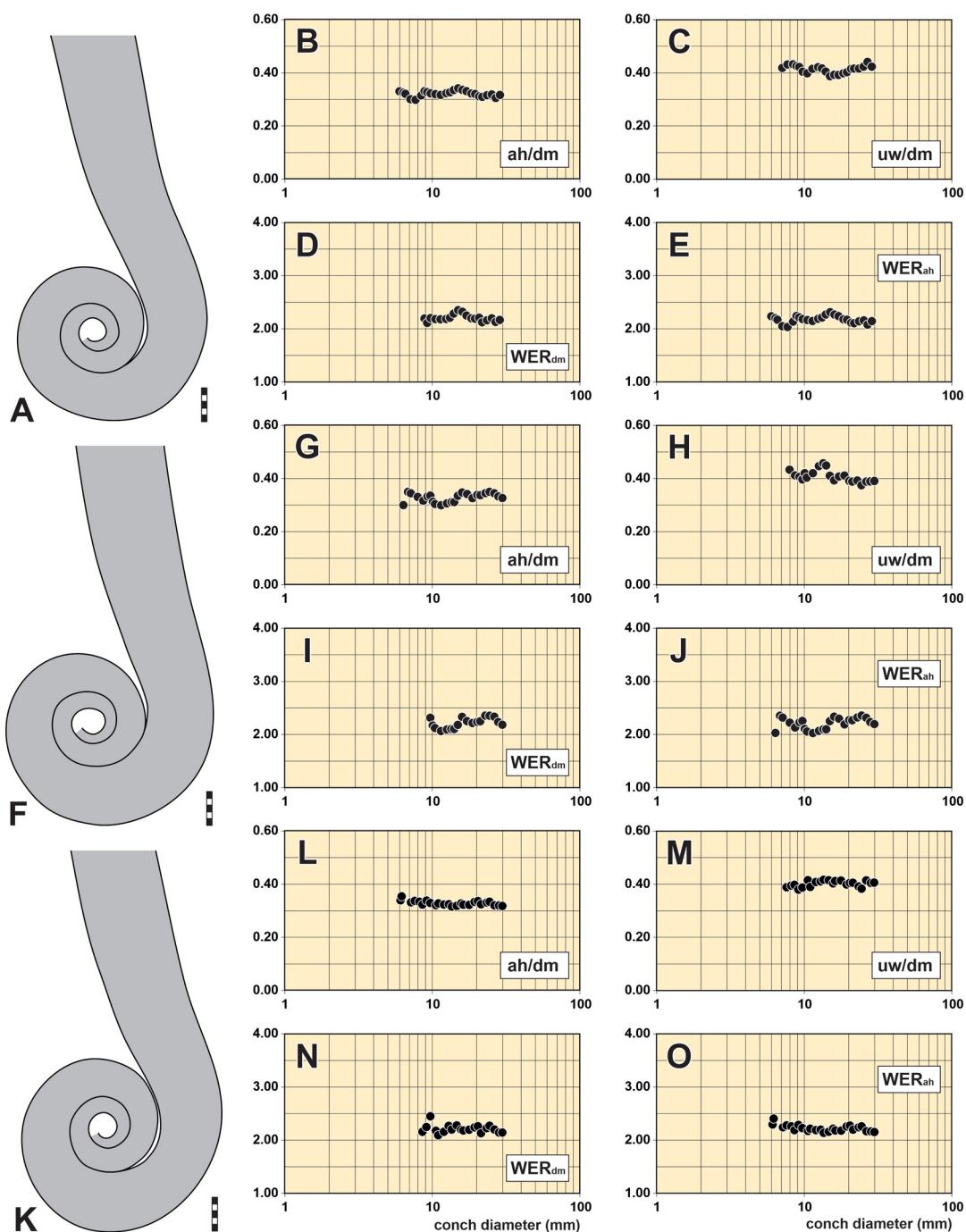


**Fig. 32.** *Lituites lituus* de Montfort, 1808 from the Upper Grey Orthoceratite Limestone; specimen MB.C.11990 (Helms 1966 Coll.) from Groß Zicker (Island of Rügen, Mecklenburg-Vorpommern). Scale bar units = 1 mm.

their interspaces. In contrast to the annuli, the growth lines are not imprinted on the internal mould. The backcoiled part is ornamented with irregularly spaced, rectiradiate to prorsiradiate lirae (0.2–0.4 mm apart) that do not leave traces on the internal mould; strong annuli are not developed. The straight part of the conch bears lirae (up to 0.5 mm apart) and the internal mould bears imprints or relatively narrow annuli; ventral sinus is deep, lateral sinus is comparatively shallow. The phragmocone chambers are variable in length, both within individual specimens and between the two specimens. In specimen MB.C.11990, the chamber length ratio varies between 0.18 and 0.56 without any ontogenetic trend. Only the chambers in front of the body chamber are shorter (Fig. 35C–D). In specimen MB.C.2497, the



**Fig. 33.** *Lituites lituus* de Montfort, 1808 (A–B) and *Lituites* cf. *lituus* de Montfort, 1808 (C) from the Upper Grey Orthoceratite Limestone. **A.** Neotype MB.C.30527 (Neben & Krueger Coll.) from Oderberg, Bralitz (Brandenburg); previously figured by Neben & Krueger (1971: pl. 31 fig. 1); magnification of the coiled part on the right. **B.** Specimen MB.C.2497 (Helms 1966 Coll.) from Groß Zicker (Island of Rügen, Mecklenburg-Vorpommern); magnification of the coiled part on the right. **C.** Specimen MB.C.30529 (Münchner Coll.) from the Island of Chrząszczewska (former Gristow), West Pomerania, Poland. Scale bar units = 1 mm.



**Fig. 34.** *Lituites lituus* de Montfort, 1808. **A**. Outline of coiled conch part of neotype MB.C.30527. **B–E**. Conch proportions and coiling rates of neotype MB.C.30527. **F**. Outline of coiled conch part of specimen MB.C.2497. **G–J**. Conch proportions and coiling rates of specimen MB.C.2497. **K**. Outline of coiled conch part of specimen MB.C. 11990. **L–O**. Conch proportions and coiling rates of specimen MB.C. 11990. Scale bar units = 1 mm.

**Table 9.** Conch measurements (in mm), ratios and rates of coiled conch parts of *Lituites* Bertrand, 1763.

<b>taxon</b>	<b>catalogue nr</b>	<b>dm</b>	<b>wh</b>	<b>uw</b>	<b>WERdm</b>	<b>WERah</b>	<b>UWI</b>
<i>L. lituus</i>	MB.C.9714	27.0	8.0	12.7	—	2.02	0.47
<i>L. lituus</i>	MB.C.11657	24.0	6.5	12.2	2.31	1.88	0.51
<i>L. lituus</i>	MB.C.2497	29.8	9.7	13.4	2.18	2.20	0.45
<i>L. lituus</i>	MB.C.11990	29.8	9.5	13.4	2.13	2.15	0.45
<i>L. lituus</i>	MB.C.30527	28.7	9.1	13.2	2.17	2.14	0.46
<i>L. lituus</i>	ZPAL N/851	24.7	7.2	12.1	2.14	1.99	0.49
<i>L. cf. lituus</i>	MB.C.30529	27.0	9.0	11.6	2.25	2.25	0.43
<i>L. cf. lituus</i>	MB.C.30530	22.1	7.4	9.3	2.42	2.26	0.42
<i>L. toernquisti</i>	MB.C.30533	18.0	7.0	7.4	—	2.68	0.41
<i>L. toernquisti</i>	MB.C.30535	—	9.0	—	—	—	—
<i>L. baculus</i>	MB.C.29654	20.8	8.2	7.7	2.81	2.73	0.37
<i>L. bottkei</i>	MB.C.29651	25.5	7.6	12.5	2.20	2.03	0.49
<i>L. clavis</i>	MB.C.30537	34.4	9.5	16.9	1.94	1.91	0.49
<i>L. dewitzii</i>	MB.C.30538	26.5	8.6	12.7	2.43	2.19	0.48
<i>L. fallax</i>	MB.C.11672.2	40.0	9.3	—	—	1.70	—
<i>L. kruegeri</i>	MB.C.30539	33.4	10.0	17.0	2.71	2.04	0.51
<i>L. cf. kruegeri</i>	MB.C.30540	27.5	9.3	12.4	2.62	2.28	0.45
<i>L. lasaulxii</i>	MB.C.11678	28.0	9.5	11.2	—	2.29	0.40
<i>L. nebeni</i>	MB.C.30541	23.7	7.2	11.4	2.01	2.06	0.48
<i>L. perfectus</i>	MB.C.30544	39.0	10.9	19.5	2.09	1.93	0.50
<i>L. perfectus</i>	MB.C.30542	33.8	10.1	17.2	2.20	2.03	0.51
<i>L. perfectus</i>	MB.C.30545	32.1	9.0	16.7	2.05	1.93	0.52
<i>L. perfectus</i>	MB.C.30543	28.9	9.1	13.6	2.49	2.13	0.47
<i>L. perfectus</i>	MB.C.11646	29.0	8.9	14.5	2.26	2.08	0.50
<i>L. procerus</i>	MB.C.2498	29.5	9.7	13.6	2.31	2.22	0.46
<i>L. procerus</i>	MB.C.30546	24.5	7.6	12.0	2.20	2.10	0.49
<i>L. procerus</i>	MB.C.30547	28.6	9.4	12.9	2.22	2.22	0.45
<i>L. tenuicaulis</i>	MB.C.5389	27.9	8.7	13.1	2.25	2.11	0.47
<i>L. tenuicaulis</i>	MB.C.30550	29.7	9.8	13.4	2.23	2.23	0.45
<i>L. tenuicaulis</i>	MB.C.30548	29.4	9.2	13.8	2.23	2.12	0.47
<i>L. tenuicaulis</i>	MB.C.30551	24.7	8.3	—	2.32	2.27	—
<i>L. sp.</i>	MB.C.9716	25.3	8.1	—	—	—	—
<i>L. sp.</i>	MB.C.29649	22.6	8.9	9.5	3.38	2.72	0.42
<i>L. sp.</i>	MB.C.11653	31.0	8.6	15.5	—	1.92	0.50
<i>L. sp.</i>	MB.C.30570	28.0	9.3	12.6	2.75	2.24	0.45
<i>L. sp.</i>	MB.C.30572	28.0	8.9	13.2	2.17	2.15	0.47
<i>L. sp.</i>	MB.C.30576	20.4	7.2	9.0	2.39	2.39	0.44
<i>L. sp.</i>	MB.C.29648	26.2	9.1	11.5	2.32	2.35	0.44
<i>L. sp.</i>	MB.C.30569	23.9	8.9	9.1	2.79	2.54	0.38
<i>L. sp.</i>	MB.C.30575	29.5	9.2	—	2.24	2.11	—
<i>L. sp.</i>	MB.C.30568	32.0	11.0	—	—	2.32	—

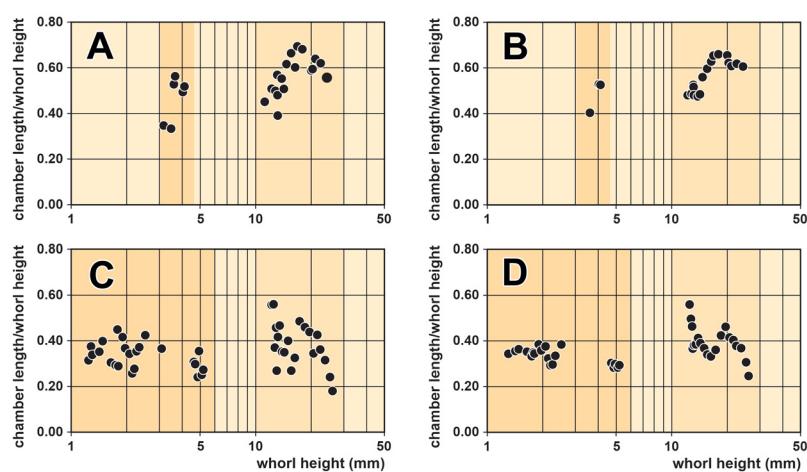
phragmocone chambers are much longer ( $CLR = 0.33\text{--}0.69$ ) and shorter chambers are usually restricted to an earlier ontogenetic stage, while longer chambers occur later in ontogeny (Fig. 35A–B).

Specimen MB.C.11657 consists of the coiled conch ( $dm = 24$  mm; the whorls are only very slightly detached from the preceding, detachment increases gradually and the maximum interspace width is 0.70 mm just before uncoiling) and the moderately curved backcoiled part of the conch (length = 100 mm;  $wh = 20$  mm). The shell ornament of the coiled part consists of annuli and very fine growth lines (preserved only on the inner half of the last whorl). In the innermost whorl, the annuli appear only as imprints on the internal mould and are 1.3 mm apart. In the remaining coiled conch, the annuli are up to 1.9 mm apart. The lateral sinus is shallow and disappears towards the end of the coiled part. At the end of the backcoiled part and in the straight part, the ornament consists of annuli, which become wider (up to ca 7 mm apart) and flat; the intercalated lirae have distances of up to 0.5 mm. Annuli as well as lirae are visible on the internal mould. The lateral sinus of the ornament elements is very shallow in the straight conch, but its depth increases during ontogeny; the dorsal projection is low and flanked by a shallow dorsolateral sinus.

### Remarks

Modéer (1796) introduced the name *Orthocera lituus* (without referring to or depicting any specimens); some authors consequently considered Modéer (1796) the author of *Lituites lituus* and the type species of *Lituites*. Most researchers, however, regarded de Montfort (1808) as the author as he was the first to use the name *Lituites lituus* and is herein assumed as the author of the species name. De Montfort (1808) himself did not refer to the work of Modéer (1796).

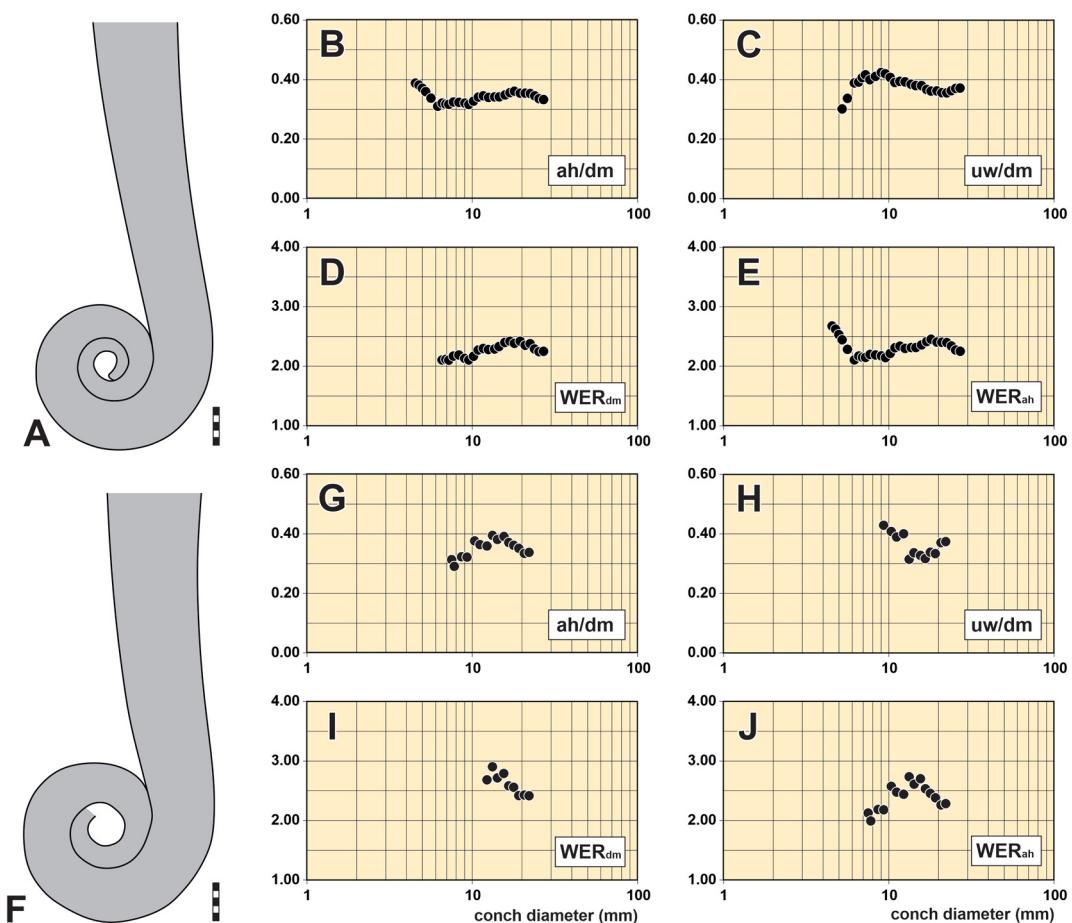
De Montfort (1808) made only a general description of the species and did not mention or describe any particular type specimens and any type locality. The only provided illustration shows a lituiticonic conch with tightly coiled apical part and a sigmoidal backcoiled part. However, since the illustration is only an artistic representation, it cannot be determined whether it shows a particular specimen of *Lituites lituus* or only a general conch morphology based on multiple specimens; moreover, there are several species of the genus *Lituites* with tightly coiled apical part of the conch, such as *L. lasaulxii*.



**Fig. 35.** Septum distances in *Lituites lituus* de Montfort, 1808 from the Upper Grey Orthoceratite Limestone. A, C = empirical data points; B, D = three data points averaged. **A–B.** Specimen MB.C.2497 (Helms 1966 Coll.) from Groß Zicker (Island of Rügen, Mecklenburg-Vorpommern). **C–D.** Specimen MB.C.11990 (Helms 1966 Coll.) from Groß Zicker (Island of Rügen, Mecklenburg-Vorpommern).

*Lituites lituus* and *L. perfectus* (discussed below) were the first and for quite some time the only species assigned to *Lituites*. Their initial descriptions were only very general and indicated that the distinction between the two species is the tightly (*L. lituus*) or loosely (*L. perfectus*) coiled apical part of the conch. The use of the names *L. lituus* and *L. perfectus* was inconsistent during the 19<sup>th</sup> century, when many authors developed own ideas for the species definition. Remelé (1880) attempted to draw firm lines between the two species based on the degree of coiling, the coiled conch diameter, the shape of whorl profile, the shape of the backcoiled conch part, the expansion angle and the ornament. He also defined some new species (Remelé 1880, 1890) of *Lituites*. Noetling (1882) and Holm (1891) stressed out the great intraspecific variation and ontogenetic changes of the characters and questioned their validity for the separation of *L. lituus* and *L. perfectus*.

Not much was added to the discussion on this particular matter during the 20<sup>th</sup> century, but several specimens were illustrated and described (Balashov 1953; Sweet 1958; Neben & Krueger 1971; Dzik 1984). In their study of Estonian lituitids, Aubrechtová & Meidla (2020) synonymised *Lituites lituus* and *L. perfectus* because of transitional morphologies between the two species and a great amount of ontogenetic variation in their material. However, the presently studied collection contains more completely preserved specimens, particularly specimens from the Neben & Krueger and the Bottke collections. The



**Fig. 36.** *Lituites* cf. *lituus* de Montfort, 1808. A. Outline of coiled conch part of specimen MB.C.30529. B–E. Conch proportions and coiling rates of specimen MB.C.30529. F. Outline of coiled conch part of specimen MB.C.30530. G–J. Conch proportions and coiling rates of specimen MB.C.30530. Scale bar units = 1 mm.

study of these specimens enabled the revision of the concepts of *L. lituus* and *L. perfectus*. Since the type material of the two species is not sufficiently known, neotypes were selected for both taxa.

The neotypes were chosen based on the most reliable and detailed descriptions and illustrations in previous literature, i.e., Remelé (1880, 1890), Noetling (1882) (Fig. 31A), Holm (1891) and Dzik (1984) (Fig. 31B).

*Lituites lituus* differs from *L. perfectus* in having a smaller diameter of the coiled conch (up to 30 mm but up to 40 mm in *L. perfectus*) and tightly or almost tightly coiled volutions (openly coiled in *L. perfectus*); in addition, the backcoiled part of *L. lituus* is moderately to strongly curved (weakly curved or straight in *L. perfectus*), the conch has a greater expansion angle ( $5^\circ$ – $8^\circ$  but  $1^\circ$ – $4^\circ$  in *L. perfectus*) and the shell has a coarser ornament (annuli along the whole conch length).

The species most similar to *L. lituus* is *L. lasaulxii*, which has more strongly curved backcoiled part and the shell ornament lacks annuli at the coiled part of the conch and the straight part only has growth lines (not lirae) on the surface of the annuli.

*Lituites procerus* Remelé, 1890 also has a tightly coiled conch up to 30 mm in diameter as *L. lituus*, but its uncoiled part is only weakly curved or straight; the shell of the coiled part has ribs instead of annuli in some specimens. *Lituites bottkei* sp. nov. has loosely coiled volutions and a finer ornament with biconvex ornament elements in the coiled part. *Lituites clavis* is tightly coiled but its coiled part has a greater diameter (34 mm) than that in *L. lituus*, the backcoiled part expands rather slowly (expansion angle of  $\sim 2^\circ$ ) and the uncoiled part is ornamented with flat (instead of prominent) annuli. The uncoiled part in *L. nebeni* sp. nov. is only weakly curved and very slender (almost tubular upon uncoiling) with expansion angle up to  $4^\circ$ ; the shell ornament consists of flat (instead of prominent) annuli.

### Geographic and stratigraphic occurrence

Norway, Sweden, Estonia (in situ) and northern Germany, northern Poland and the Kaliningrad Region (Russia) (in erratics within Pleistocene gravels); Darriwilian to early Sandbian (Middle to early Late Ordovician).

*Lituites lituus* is a stratigraphically significant species in Baltoscandia indicating a mid-Lasnamägian age (e.g., Jaanusson 1960; Evans *et al.* 2014).

***Lituites cf. lituus* de Montfort, 1808**  
Figs 33C, 36, Tables 9–10

### Material examined

POLAND • 2 specs; West Pomerania, Island of Chrząszczewska (former Gristow); Ordovician, Upper Grey Orthoceratite Limestone; Müchner Coll.; MB.C.30529, MB.C.30530.

SWEDEN • 1 spec.; Island of Öland, Island of Öland; Ordovician; Technische Universität Berlin Coll.; MB.C.30531.

COUNTRY UNKNOWN • 1 spec.; Ordovician; MB.C.11650.

### Description

Specimen MB.C.30529 (Fig. 33C) consists of the coiled part (2.25 tightly coiled volutions; dm = 27 mm; WER 2.3; Fig. 36A–E) and the weakly curved backcoiled part (length = 102 mm; wh = 18 mm; EA  $\sim 5^\circ$ ). The initial chamber of the phragmocone is cup-shaped and small (whorl height ca 1.4 mm). The initial

**Table 10.** Conch measurements (in mm), and expansion rates of uncoiled conch parts of *Lituites* Bertrand, 1763.

<b>taxon</b>	<b>catalogue nr</b>	<b>max. wh</b>	<b>max. ww</b>	<b>min. wh</b>	<b>min. ww</b>	<b>fragm. length</b>	<b>EA (°)</b>
<i>L. lituus</i>	MB.C.2497	25.4	24.0	12.3	9.8	156.3	4.8
<i>L. lituus</i>	MB.C.11990	25.0	—	11.4	—	146.9	5.3
<i>L. lituus</i>	MB.C.29650	35.8	—	25.8	24.4	88.0	6.5
<i>L. lituus</i>	MB.C.30527	32.0	32.0	10.5	9.4	195.3	6.3
<i>L. lituus</i>	MB.C.30528	45.0	—	35.0	—	127.2	4.5
<i>L. lituus</i>	ZPAL N/851	30.8	—	8.7	—	210.8	6.0
<i>L. cf. lituus</i>	MB.C.30529	18.3	18.0	9.8	8.0	99.3	4.9
<i>L. cf. lituus</i>	MB.C.30530	13.0	—	9.0	7.3	41.6	5.5
<i>L. toernquisti</i>	MB.C.30532	12.0	—	9.6	7.8	25.4	5.4
<i>L. toernquisti</i>	MB.C.30533	10.0	8.5	7.2	6.3	43.3	3.7
<i>L. toernquisti</i>	MB.C.30534	13.0	—	8.0	—	54.0	5.3
<i>L. toernquisti</i>	MB.C.30535	15.6	15.0	7.7	—	83.7	5.4
<i>L. baculus</i>	MB.C.29654	15.6	—	8.1	—	97.6	4.4
<i>L. bottkei</i>	MB.C.29651	41.9	—	9.7	—	287.9	6.4
<i>L. bottkei</i>	MB.C.30536	36.0	—	19.5	—	134.9	7.0
<i>L. cf. bottkei</i>	MB.T.4492.52	40.0	38.0	28.0	—	109.0	6.3
<i>L. clavis</i>	MB.C.30537	16.0	15.6	12.0	—	109.1	2.1
<i>L. dewitzii</i>	MB.C.30538	14.1	—	9.1	—	60.9	4.7
<i>L. kruegeri</i>	MB.C.30539	11.0	10.4	10.8	9.3	12.7	0.9
<i>L. lasaulxii</i>	MB.C.11678	18.4	—	10.4	—	81.8	5.6
<i>L. lasaulxii</i>	MB.C.11645	16.2	—	10.0	—	64.5	5.5
<i>L. cf. lasaulxii</i>	MB.C.11677	24.0	—	19.0	—	75.4	3.8
<i>L. nebeni</i>	MB.C.30541	12.7	12.3	8.6	7.3	61.8	3.8
<i>L. perfectus</i>	MB.C.30544	11.4	10.2	11.3	9.7	10.0	0.8
<i>L. perfectus</i>	MB.C.30542		11.0	10.3	9.0	229.2	0.5
<i>L. perfectus</i>	MB.C.30543	15.2	13.7	10.9	9.6	82.1	3.0
<i>L. procerus</i>	MB.C.2498	9.8	—	9.7	—	19.1	0.3
<i>L. procerus</i>	MB.C.30546	10.0	9.0	8.7	—	49.6	1.5
<i>L. procerus</i>	MB.C.30547	12.8	—	10.6	—	25.7	4.9
<i>L. tenuicaulis</i>	MB.C.5389	12.4	—	10.3	—	44.5	2.7
<i>L. tenuicaulis</i>	MB.C.30550	11.7	—	10.2	—	34.4	2.5
<i>L. sp.</i>	MB.C.11673.2	19.2	19.0	14.0	—	59.5	5.0
<i>L. sp.</i>	MB.C.29649	20.7	—	10.1	—	77.7	7.8
<i>L. sp.</i>	MB.C.11628	47.4	—	22.7	22.2	204.8	6.9
<i>L. sp.</i>	MB.C.11653	11.1	—	10.1	—	28.6	2.0
<i>L. sp.</i>	MB.C.30572	11.9	—	9.7	—	42.0	3.0
<i>L. sp.</i>	MB.C.30576	11.8	11.0	9.1	7.4	44.2	3.5
<i>L. sp.</i>	MB.C.29648	16.6	—	10.0	—	63.0	6.0
<i>L. sp.</i>	MB.C.30569	21.4	21.4	10.6	9.2	103.0	6.0
<i>L. sp.</i>	MB.C.9706	37.0	—	29.0	—	86.4	5.3
<i>L. sp.</i>	MB.C.30575	12.4	12.0	10.0	8.3	43.0	3.2
<i>L. sp.</i>	MB.C.30568	19.0	—	12.7	11.0	52.2	6.9

ca 4 mm of conch length is ornamented by fine growth lines (0.1–0.2 mm apart); after that pairs of raised lirae appear (up to 0.7 mm apart) with extremely fine growth lines in between them. From about the beginning of the second whorl, a weak lateral sinus is developed. The ornament of the rest of the coiled and backcoiled part of the conch consists of biconvex lirae and flat ribs. The ribs are barely discernible in the second half of the specimen and only coarse lirae are visible (1.3 mm apart). Lateral sinus is either very shallow or the ornament elements are straight, ventral sinus is deep and rounded, dorsal projection and dorsolateral sinuses are not developed. At the end of the specimen, only lirae (1 mm apart) are present.

### Remarks

The specimens resemble *Lituites lituus* in their overall dimensions, but the backcoiled part in specimens MB.C.30529, MB.C.30530 (Fig. 36F–J) and MB.C.30531 is only weakly curved and the shell ornament is slightly finer. Specimen MB.C.30529 differs with its biconvex lirae and flat ribs on the shell surface. Specimen MB.C.11650 is a fragmentary and slightly deformed body chamber, which has a finer shell ornament; the ornament elements form a flatter lateral sinus compared to *L. lituus*.

***Lituites perfectus*** Wahlenberg, 1818  
Figs 37–42, Tables 9–11

*Lituites perfectus* Wahlenberg, 1818: 83.

*Lituites perfectus* – Remelé 1880: pl. 1 fig. 2; 1890: pl. 1 fig. 2, pl. 6 fig. 3. — Holm 1891: 12, pl. 2 figs 1–5. — Hardt 1953: 45, text-fig. 10.

*Lituites lituus*? – Aubrechtová & Meidla 2020: 286, text-fig. 14l.

? *Lituites perfectus* – Balashov 1953: pl. 14 fig. 4. — Sweet 1958: 144, pl. 16 fig. 4.

### Diagnosis

Species of the genus *Lituites* with coiled part ca 29–40 mm in diameter; coiling open, eccentric, only innermost whorls contiguous, end part of the last whorl might be in the proximity or in contact with preceding whorl; whorl expansion rate ca 2.00. Backcoiled part of the conch weakly curved, expansion angle ca 1°, later up to 4°. Shell ornament with growth lines and annuli or ribs; rectiradiate in the coiled part and prorsiradiate in the backcoiled part. Ventral sinus deep with a ventral band, shallow lateral sinus just in front of the moderately high ventrolateral projection.

### Type material

#### Neotype

GERMANY • Mecklenburg-Vorpommern, Lansen (Malchin); Ordovician (late Lasnamägi or Uhaku regional stages, late Darriwilian), Upper Grey Orthoceratite Limestone; Krueger Coll.; MB.C.30544 (illustrated in Fig. 38A).

### Additional material

GERMANY • 2 specs; Brandenburg, Eberswalde; Ordovician, Upper Grey Orthoceratite Limestone; Kgl. Forstakademie Eberswalde Coll.; MB.C.11622, MB.C.11646 • 1 spec.; Brandenburg, Niederfinow; Ordovician, Upper Grey Orthoceratite Limestone; Neben Coll.; MB.C.30542 • 1 spec.; Brandenburg, Oderberg (Bralitz); Ordovician, Upper Grey Orthoceratite Limestone; Krueger Coll.; MB.C.30543.

POLAND • 1 spec.; Kujawi-Pomerania, Bydgoszcz (former Bromberg); Ordovician, Upper Grey Orthoceratite Limestone; MB.C.30545.

### Description

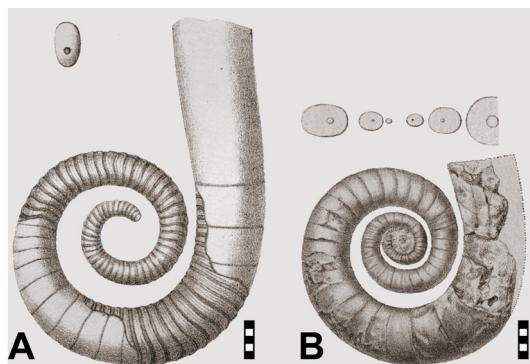
Neotype MB.C.30544 (Fig. 38A) consists of the coiled part ( $dm = 39$  mm, 2.5 openly, eccentrically coiled volutions not touching each other, Fig. 39A–E) and a short part of the backcoiled part (length = 32 mm;  $wh = 11.4$  mm; EA  $< 1^\circ$ ). The shell ornament is best preserved at the transition of the coiled part to the backcoiled part of the conch. Here, it consists of narrow annuli (1.8–2.4 mm apart) and delicate growth lines (up to 0.2 mm apart). They extend with a broad and shallow lateral sinus across the flanks and then turn forward for a moderately high ventrolateral projection. On the venter they form a deep sinus. The close approximation of the growth lines leads to the formation of a ventral band (Fig. 42). The dorsal projection is very low. The ornament elements are concavo-convex and change from rectiradiate to prorsiradiate towards the backcoiled part of the conch. The phragmocone chambers are 0.60 of whorl height.

Specimen MB.C.30542 (Figs 38B, 39F–J) consists of a coiled and uncoiled part of the conch and has essentially the same dimensions as the neotype. The shell ornament, however, differs as it possesses much coarser growth lines that stand in distances of 0.3–0.6 mm at the beginning of the backcoiled part. In the coiled part, at 18 mm diameter, there are sharp annuli standing about 1.2 mm apart (mid-flank area); they weaken out in the outer flank area. Sharp growth lines (irregularly spaced 0.05–0.2 mm) occur between and on the crests of the annuli. In the backcoiled part, the shell wall is mostly not preserved; ornament is visible only as imprints of narrow annuli. The ornament elements extend straight across the flank with a very shallow sinus close to the ventrolateral projection. The CLR is  $\sim 0.57$ , with an increasing trend during ontogeny; however, a rapid decrease in the CLR followed by a rapid increase occurs at the end of the coiled part (Fig. 41A–B).

Specimen MB.C.11646 (Figs 37B, 38C) is a coiled part of a conch with 29 mm diameter; only a very short portion of the uncoiled part preserved. The volutions are slightly more regularly coiled compared to the other specimens (Fig. 39K–O). The CLR is ca 0.38 with a general decreasing ontogenetic trend up to the end of the coiled part, where the CLR starts to increase (Fig. 41E–F). In specimen MB.C.30543, the CLR also appears to be relatively higher, where the conch uncoiling starts (Fig. 41C–D).

### Remarks

The name *Lituites perfectus* was introduced by Wahlenberg (1818); the original work was then republished later (Wahlenberg 1821); this caused some later authors to erroneously use the latter year of the species description. Wahlenberg (1818) did not describe or illustrate any type material and only referred to a



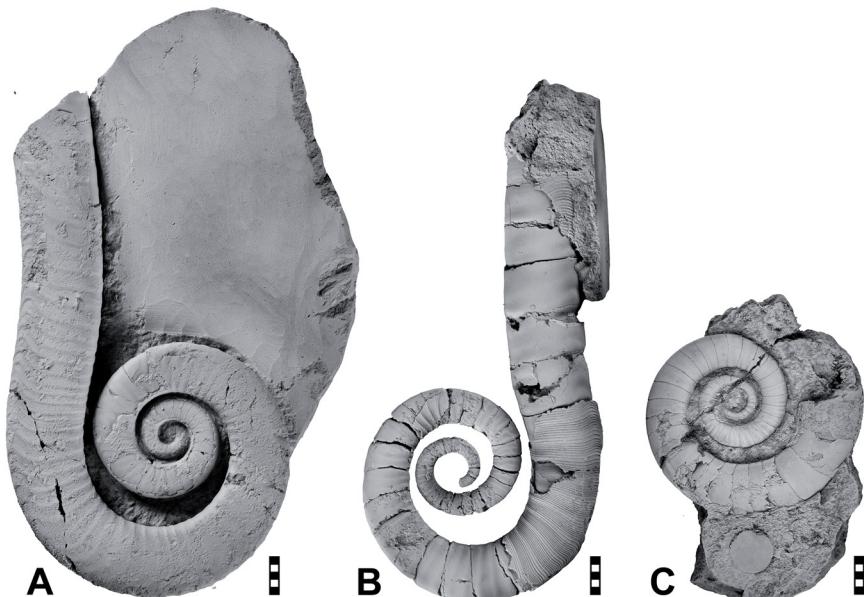
**Fig. 37.** *Lituites perfectus* Wahlenberg, 1818; reproductions of illustrations of Remelé (1890).  
**A.** Specimen MB.C.11622 from Eberswalde (Brandenburg), illustrated by Remelé (1890: pl. 1 fig. 2).  
**B.** Specimen MB.C.11646 from Eberswalde (Brandenburg), illustrated by Remelé (1890: pl. 6 fig. 3).

specimen depicted previously by Walch (1771: pl. 4 fig. 1) as “the best example” of *L. perfectus*. Later, Holm (1891) reviewed the species and identified two probable originals of Wahlenberg (1818) in the collections of the Uppsala University, Sweden. However, Holm (1891) concluded that both specimens are too poorly preserved to be determined and might even represent two different species. He also pointed out that the specimen figured by Walch (1771) contradicts the brief description of Wahlenberg (1818) because its apical part is loosely, not tightly coiled. Despite that, Holm (1891) and other authors regarded the specimen of Walch (1771) as the type of *Lituites perfectus*.

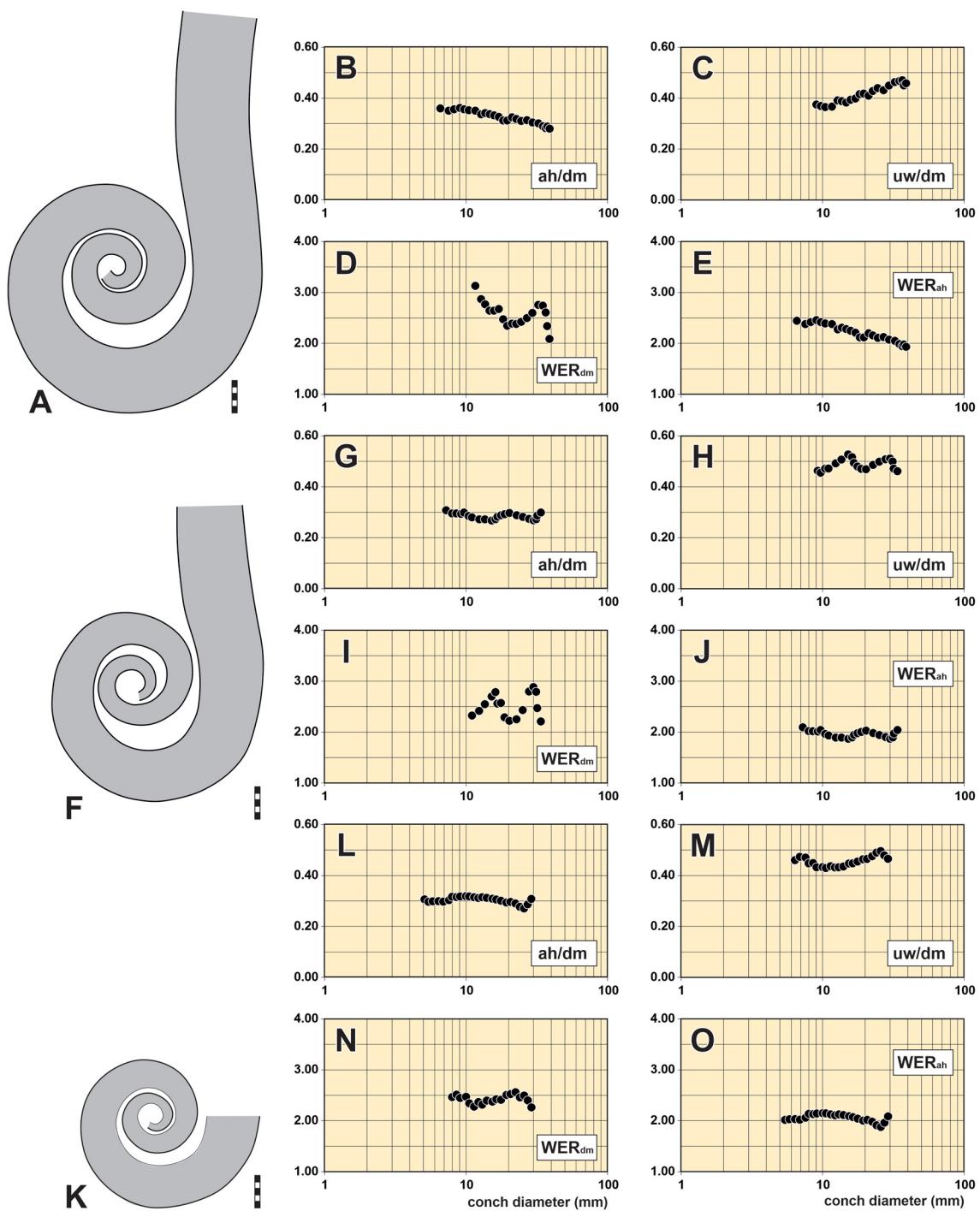
The illustration of the specimen of Walch (1771: pl. 4 fig. 1) is a drawing, which shows a section through a lituiticonic conch with loosely coiled apical portion and a slightly curved, almost tubular uncoiled portion. Based on this illustration, it is not possible to determine the species identity of the specimen because the shell ornament is not shown and the above combination of characters is present in several lituitid species, such as *Lituites nebeni* sp. nov., *Trilacinoceras discors* or *T. filix* sp. nov.

The ambiguous interpretation of *Lituites perfectus* led to an inconsistent use of the name and specimens with variable conch shapes were thus assigned to the species. *Lituites perfectus* was most commonly confused with *L. lituus*. The herein studied material enabled the recovery and re-definition of *L. perfectus* and selection of a neotype. For further discussion, see remarks under *L. lituus* above.

*Lituites perfectus* differs from *L. lituus* in the larger diameter of the coiled conch, openly coiled volutions (tightly or almost tightly coiled in *L. lituus*), in the backcoiled part being weakly curved or straight (moderately to strongly curved in *L. lituus*), in the lower expansion angle of the conch (less than 1°–4° but 5°–8° in *L. lituus*) and in the generally finer ornament of the shell (*L. lituus* has annuli along the whole conch length).



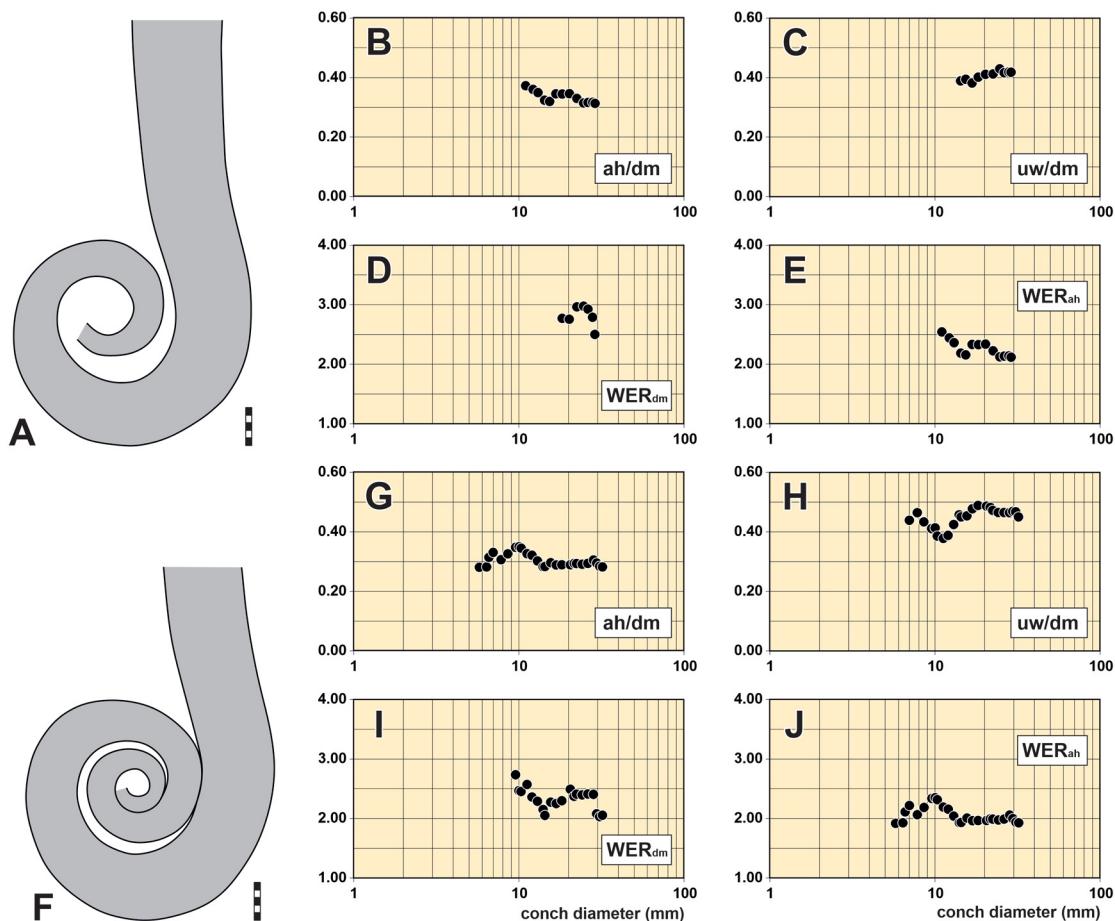
**Fig. 38.** *Lituites perfectus* Wahlenberg, 1818 from the Upper Grey Orthoceratite Limestone. **A.** Neotype MB.C.30544 (Krueger Coll.) from Lansen near Malchin (Mecklenburg-Vorpommern, Germany). **B.** Specimen MB.C.30542 (Neben Coll.) from Niederfinow (Brandenburg). **C.** Specimen MB.C.11646 (Kgl. Forstakademie Eberswalde Coll.) from Eberswalde (Brandenburg). Scale bar units = 1 mm.



**Fig. 39.** *Lituites perfectus* Wahlenberg, 1818. A. Outline of coiled conch part of neotype MB.C.30544. B–E. Conch proportions and coiling rates of neotype MB.C.30544. F. Outline of coiled conch part of specimen MB.C.30542. G–J. Conch proportions and coiling rates of specimen MB.C.30542. K. Outline of coiled conch part of specimen MB.C.11646. L–O. Conch proportions and coiling rates of specimen MB.C.11646. Scale bar units = 1 mm.

**Table 11.** Siphuncular diameter ratio (SDR) and siphuncular distance ratio (SPR) at their corresponding whorl height in specimens of *Lituites* Bertrand, 1763.

taxon	catalogue nr	wh	SDR	wh	SPR
<i>L. baculus</i>	MB.C.29654	16.0	0.16	16.0	0.46
<i>L. kruegeri</i>	MB.C.30539	11.0	0.18	11.0	0.35
<i>L. lasaulxii</i>	MB.C.11678	18.4	0.11	—	—
<i>L. perfectus</i>	MB.C.30543	15.2	0.16	15.2	0.29
<i>L. tenuicaulis</i>	MB.C.5389	12.5	0.18	12.5	0.32
<i>L. sp.</i>	MB.C.11628	22.7	0.13	22.7	0.34
<i>L. sp.</i>	MB.C.30576	—	—	11.8	0.30
<i>L. sp.</i>	MB.C.29648	10.0	0.16	—	—

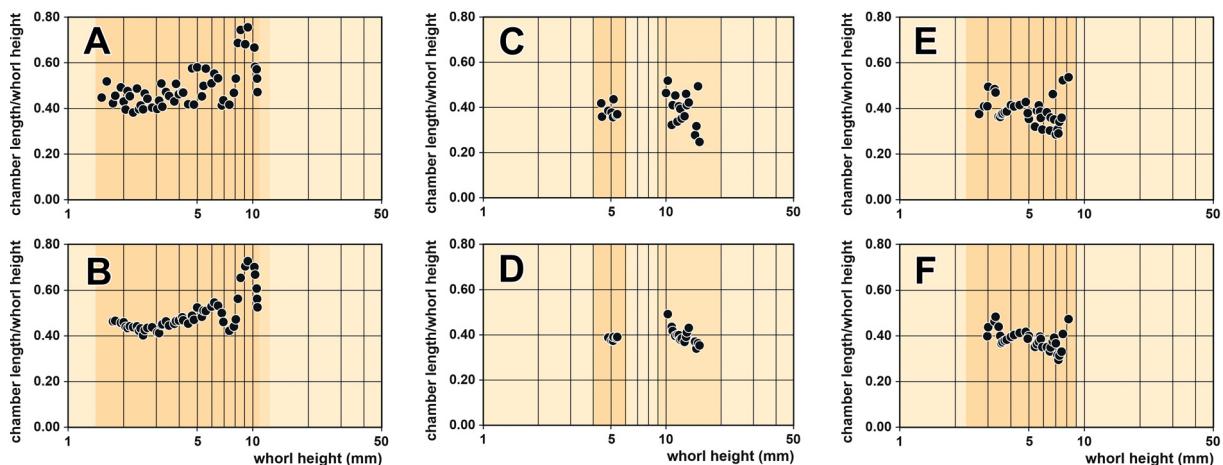


**Fig. 40.** *Lituites perfectus* Wahlenberg, 1818. A. Outline of coiled conch part of specimen MB.C.30543. B–E. Conch proportions and coiling rates of specimen MB.C.30543. F. Outline of coiled conch part of specimen MB.C.30545. G–J. Conch proportions and coiling rates of specimen MB.C.30545. Scale bar units = 1 mm.

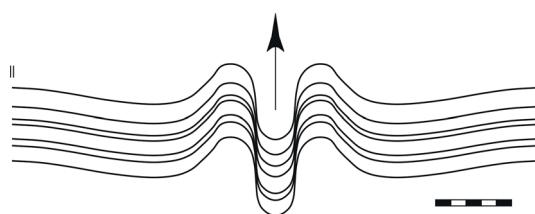
The species most similar to *L. perfectus* is *L. kruegeri* sp. nov.; the coiled part of both species is relatively large (more than 30 mm in diameter), the volutions are openly coiled and the uncoiled part is almost straight with a low expansion angle ( $\sim 1^\circ$ ). However, *L. perfectus*, has a less regular (eccentric) coiling geometry and a more prominent shell ornament compared to *L. kruegeri* sp. nov.

*Lituites bottkei* sp. nov. is openly coiled but its conch diameter is smaller (26 mm) compared to *L. perfectus*, the coiling is regular (not eccentric) and the uncoiled part is moderately curved with a greater expansion angle ( $6^\circ$ – $7^\circ$  vs  $1$ – $3^\circ$  in *L. perfectus*). In *L. dewitzi* sp. nov., only the last half whorl is detached from the preceding (inner volutions are tightly coiled), the coiled part diameter is smaller (27 mm) than in *L. perfectus*, the uncoiled part has an expansion angle of  $5^\circ$  and the general character of ornament is different (especially in the prorsiradiate direction of ornament elements in the coiled part of the conch).

The variation in *L. perfectus* concerns mainly the conch diameter and the degree of eccentricity of coiling (Figs 39–40).



**Fig. 41.** Septum distances in *Lituites perfectus* Wahlenberg, 1818 from the Upper Grey Orthoceratite Limestone. Upper row = empirical data points; lower row = three data points averaged. **A–B.** Specimen MB.C.30542 (Neben Coll.) from Niederfinow (Brandenburg). **C–D.** Specimen MB.C.30543 (Krueger Coll.) from Oderberg (Bralitz) (Brandenburg). **E–F.** Specimen MB.C.11646 (Kgl. Forstakademie Eberswalde Coll.) from Eberswalde (Brandenburg).



**Fig. 42.** *Lituites perfectus* Wahlenberg, 1818 from the Upper Grey Orthoceratite Limestone; lirae in the neotype MB.C.30544 (Neben Coll.) from Niederfinow (Brandenburg), at wh = 11 mm. Scale bar units = 1 mm.

The illustration of specimen MB.C.11622 in Remelé (1890: pl. 1 fig. 2; reproduced here in Fig. 37A) is an idealised reconstruction of a rather poorly preserved, fragmentary specimen. Re-study of the specimen revealed, however, that the diagnostic characters of *L. perfectus* are present and the assignment to this species is plausible.

### Geographic and stratigraphic occurrence

Norway (?), Sweden (?), Estonia (*in situ*) and northern Germany and northern Poland (in erratics within Pleistocene gravels); late Darriwilian, Middle Ordovician.

*Lituites perfectus* is a stratigraphically significant species in Baltoscandia indicating the late Lasnamägian age (e.g., Jaanusson 1960; Evans *et al.* 2014).

***Lituites toernquisti*** Holm, 1891  
Figs 43–44, Tables 9–10

*Lituites Törnquisti* Holm, 1891: 9, pl. 1 figs 1–4.

*Lituites törnquisti* – Sweet 1958: 124, 147.

? *Lituites lituus* – Hucke 1967: 56, pl. 17 fig. 5.

*Lituites* sp. – Neben & Krueger 1971: pl. 21 fig. 7.

*Lituites toernguisti* – Chen 1987: 77.

non *Lituites tornquisti* – Jaanusson & Mutvei 1953: text-fig. 3a.

non *Lituites törnquisti* – Neben & Krueger 1971: pl. 21 fig. 8.

### Diagnosis

Species of the genus *Lituites* with coiled conch diameter of 16–20 mm; whorls contiguous but not in contact. Uncoiled part moderately curved, expansion angle of 3–5.5° in early growth stages and 7° in later growth stages; whorl height at maturity of ca 25 mm. Mature aperture with broad lateral sinuses and a deep ventral sinus; dorsolateral lappets not indicated by the shape of ornament elements (after Holm 1891 and Sweet 1958).

### Type material

Not available for study; Holm (1891: pl. 1 figs 1–4) illustrated one specimen (reproduced here in Fig. 43A), it is from Sollerön (Dalarna, Sweden), Red *Lituites* Limestone (*Lituites tornquisti* Zone, Segerstad Limestone, upper part of the Upper Red Orthoceratite Limestone, Aseri Regional Stage, middle Darriwilian, Middle Ordovician).

### Material examined

GERMANY • 1 spec.; Brandenburg, Niederfinow; Ordovician, Upper Red Orthoceratite Limestone; Neben Coll.; MB.C.30532 • 3 specs; Brandenburg, Niederfinow; Ordovician, Upper Red Orthoceratite Limestone; Neben and Krueger Coll.; MB.C.30533 to MB.C.30535.

### Description

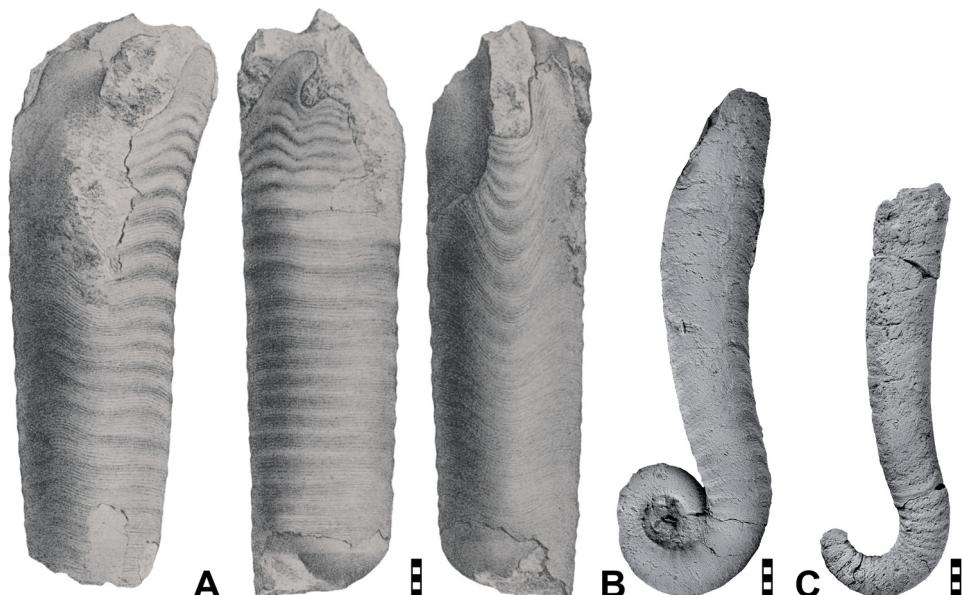
Specimen MB.C.30533 (Fig. 43C) is a fragment of a coiled part (last half of a coiled volution preserved) and a short part of the moderately curved backcoiled part (length = 20 mm; wh = 12.4 mm; EA ~ 4°) of a conch with a compressed whorl profile (WWI = 0.85). The shell surface is weathered but coarse annuli are well-discernible even in the coiled part of the conch; just behind the coiled part of the conch, fine lirae or growth lines are preserved between the annuli.

Additional information about the ornament is provided by the specimens MB.C.30532 (Fig. 43B) and MB.C.30534 (Fig. 44), which have coarse, prorsiradiate annuli and lirae; the elements form a relatively deep and sharp ventral sinus, while the lateral sinus and dorsal projection are not developed.

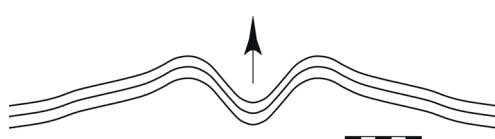
### Remarks

Specimen MB.C.30533 corresponds to the species description given by Holm (1891) in the very small dimensions, the low expansion angle of the backcoiled part and a relatively coarse ornament. The other three specimens differ in larger expansion angles ( $5.3^\circ$  in MB.C.30534, and  $5.4^\circ$  in MB.C.30532 and MB.C.30535), but they are also assigned to *L. toernquisti* here, since they correspond to specimen MB.C.30533 both in size and ornament.

On the contrary, specimen MB.C.30568 (Neben & Krueger 1971: pl. 21 fig. 8) and also the specimen figured by Jaanusson & Mutvei (1953: text-fig. 3a) are not included in *L. toernquisti* here because they



**Fig. 43.** *Lituites toernquisti* Holm, 1891 from the Upper Grey Orthoceratite Limestone. **A.** Reproduction of the illustration by Holm (1891: pl. 1 figs 1–3); from left to right – lateral, dorsal and ventral view of specimen (mature aperture). **B.** Specimen MB.C.30532 (Neben Coll.) from Niederfinow (Brandenburg); previously figured by Neben & Krueger (1971: pl. 21 fig. 7); lateral view of specimen. **C.** Specimen MB.C.30533 (Neben & Krueger Coll.) from Niederfinow (Brandenburg); lateral view of specimen. Scale bar units = 1 mm.



**Fig. 44.** *Lituites toernquisti* Holm, 1891 from the Upper Grey Orthoceratite Limestone; lirae in specimen MB.C.30534 (Neben & Krueger Coll.) from Niederfinow (Brandenburg), at wh = 11 mm. Scale bar units = 1 mm.

are much larger in overall proportions (diameter of the coiled part  $\sim$  30 mm) and have greater expansion angles ( $7^\circ$ ).

*Lituites toernquisti* may be difficult to distinguish from *Trilacinoceras discors* when the body chamber is not completely preserved. However, *L. toernquisti* belongs to *Lituites* because it possesses a five-lappeted aperture (Fig. 43A), i.e., not three-lappeted as is diagnostic for *Trilacinoceras* (for further discussion, see Holm 1891; Sweet 1958; Aubrechtová & Meidla 2020). *Lituites toernquisti* differs from other species of the genus *Lituites* chiefly by the small size of its conch (coiled part diameters up to 20 mm, whorl height at maturity about 25 mm). The only exception to this is *L. baculus* sp. nov., which is comparable in overall size to *L. toernquisti*; however, the coiled part in the former species is composed of only 1.5 rapidly expanding volutions and the shell ornament is different (annuli in the coiled part are absent and ornament elements in the backcoiled part have prorsiradiate direction).

### Geographic and stratigraphic occurrence

Sweden (in situ) and northern Germany (in erratics within Pleistocene gravels); Aseri and possibly Lasnamägi regional stages, Darriwilian, Middle Ordovician.

*Lituites toernquisti* is a stratigraphically significant species in the Upper Red Orthoceratite Limestone of Baltoscandia indicating the late Aserian *Lituites toernquisti* Zone (Jaanusson & Mutvei 1953; Evans *et al.* 2014).

### *Lituites lasaulxii* Remelé, 1890

Fig. 45, Tables 9–11

*Lituites Lasaulxii* Remelé, 1890: pl. 3 fig. 1.

? *Lituites* cf. *Lasaulxii* – Remelé 1890: pl. 6 fig. 2.

*Lituites perfectus*? – Remelé 1890: pl. 6 fig. 4.

### Diagnosis

Species of the genus *Lituites* with diameter of the coiled conch of 25–27 mm; coiling tight or almost tight; backcoiled part strongly curved; juvenile expansion angle of ca  $5.5^\circ$ . Shell surface with narrow annuli and very fine lirae in the coiled part and more prominent annuli and lirae after uncoiling; ventral sinus deeply rounded, becoming shallow and wide on the backcoiled part.

### Type material

#### Lectotype (designated here)

GERMANY • Brandenburg, Heegermühle; Ordovician (late Lasnamägi Regional Stage, late Darriwilian), Upper Grey Orthoceratite Limestone; Kgl. Forstakademie Eberswalde Coll.; illustrated by Remelé (1890: pl. 3 fig. 1), re-illustrated here in Fig. 45A; MB.C.11678.

### Additional material

GERMANY • 1 spec.; Brandenburg, Eberswalde; Ordovician, Upper Grey Orthoceratite Limestone; Remelé Coll.; MB.C.11645 • 1 spec.; Brandenburg, Heegermühle; Ordovician, Upper Grey Orthoceratite Limestone; Kgl. Forstakademie Eberswalde Coll.; MB.C.11677.

### Description

Lectotype MB.C.11678 (Fig. 45A) consists of the coiled part (dm = 28 mm; only the last three quarters of the last volution are preserved, coiling is probably nearly tight or tight) and the backcoiled part (length = 93 mm; wh = 18.4 mm; EA =  $5.6^\circ$ ) of the conch. The shell surface is preserved mainly in the

coiled part and the beginning of the backcoiled part; there the ornament consists of raised lirae (up to 1.2 mm apart); ventrolaterally they bend steeply backwards to form a deep, U-shaped ventral sinus. The ornament grades into marked annuli (up to 3.4 mm apart) with lirae during ontogeny; the ventral sinus becomes wide. After uncoiling of the conch, there are two conspicuous, raised lines of ornament. The development of the ornament can be subdivided into four successive stages: (1) The last whorl bears lirae, which run almost straight on the inner half of the flank and bend into a narrow projection in the ventrolateral area. The lirae are almost 1 mm apart (on the mid-flank). (2) In the transition from the coiled part to the backcoiled part, the distances between the lirae decrease for a length of 11 mm. The distances between the lirae are somewhat irregular between 0.3 and 0.5 mm. (3) In the following area of the backcoiled part of about 7.5 mm in length, flat annuli appear for the first time; these are superimposed by very fine growth lines. The annuli alternate with some intermediate lirae that form groups of three or four. (4) The remaining extent of the backcoiled and straight part has then only annuli with intervals of 2.5 to 3.5 mm. They are occupied by fine growth lines with 0.1 to 0.15 mm wide intervals. At this stage the growth lines extend with shallow lateral sinuses, low ventrolateral projection, and shallow, broadly rounded ventral sinus.



**Fig. 45.** *Lituites lasaulxii* Remelé, 1890 from the Upper Grey Orthoceratite Limestone. **A.** Lectotype MB.C.11678 (Kgl. Forstakademie Eberswalde Coll.) from Heegermühle (Brandenburg); photograph and reproduction of the illustration by Remelé (1890: pl. 3 fig. 1). **B.** Specimen MB.C.11645 (Remelé Coll.) from Eberswalde (Brandenburg); photograph and reproduction of the illustration by Remelé (1890: pl. 6 fig. 4). Scale bar units = 1 mm.

Specimen MB.C.11645 (Fig. 45B) is similar to the lectotype in general proportions and shape. The shell ornament has wider and flatter annuli in the uncoiled part of the conch.

### Remarks

Specimen MB.C.11677 (Remelé 1890: pl. 6 fig. 2) is a laterally compressed and crushed, straight phragmocone, which is ornamented by narrow, regularly spaced annuli similar to those of the lectotype. However, the specimen differs from the lectotype in having a lower expansion angle ( $4^\circ$ ). Because the specimen in discussion does not have anything of the coiled part preserved, it is placed in open nomenclature as *Lituites* cf. *lasaulxii*.

*Lituites lasaulxii* is most similar to *L. lituus* but differs in the stronger curvature of the backcoiled part; also, in *L. lasaulxii*, annuli are not developed at the coiled part of the conch and in the straight part, annuli are covered by growth lines instead of lirae.

### Geographic and stratigraphic occurrence

Northern Germany (in erratics within Pleistocene gravels); late Darriwilian, Middle Ordovician.

*Lituites fallax* Remelé, 1890  
Fig. 46, Table 9

*Lituites fallax* Remelé, 1890: 59, pl. 5 fig. 1.

### Diagnosis

Species of the genus *Lituites* with coiled conch diameter of ca 40 mm; whorl expansion rate 1.70. Shell surface of the coiled part of lirae (0.5–1.0 mm apart), raised in ca 2 mm wide intervals. Deep, rounded ventral sinus, very low dorsal projection; lirae straight laterally, direction rectiradiate.

### Type material

#### Lectotype (designated herein)

GERMANY • Brandenburg, Heegermühle; Ordovician (late Lasnamägi Regional Stage, late Darriwilian), Upper Grey Orthoceratite Limestone; Ramann Coll.; previously illustrated by Remelé (1890: pl. 5 fig. 1), re-illustrated here in Fig. 46; MB.C.11672.2.

### Description

Lectotype MB.C.11672.2 (Fig. 46) is a fragment of a third of the last whorl of the coiled part (40 mm estimated diameter;  $WER_{ah} \sim 1.70$ ) of a conch. The ornament consists of sharp lirae (0.5–1.0 mm apart), raised in more or less regular intervals (every ca 2 mm); the lirae are straight on the flanks, with a narrow ventrolateral projection. The ventral sinus is deep and rounded, dorsal projection is very low with a shallow dorsolateral sinus.

### Remarks

The lectotype of *Lituites fallax* is incompletely preserved and therefore, it cannot be excluded that it represents a morphological variant of some other species of the genus *Lituites*. Most similar to *L. fallax* are *L. kruegeri* sp. nov. and *L. cf. kruegeri*, both of which differ from *L. fallax* in having a smaller conch diameter (33 and 28 mm, respectively) and a higher  $WER_{ah}$  (2 and 2.30, respectively). Also, *L. fallax* is ornamented with lirae, which are straight on the flanks, while prorsiradiate lirae and flat annuli are developed in *L. kruegeri* sp. nov. (Fig. 8) and also in *L. cf. kruegeri*. Some specimens of *L. perfectus* have a large conch diameter (39 mm in the neotype MB.C.30544) and a low  $WER_{ah}$  (1.9 in MB.C.30544 and MB.C.30545) as *L. fallax* but the former species differs in the shell ornament of the coiled part;



**Fig. 46.** *Lituites fallax* Remelé, 1890 from the Upper Grey Orthoceratite Limestone. Lectotype MB.C.11672.2 (Ramann, Kgl. Forstakademie Eberswalde Coll.) from Heegermühle (Brandenburg, Germany); photograph (with dorsal, lateral and ventral views) and reproduction of the illustration by Remelé (1890: pl. 5 fig. 1). Scale bar units = 1 mm.

it consists of growth lines and rectiradiate annuli or ribs instead of sharp lirae. With only the holotype MB.C.11672.2 at hand, it is therefore not possible to confidently synonymise *L. fallax* with any other species of the genus *Lituites*.

Remelé (1890: pl. 1 fig. 3) assigned a second specimen (MB.C.11673.2) from coeval strata to *Lituites fallax*? but in this specimen nothing of the coiled part is preserved and hence its correspondence to the holotype cannot be validated. Holm (1891) and Sweet (1958) argued that the specimen probably represents *Trilacinoceras discors*. Indeed, this specimen is similar in ornament, expansion angle and general adult size to *T. discors*. However, the specimen is still chambered and its whorl profile is circular. Its identity is thus left unresolved herein; the holotype remains the only specimen unequivocally attributable to *L. fallax*.

***Lituites procerus* Remelé, 1890**  
Figs 47–49, Tables 9–10

*Lituites procerus* Remelé, 1890: 57, pl. 6 fig. 1.

non *Lituites procerus* – Foerste 1932: 166, text-fig. 7.

#### Diagnosis

Species of the genus *Lituites* with a coiled conch 24–30 mm in diameter; coiling tight or almost tight, 2.5–3 volutions; whorl expansion rate 2.10–2.50. Uncoiled part straight or slightly curved, juvenile expansion angle of up to 5°. Shell surface with widely spaced ribs or annuli and prominent, widely spaced lirae. Ornament elements biconvex or concavo-convex in the coiled part, and concavo-convex in the backcoiled part; ventral sinus deep and rounded, with ventral band (after Balashov 1953, emended).

## Type material

### Lectotype

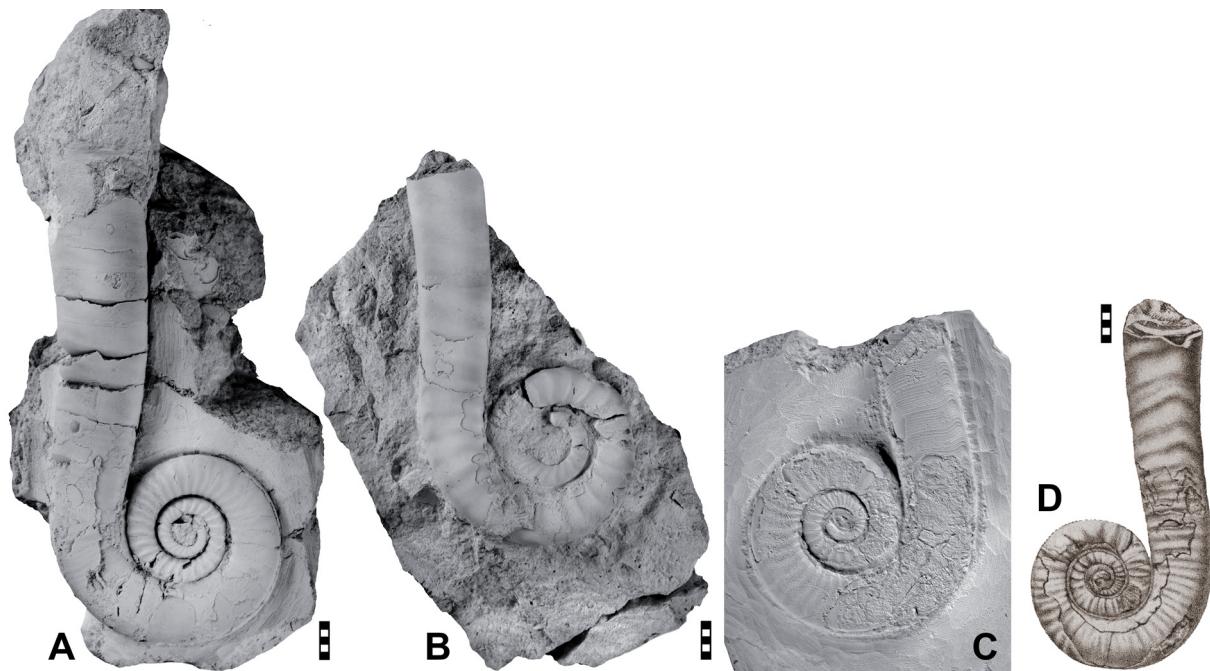
Not available for study, designated by Balashov (1953); illustrated by Remelé (1890: pl. 6 fig. 1) and reproduced here in Fig. 47D. It is from Drewin near Neustrelitz (Mecklenburg-Vorpommern, Germany), Upper Grey Orthoceratite Limestone erratics from Pleistocene gravel (late Darriwilian, Middle Ordovician).

## Material examined

GERMANY • 1 spec.; Brandenburg, Hohensaaten; Ordovician, Upper Grey Orthoceratite Limestone; Neben and Krueger Coll.; MB.C.30546 • 1 spec.; Brandenburg, Niederfinow; Ordovician, Upper Grey Orthoceratite Limestone; MB.C.2498 • 1 spec.; Brandenburg, Oderberg; Ordovician, Upper Grey Orthoceratite Limestone; Krueger Coll.; MB.C.30547.

## Description

Specimen MB.C.2498 (Fig. 47C) consists of a nearly complete coiled part ( $dm = 30$  mm; 2.5 essentially tight, barely detached volutions; Fig. 48F–J) and a short part of the backcoiled part (length = 15 mm;  $wh = 9.8$  mm;  $EA < 1^\circ$ ). The ornament is produced by ribs (up to 3.5 mm apart) and lirae (up to 0.5 mm apart). The spacing of ribs and lirae increases gradually and regularly during ontogeny. Their ventral sinus is deep and rounded. In the coiled part of the conch, the ornament elements are biconvex; in the backcoiled part, they are concavo-convex and form a shallow lateral sinus.



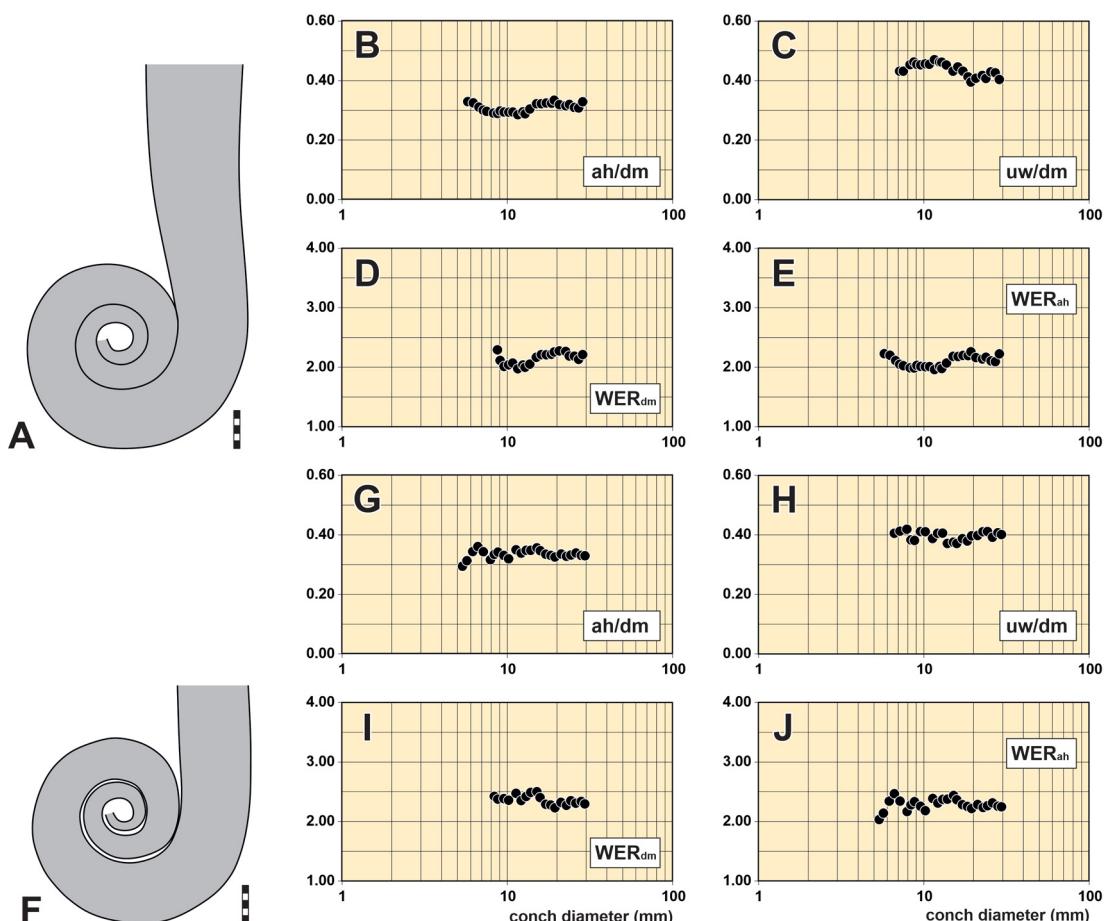
**Fig. 47.** *Lituites procerus* Remelé, 1890 from the Upper Grey Orthoceratite Limestone. **A.** Specimen MB.C.30547 (Krueger Coll.) from Oderberg (Brandenburg). **B.** Specimen MB.C.30546 (Neben & Krueger Coll.) from Hohensaaten (Brandenburg). **C.** Specimen MB.C.2498 from Niederfinow (Brandenburg). **D.** Reproduction of the illustration by Remelé (1890: pl. 6 fig. 1). Scale bar units = 1 mm.

Specimen MB.C.30546 (Fig. 47B) is a part and counterpart of the coiled part ( $dm = 25$  mm; 1.5 nearly tight, slightly detached volutions;) and a short part of the backcoiled part (length = 28 mm;  $wh = 10$  mm; EA  $\sim 1.5^\circ$ ). The ornament has coarse annuli, which are less than 1 mm in distance in the coiled part and towards backcoiled part of the specimen they are broad and flat and 4 mm apart. The spacing of annuli increases gradually and regularly during ontogeny. Lirae are not visible. The CLR is between 0.53 and 0.79, without an ontogenetic trend.

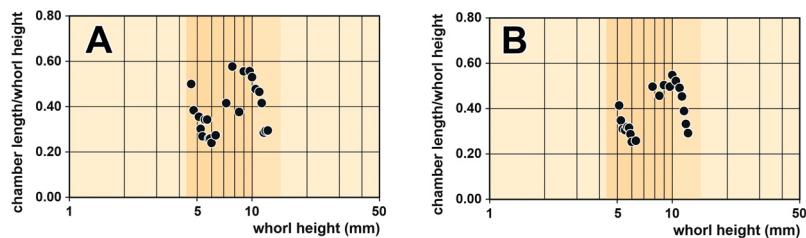
Specimen MB.C.30547 (Fig. 47A) consists of the nearly complete coiled part ( $dm = 33$  mm; 2.5 tightly coiled volutions; Fig. 48A–E) and a short part of the backcoiled part (length = 33 mm;  $wh = 13$  mm; EA  $\sim 5^\circ$ ). The ornament has coarse annuli (1–2 mm apart), lirae are not visible. The phragmocone chambers are variable in length (CLR between 0.24 and 0.58), without an ontogenetic trend (Fig. 49).

### Remarks

*Lituites procerus* is most similar to *L. lituus*, because it is tightly coiled with conch diameters of up to 30 mm; however, the uncoiled part in *L. lituus* is moderately curved with a greater expansion angle ( $5^\circ$ – $8^\circ$ ). *Lituites clavis* sp. nov. is also tightly coiled but its conch diameter is larger (34 mm) and the uncoiled conch part is moderately curved.



**Fig. 48.** *Lituites procerus* Remelé, 1890. **A.** Outline of coiled conch part of specimen MB.C.30547. **B–E.** Conch proportions and coiling rates of specimen MB.C.30547. **F.** Outline of coiled conch part of specimen MB.C.2498. **G–J.** Conch proportions and coiling rates of specimen MB.C.2498. Scale bar units = 1 mm.



**Fig. 49.** *Lituites procerus* Remelé, 1890, chamber length/whorl height of specimen MB.C.30547 (Krueger Coll.) from Oderberg (Brandenburg). **A.** Empirical data. **B.** Three data point averaged.

The variation of *Lituites procerus* concerns mainly the expansion angle at the beginning of the uncoiled stage; it is lower in specimens MB.C.2498 and MB.C.30546 but higher in the specimen figured by Remelé (1890) and specimen MB.C.30547. Furthermore, the latter specimen has narrower lirae at the end of the uncoiled part. Specimen MB.C.2498 is also unique due to the presence of biconvex ribs in the coiled part of the conch.

The late Darriwilian specimen figured by Balashov (1953: pl. 14 fig. 2) from northern Estonia has coarse annuli in the coiled and uncoiled part of the conch and the backcoiled part is rather strongly curved; the specimen is thus here attributed to *L. lituus*.

#### Geographic and stratigraphic occurrence

Northern Germany, Upper Grey Orthoceratite Limestone erratics from Pleistocene gravel (late Darriwilian, Middle Ordovician).

***Lituites tenuicaulis*** Remelé, 1890  
Figs 50–53, Tables 9–11

*Lituites tenuicaulis* Remelé, 1890: pl. 3 fig. 2.

*Lituites procerus* – Foerste 1932: 166, text-fig. 7.

*Lituites tenuicaulis* – Balashov 1953: 231, pl. 14 fig. 1. — Aubrechtová & Meidla 2020: 278.

#### Diagnosis

Species of the genus *Lituites* with the coiled conch 30 mm in diameter; 2–3 tightly coiled whorls, only the mid-part of the last whorl sometimes detached; whorl expansion rate 1.90–2.30. Uncoiled part straight in shape or slightly curved, expansion angle 2–3°. Shell surface in coiled part with fine growth lines and sharp lirae, sometimes with narrow annuli; in the backcoiled part with lirae and low annuli (after Balashov 1953; emended).

#### Type material

##### Lectotype

GERMANY • Brandenburg, Oderberg; Ordovician (late Lasnamägi Regional Stage, late Darriwilian), Upper Grey Orthoceratite Limestone; Kgl. Forstakademie Eberswalde Coll.; designated by Balashov (1953); illustrated by Remelé (1890: pl. 3 fig. 2), re-illustrated here in Fig. 50A; MB.C.5389.

### Additional material

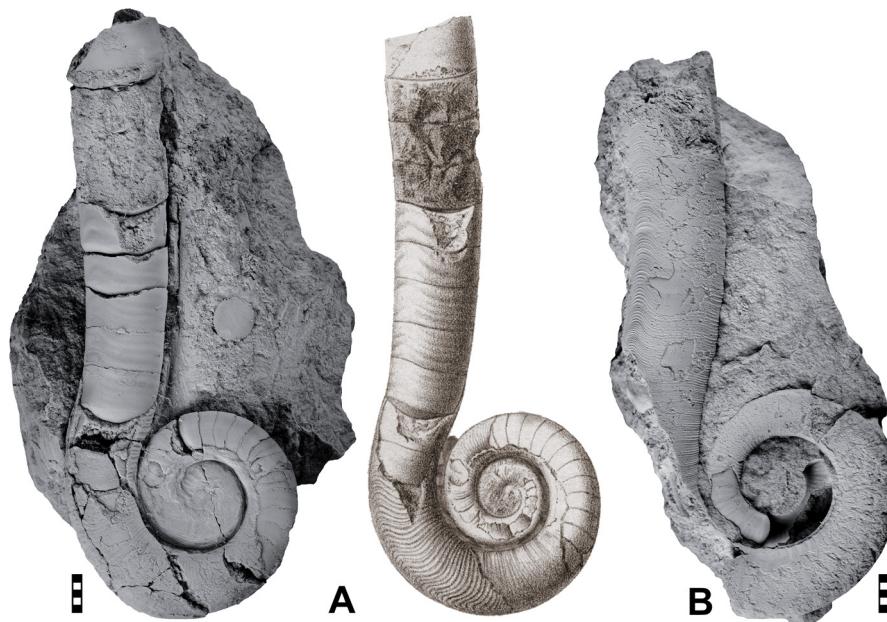
GERMANY • 1 spec.; Brandenburg, Eberswalde; Ordovician, Upper Grey Orthoceratite Limestone; Remelé 1884 Coll.; MB.C.11651 • 2 specs; Brandenburg, Niederfinow; Ordovician, Upper Grey Orthoceratite Limestone; Neben and Krueger Coll.; MB.C.30548, MB.C.30549 • 1 spec.; Brandenburg, Ringenwalde; Ordovician, Upper Grey Orthoceratite Limestone; Neben and Krueger Coll.; MB.C.30550.

POLAND • 1 spec.; West Pomerania, Island of Chrząszczewska (former Gristow); Ordovician, Upper Grey Orthoceratite Limestone; Müchner Coll.; MB.C.30551.

### Description

Lectotype MB.C.5389 (Fig. 50A) consists of the coiled part ( $dm = 28$  mm; 1.5 tightly coiled volutions slightly detached in the last half volution) and a part of the backcoiled part ( $length = 50$  mm;  $wh = 12.4$  mm;  $EA = 2.7^\circ$ ). The whorl profile is compressed ( $WWI = 0.88$ ). The shell wall is preserved only in the last portion of the coiled part; there the ornament consists of sharp lirae (less than 1 mm apart) and fine growth lines between them. The backcoiled part of the specimen additionally shows imprints of annuli of about 1 mm apart. The chamber length increases during ontogeny from  $CLR \sim 0.36$  to  $\sim 0.52$  (Fig. 52A–B). The siphuncle is visible at the last preserved septum, where it has a relative diameter of 0.18 and a position of 0.32.

A more completely preserved ornament is seen in the specimen MB.C.30551 (Fig. 50B). In this specimen, the coiled part has lirae and narrow annuli, which grade into flat annuli after uncoiling (3–4 mm apart). The annuli of the backcoiled part have coarse lirae in between them (0.3–0.5 mm apart). The ventral sinus of ornament elements is deep and rounded (Fig. 53). In the coiled part, the ornament elements are laterally straight, while in the backcoiled part, they have a shallow lateral sinus.

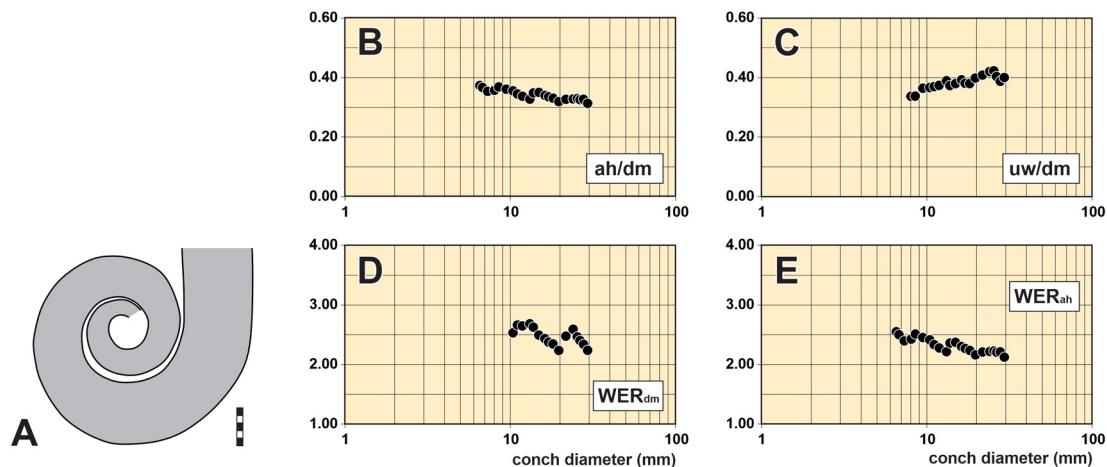


**Fig. 50.** *Lituites tenuicaulis* Remelé, 1890 from the Upper Grey Orthoceratite Limestone. **A.** Lectotype MB.C.5389 (Kgl. Forstakademie Eberswalde Coll.) from Oderberg (Brandenburg); photograph and reproduction of the illustration by Remelé (1890: pl. 3 fig. 2). **B.** Specimen MB.C.30551 (Münchner Coll.) from Island of Chrząszczewska (former Gristow; West Pomerania, Poland). Scale bar units = 1 mm.

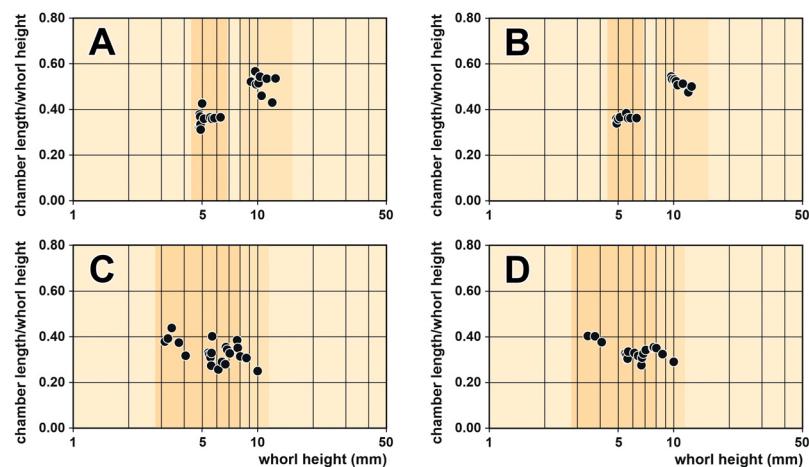
Specimen MB.C.30548 has a well-preserved coiled part (Fig. 51), which consists of nearly two tightly coiled volutions that are slightly detached in the last half volution. By contrast to the lectotype, the chamber length in MB.C.30548 decreases during ontogeny from CLR ~ 0.40 to ~ 0.25 (Fig. 52C–D).

### Remarks

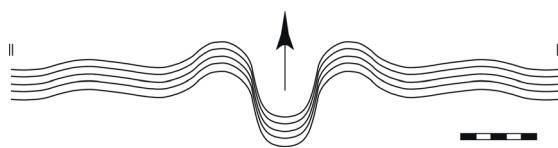
*Lituites tenuicaulis* is distinguished from other species of *Lituites* by a comparatively large, tightly or nearly tightly coiled conch, an almost straight, slowly expanding backcoiled part and an ornament with lirae in the coiled part, low and wide annuli in the backcoiled part. In these characters, the species is similar to *Trilacinoceras discors* but that species has smaller, more slender and openly coiled conch.



**Fig. 51.** *Lituites tenuicaulis* Remelé, 1890. A. Outline of coiled conch part of specimen MB.C.30548. B–E. Conch proportions and coiling rates of specimen MB.C.30548. Scale bar units = 1 mm.



**Fig. 52.** Septum distances in *Lituites tenuicaulis* Remelé, 1890 from the Upper Grey Orthoceratite Limestone. A, C = empirical data points; B, D = three data points averaged. A–B. Lectotype MB.C.5389 (Kgl. Forstakademie Eberswalde Coll.) from Oderberg (Brandenburg). C–D. Specimen MB.C.30548 (Neben & Krueger Coll.) from Niederfinow (Brandenburg).



**Fig. 53.** *Lituites tenuicaulis* Remelé, 1890 from the Upper Grey Orthoceratite Limestone; lirae in specimen MB.C.30551 (Münchner Coll.) from Island of Chrząszczewska (former Gristow; West Pomerania, Poland), at wh = 12.5 mm. Scale bar units = 1 mm.

### Geographic and stratigraphic occurrence

Estonia (in situ), northern Germany and northern Poland (in erratics within Pleistocene gravels); late Darriwilian, Middle Ordovician.

### *Lituites baculus* sp. nov.

urn:lsid:zoobank.org:act:4683F88A-1A93-436C-87E0-6A8E2996F9A8

Figs 54A, 55, Tables 9–11

### Diagnosis

Species of the genus *Lituites* with a small coiled part (ca 21 mm in diameter); 1.5 tightly coiled volutions (only the last half volution slightly detached). Whorl expansion rate 2.70. Uncoiled part weakly curved, expansion angle 4°. Shell ornament with rectiradiate lirae in the coiled part and lirae (up to 0.5 mm distance) and annuli (up to 4 mm apart) in the uncoiled part. Ornament elements in the backcoiled part prorsiradiate with shallow lateral sinus.

### Etymology

From the Latin ‘*baculus*’ (nomen) = ‘a stick’, referring to the shape of the holotype.

### Type material

#### Holotype

SWEDEN • Island of Öland, Gärdslösa; Middle Ordovician; Bottke Coll.; MB.C.29654 (illustrated in Fig. 54A).

### Description

Holotype MB.C. 29654 (Fig. 54A) consists of the complete coiled part (dm = 20.8 mm; 1.5 tightly coiled volutions, of which the last half volution is slightly detached from the preceding;  $WER_{ah} = 2.70$ ; Fig. 55) and the weakly curved backcoiled and straight parts (length = 110 mm; wh = 15.6 mm; EA ~ 4°). The whorl profile is compressed (WWI = 0.88). The initial chamber of the phragmocone is 0.46 mm in length and the whorl height at the first septum is 0.94 mm. The ornament is rather coarse and regular. In the coiled part, only transverse, rectiradiate lirae are visible (<0.5 mm apart). In the backcoiled and straight part, coarse annuli are added and are up to 4 mm apart with lirae of up to 0.5 mm distance; the ornament elements are prorsiradiate with a shallow lateral sinus. The chamber length ratio is ca 0.44 and increases during ontogeny.

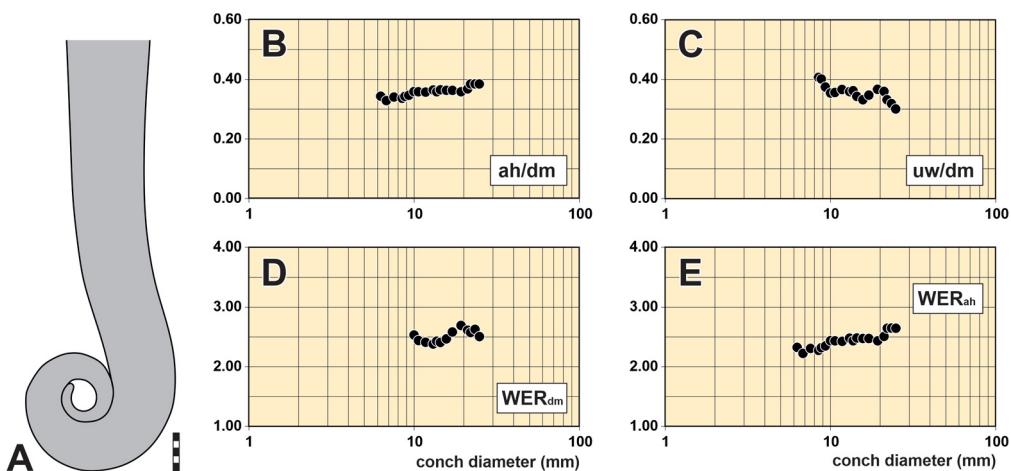
### Remarks

*Lituites baculus* sp. nov. is most similar to *Lituites toernquisti* because of the small overall size, the weak curvature of the backcoiled part and relatively low expansion angle of the backcoiled part. However,

the new species has only 1.5 volutions, which expand rather rapidly (WER 2.70). The shell ornament is also different: *L. baculus* sp. nov. lacks annuli in the coiled conch part and in the backcoiled part, the ornament elements have prorsiradiate direction.



**Fig. 54.** Species of *Lituites* from the Middle Ordovician of Gärdslösa (Island of Öland, Sweden). **A.** *Lituites baculus* sp. nov., holotype MB.C.29654 (Bottke Coll.). **B.** *Lituites bottkei* sp. nov., holotype MB.C.29651 (Bottke Coll.). Scale bar units = 1 mm.



**Fig. 55.** *Lituites baculus* sp. nov. A. Outline of coiled conch part of holotype MB.C.29654. B–E. Conch proportions and coiling rates of holotype MB.C.29654. Scale bar units = 1 mm.

***Lituites bottkei* sp. nov.**  
 urn:lsid:zoobank.org:act:E0CCF553-04EB-4E2C-9E3F-6653ABF2432A  
 Figs 54B, 56–57, Tables 9–10

### Diagnosis

Species of the genus *Lituites* with coiled part ca 26 mm in diameter; coiling open, the last whorl approaches preceding whorls just before uncoiling. Uncoiled part moderately curved, expansion angle 6–7°. Shell ornament with growth lines, transverse lirae and annuli; irregularly developed in thickness and spacing. Ornament elements biconvex in the coiled conch. Ventral sinus moderately deep, lateral sinus wide and shallow, dorsolateral sinus shallow, dorsal projection low.

### Etymology

After the late Werner Bottke (1943–2020), the collector of the holotype.

### Type material

#### Holotype

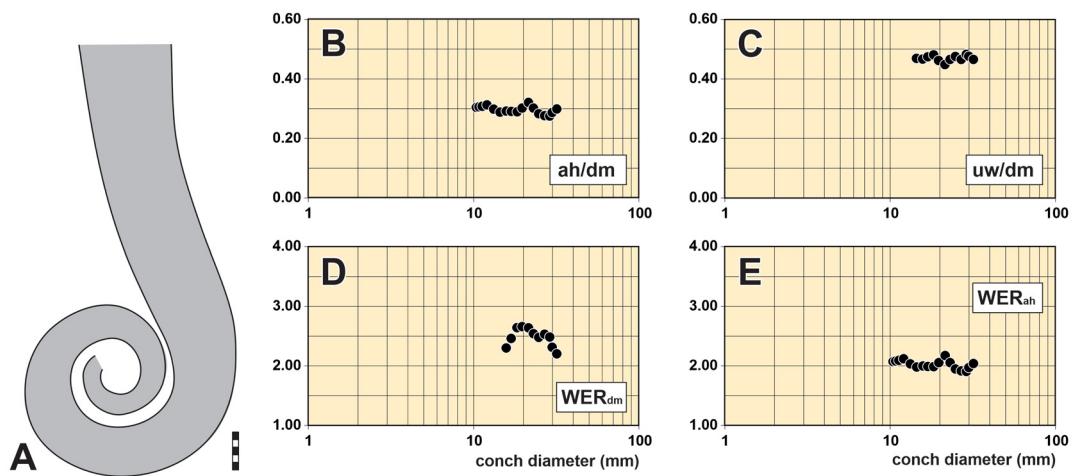
SWEDEN • Island of Öland, Gärdslösa; Middle Ordovician; Bottke Coll.; MB.C.29651 (illustrated in Fig. 54B).

#### Paratype

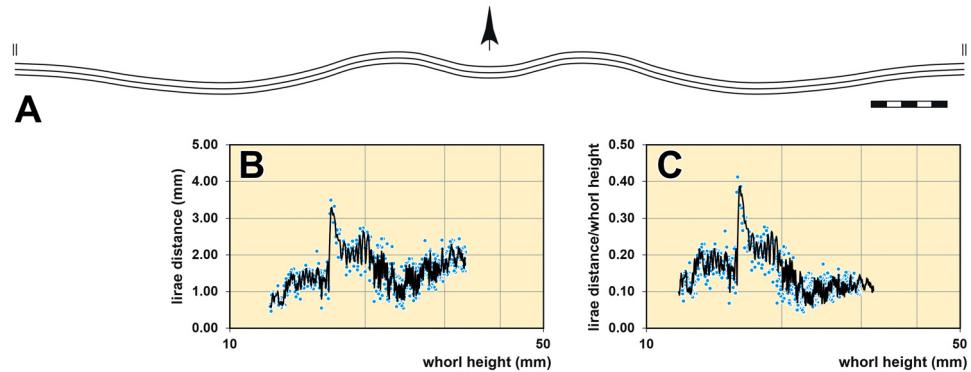
POLAND • West Pomerania, Ustronie Morskie (former Henkengahlen); Ordovician; Müldner? Coll.; MB.C.30536.

### Description

Holotype MB.C.29651 (Fig. 54B) consists of the coiled part (dm = 26 mm; coiling is open with the whorls not in contact; only the last whorl nearly touches the preceding just before uncoiling; Fig. 56) and the moderately curved backcoiled and straight parts (length = 300 mm; wh = 42 mm; EA ~ 6°). The ornament is best preserved in the penultimate whorl. It is here composed of various successive elements including shallow, rounded annuli, irregularly spaced growth lines and raised lirae. In the backcoiled part, very weak annuli are developed with irregular distances (between 0.5 and 1.0 mm apart); they



**Fig. 56.** *Lituites bottkei* sp. nov. A. Outline of coiled conch part of holotype MB.C.29651. B–E. Conch proportions and coiling rates of holotype MB.C.29651. Scale bar units = 1 mm.



**Fig. 57.** *Lituites bottkei* sp. nov. A. Lirae of holotype MB.C.29651 (Bottke Coll.) from Gärdslösa (Island of Öland, Sweden), at wh = 32 mm. B–C. Ontogenetic development of lirae distance (in mm) and lirae distance/whorl height of holotype MB.C.29651. Blue dots = individual measurements, black lines = three data point averaged values. Scale bar units = 1 mm.

are particularly well-visible in the ventrolateral area. Lirae (0.1–0.3 mm apart) cover the annuli and their interspaces. They are slightly coarser on the ridges of annuli. The ornament elements become progressively more prominent until the beginning of the straight part (wh ~ 17 mm, Fig. 57), where the shell bears traces of healed injuries (Fig. 6A). For another 21 mm of conch length following the position of the damage, the shell ornament is composed of widely spaced annuli (ca 4 mm apart) and lirae (0.6 mm apart). After that, the annuli become weaker, less regularly developed; at the end of the straight part of the conch, the annuli attain a maximum distance of ca 3 mm. The ornament elements extend with moderately deep ventral sinus, wide and shallow lateral sinus, shallow dorsolateral sinus and low dorsal projection. The chamber length can be measured only locally (CLR between 0.36 and 0.42).

## Remarks

*Lituites bottkei* sp. nov. differs from *L. lituus* in the loosely coiled part of the conch and in the ornament, which is generally finer with biconvex course in the coiled conch. *Lituites bottkei* sp. nov. differs from *L. perfectus* in regular coiling (i.e., the whorls are not eccentric) and greater expansion angle ( $6^\circ$  vs  $1-3^\circ$ ) of the uncoiled part.

Specimen MB.T.4492.52 is a nearly complete body chamber with several chambers of the phragmocone, which corresponds to the dimensions and expansion angle of *L. bottkei* sp. nov. However, the ornament is coarser (annuli up to 4 mm apart) and the specimen is therefore classified as *Lituites* cf. *bottkei*.

## Geographic and stratigraphic occurrence

Sweden (in situ) and Poland (in erratics within Pleistocene gravels); Middle Ordovician.

### *Lituites clavis* sp. nov.

urn:lsid:zoobank.org:act:717047ED-9C20-4AE7-B9F8-33C72291029F

Figs 58A, 59, Tables 9–10

*Lituites* sp. Neben & Krueger 1971: pl. 31 fig. 3.

## Diagnosis

Species of the genus *Lituites* with coiled part ca 34 mm in diameter; three tightly coiled whorls; whorl expansion rate  $\sim 2.00$ . Backcoiled part moderately curved, expansion angle  $\sim 2^\circ$ . Shell surface in the coiled part with annuli and growth lines and in the uncoiled part with very flat annuli a lirae. Ornament elements in the uncoiled part prorsiradiate.

## Etymology

From the Latin ‘*clavis*’ (nomen) = ‘a key’, referring to the shape of the holotype.

## Type material

### Holotype

GERMANY • Brandenburg, Niederfinow; Ordovician (late Lasnamägi Regional Stage, late Darriwilian), Upper Grey Orthoceratite Limestone; Neben Coll.; MB.C.30537 (illustrated in Fig. 58A).

## Description

Holotype MB.C.30537 (Fig. 58A) consists of the nearly complete coiled part (dm = 34 mm; three tightly coiled volutions; WER = 1.90; Fig. 59) and the moderately curved backcoiled part (length = 100 mm; wh = 16 mm; EA  $\sim 2^\circ$ ). The ornament undergoes some ontogenetic change: (1) Up to 20 mm diameter of the coiled conch, annuli are the dominant ornament element; these are particularly coarse and sharp on the inner half of the flank. They stand at distances of about 1 mm and carry fine growth lines that are strengthened to sharp lirae on the crests of the annuli. Between the crests of the annuli, the growth lines are extremely fine and have distances of less than 0.1 mm. (2) On the last half whorl of the coiled part, the annuli become significantly weaker and are only recognisable as low undulations. The growth lines are now stronger and stand at distances of about 0.15 mm. They are periodically raised to sharp lirae at intervals of about 1 mm. (3) The backcoiled part of the conch shows some remains of the shell with lamellar radial elements. These are flat annuli (3–4 mm apart) and irregularly placed, flat lirae at distances of 0.5–1.0 mm; both ornament elements leave a faint impression on the internal mould. Lateral sinus is shallow, ornament elements in the uncoiled part are prorsiradiate. The ventral sinus is moderately deep and rounded. The chamber length declines from CLR = 0.50–0.23 during ontogeny.

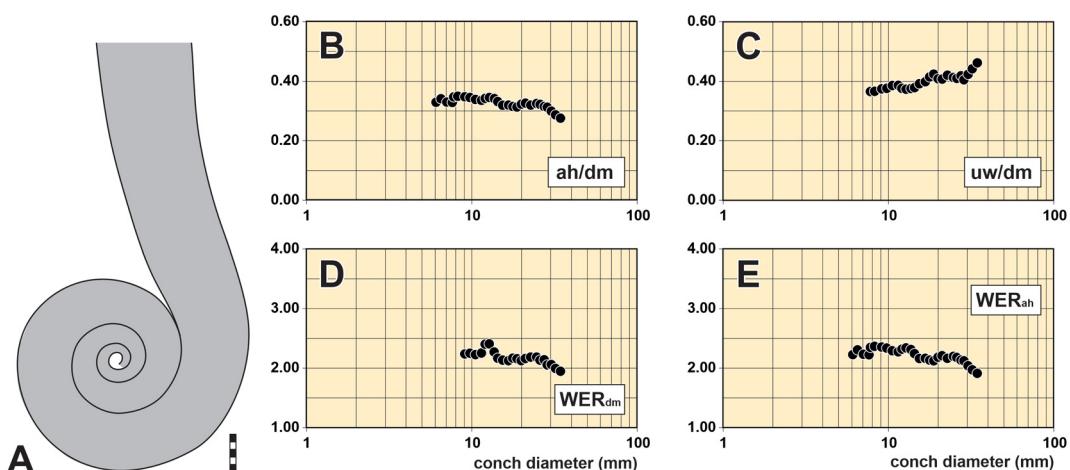
### Remarks

*Lituites clavis* sp. nov. has a relatively large coiled part, which consists of as many as three volutions. In these characters, the new species is similar to *Trilacinoceras knoeffleri* sp. nov., which differs in the finer shell ornament and a greater expansion angle. Since the mature aperture is not preserved in *L. clavis* sp. nov., it cannot be decided whether the species is indeed a *Lituites* or a *Trilacinoceras*. However, the rather coarse shell ornament and the circular whorl profile of the backcoiled part of the conch justifies the classification of *L. clavis* sp. nov. in the genus *Lituites*.

*Lituites clavis* sp. nov. differs from *L. lituus* by a greater diameter of the coiled part (34 mm but only up to 30 mm in *L. lituus*) and a lower expansion angle of the uncoiled part ( $2^\circ$  but  $5^\circ$ – $8^\circ$  in *L. lituus*); in addition, the annuli at the backcoiled part in *L. clavis* sp. nov. are flat, not prominent as in *L. lituus*. *Lituites clavis* sp. nov. differs from *L. procerus* because its coiled part is larger in diameter (34 mm but only up to 30 mm in *L. procerus*) and its uncoiled part is moderately curved slightly curved or straight in *L. procerus*.



**Fig. 58.** Species of *Lituites* from glacial erratics. **A.** *Lituites clavis* sp. nov., holotype MB.C.30537 (Neben Coll.) from the Upper Grey Orthoceratite Limestone of Niederfinow (Brandenburg, Germany); previously figured by Neben & Krueger (1971: pl. 31 fig. 3). **B.** *Lituites dewitzi* sp. nov., holotype MB.C.30538 (Neben Coll.) from the *Schroeteri* Limestone of Boltenhagen near Gross Klütz Höved (Mecklenburg-Vorpommern, Germany). **C.** *Lituites nebeni* sp. nov., holotype MB.C.30541 (Neben Coll.) from Upper Grey Orthoceratite Limestone of Niederfinow (Brandenburg, Germany); previously figured by Neben & Krueger (1971: pl. 31 fig. 2). Scale bar units = 1 mm.



**Fig. 59.** *Lituites clavis* sp. nov. A. Outline of coiled conch part of holotype MB.C.30537. B–E. Conch proportions and coiling rates of holotype MB.C.30537. Scale bar units = 1 mm.

#### *Lituites dewitzii* sp. nov.

urn:lsid:zoobank.org:act:8A82E920-AAD0-4EC3-A56B-B8D99B40D453

Figs 58B, 60, Tables 9–10

#### Diagnosis

Species of the genus *Lituites* with coiled part diameter of 27 mm; tightly coiled inner volutions, last half whorl detached from the preceding; whorl expansion rate based on conch shape 2.40 and based on whorl height 2.20. Uncoiled part faintly curved, expansion angle 5°. Shell surface of the coiled conch with sharp, prorsiradiate growth lines and lirae, backcoiled part with wide, lamellar lirae and growth lines. Annuli very flat and widely spaced in the backcoiled part.

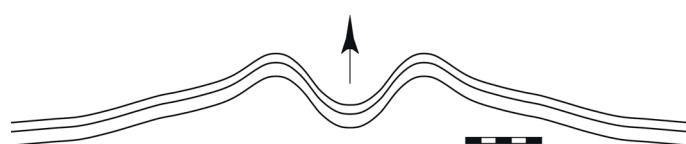
#### Etymology

After H.H. Dewitz, who published several important studies on Ordovician cephalopods during the 19<sup>th</sup> century.

#### Type material

##### Holotype

GERMANY • Mecklenburg-Vorpommern, Boltenhagen (Gross Klütz Höved); Ordovician (Lasnamägi Regional Stage, late Darriwilian), Upper Grey Orthoceratite Limestone; MB.C.30538 (illustrated in Fig. 58B).



**Fig. 60.** *Lituites dewitzii* sp. nov. from the *Schroeteri* Limestone; lirae on the venter in holotype MB.C.30538 (Neben Coll.) from Boltenhagen near Gross Klütz Höved (Mecklenburg-Vorpommern, Germany), at wh = 11 mm. Scale bar units = 1 mm.

## Description

Holotype MB.C.30538 (Fig. 58B) consists of the coiled part ( $dm = 27$  mm; 1.5 volutions preserved, coiling of inner volutions almost tight or tight, only the last 0.5 volution detached) and the faintly curved backcoiled part (length = 68 mm;  $wh = 14$  mm; EA  $\sim 5^\circ$ ). The ornament reveals two successive stages: (1) The coiled part (except for the last  $60^\circ$ ) shows sharp growth lines, strengthened to lirae, and annuli, which run almost straight but with a forward direction across the flank. In the ventrolateral area they bend into a shallow ventral sinus. (2) At the end of the coiled part, the narrow lirae transform into wide, lamellar lirae with distances of 0.5 to 1.2 mm. This ornament is retained in the entire preserved backcoiled part. There are delicate growth lines between the raised lirae. Annuli are present in the coiled part and then flatten out towards the backcoiled part, where they are visible only as very flat undulations of the shell wall. In the coiled part, the lateral sinus of ornament elements is not distinctly developed; after uncoiling, it remains shallow and oblique, sloping towards the dorsum. The ventral sinus is deep and rounded with a ventral band (up to  $wh$  of 10 mm; Fig. 60); the dorsal projection is very low.

## Remarks

The type of coiling in *Lituites dewitzi* sp. nov. is similar to that in *L. kruegeri* sp. nov. described below, but the former has a much coarser shell ornament, particularly with regard to the lirae. *Lituites perfectus* differs from *L. dewitzi* sp. nov. in being eccentrically and openly coiled with conch diameters of up to 40 mm; the backcoiled part in *L. perfectus* is nearly straight in shape with a lower expansion angle ( $1^\circ$ – $4^\circ$ ). *Lituites dewitzi* sp. nov. stands out among the species of the genus *Lituites* in the prorsiradiate direction of ornament elements in the coiled part of the conch.

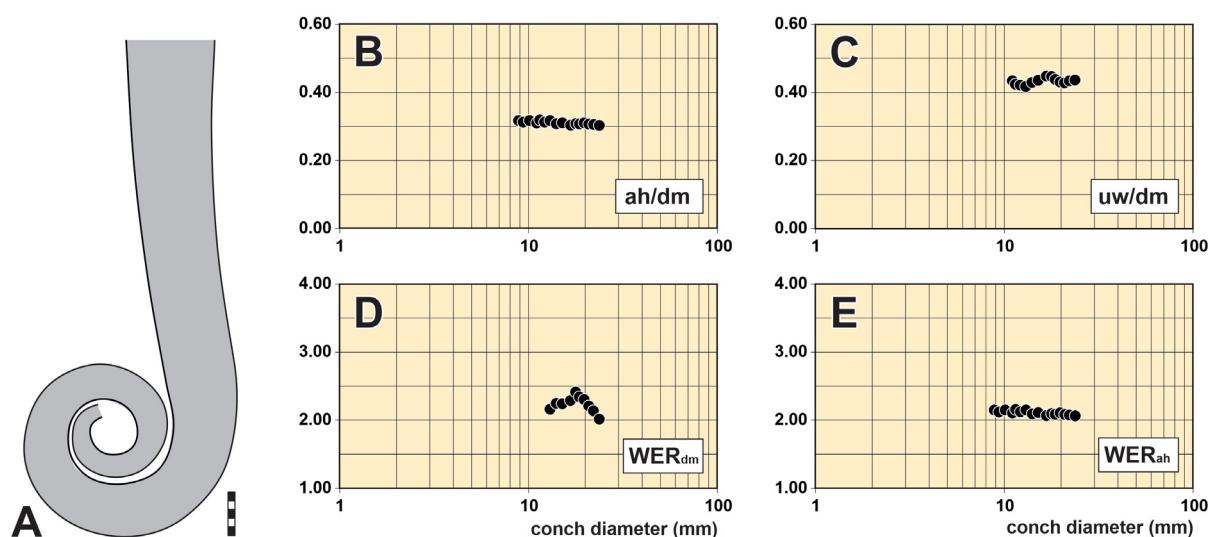
### *Lituites nebeni* sp. nov.

urn:lsid:zoobank.org:act:7DBAADFC-3AC7-41C1-B0BF-894C3FE9D6FE

Figs 58C, 61–62, Tables 9–10

*Lituites* cf. *lituus* – Hardt 1953: 45, text-fig. 10.

*Lituites* sp. – Neben & Krueger 1971: pl. 31 fig. 2.



**Fig. 61.** *Lituites nebeni* sp. nov. A. Outline of coiled conch part of holotype MB.C.30541 (Neben Coll.). B–E. Conch proportions and coiling rates of holotype MB.C.30541. Scale bar units = 1 mm.

## Diagnosis

Species of the genus *Lituites* with coiled part diameter of 24 mm; conch tightly coiled; whorl expansion rate ca 2.00. Uncoiled part weakly curved, very slender and almost tubular upon uncoiling, later reaching an expansion angle of 4°. Shell surface with very flat, widely spaced annuli (up to 4 mm apart) and sharp lirae (up to 1.2 mm apart).

## Etymology

After the late W. Neben (1901–1971), a private collector, who collected important specimens studied herein.

## Type material

### Holotype

GERMANY • Brandenburg, Niederfinow; Ordovician (late Lasnamägi Regional Stage, late Darriwilian), Upper Grey Orthoceratite Limestone; Neben Coll.; MB.C.30541 (illustrated in Fig. 58C).

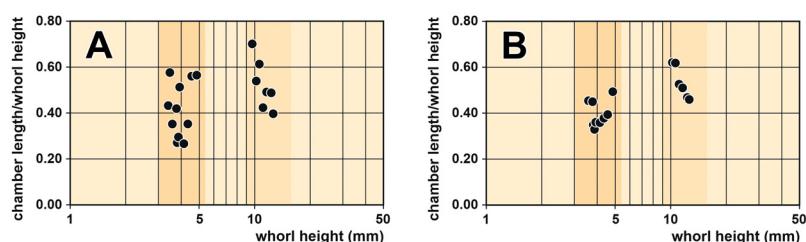
## Description

Holotype MB.C.30541 (Fig. 58C) consists of the coiled part ( $dm = 24$  mm; 1.25 whorls, tightly coiled, WER ~ 2.00; Fig. 61) and the faintly curved backcoiled part (length = 73 mm; wh = 13 mm); the backcoiled part is almost tubular after uncoiling and later reaches an expansion angle of 4°. The ornament of the coiled part consists of flat, widely spaced annuli (arranged up to 1.5 mm apart) with very fine growth lines in between; the backcoiled part possesses sharp lirae (0.5–1.2 mm apart), which are also visible on the internal mould, and very flat, widely spaced annuli (up to 4 mm apart). In the uncoiled part of the conch, the course of ornament elements is rectiradiate to slightly prorsiradiate; lateral sinus is shallow, dorsal projection is very low. The phragmocone chambers are ca 0.46 of whorl height with an increase up to 0.70 during ontogeny (Fig. 62).

## Remarks

*Lituites nebeni* sp. nov. is somewhat similar to *Trilacinoceras filix* sp. nov. described below, which differs in the more delicate shell ornament, the less prominent curvature of the conch after uncoiling and a compressed whorl profile in late growth stages. The character of ornament and the circular whorl profile of the backcoiled part of the conch suggests, however, that *L. nebeni* sp. nov. should be classified in *Lituites*.

The new species is similar to *L. anguinus* but the latter has an openly coiled juvenile conch and a lower expansion angle of the uncoiled part. *Lituites lituus* differs from *L. nebeni* sp. nov. in the moderate curvature of the uncoiled part, which also has a greater expansion angle (5°–8°); the shell ornament in *L. lituus* consists of prominent (instead of flat) annuli.



**Fig. 62.** *Lituites nebeni* sp. nov., chamber length/whorl height of holotype MB.C.30541 (Neben Coll.) from Niederfinow (Brandenburg, Germany). **A.** Empirical data. **B.** Three data point averaged.

*Lituites kruegeri* sp. nov.  
urn:lsid:zoobank.org:act:52BE9C66-AE91-46CA-893A-B1749CC2980E  
Figs 63B, 64A–E, 65, Tables 9–11

*Lituites* sp. – Neben & Krueger 1971: pl. 31 fig. 5.

**Diagnosis**

Species of the genus *Lituites* with coiled part 33 mm in diameter; inner whorls contiguous, last whorl detached, coiling widely open. Whorl expansion rate based on conch shape 2.70, whorl expansion rate based on whorl height 2.00. Uncoiled part almost straight, tubular (expansion angle 1°). Shell surface with growth lines, sharp lirae and flat annuli. Ornament elements rectiradiate in the coiled part and prorsiradiate in the backcoiled part, closer together in the last quarter of the last whorl and further apart in distance upon uncoiling; ventral sinus deep and rounded, with a ventral band, lateral sinus very shallow or ornament elements straight across flanks.

**Etymology**

After Hans-Hartmut Krueger, a skilled preparator of the Museum für Naturkunde, Berlin, who masterfully prepared the holotype.

**Type material**

**Holotype**

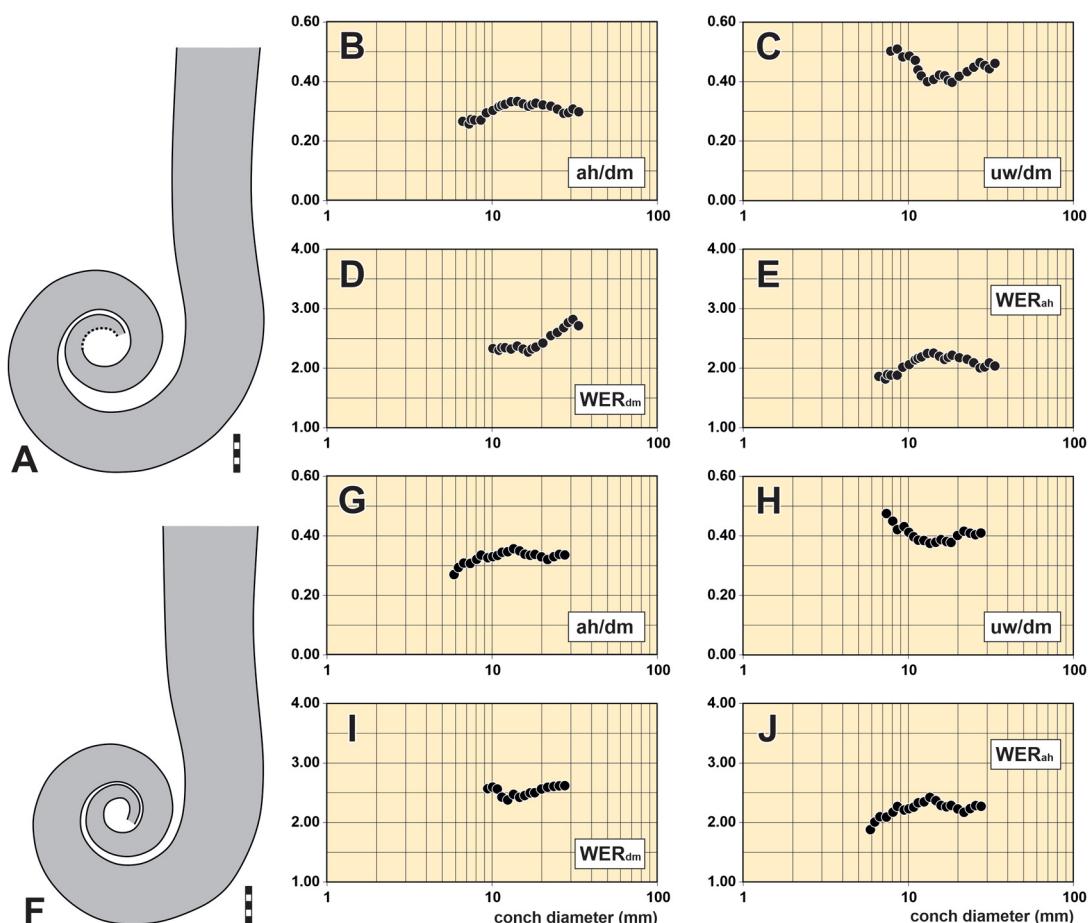
GERMANY • Brandenburg, Werbellinsee; Ordovician (late Lasnamägi Regional Stage, late Darriwilian), Upper Grey Orthoceratite Limestone; Neben and Krueger Coll.; previously illustrated by Neben & Krueger (1971: pl. 31 fig. 5), re-illustrated here in Fig. 63B; MB.C.30539.



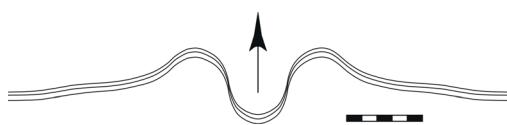
**Fig. 63.** *Lituites kruegeri* sp. nov. and *L. cf. kruegeri* from the Upper Grey Orthoceratite Limestone. **A.** *L. cf. kruegeri* – specimen MB.C.30540 (Neben & Krueger Coll.) from Hohensaaten (Brandenburg); lateral view. **B.** *L. kruegeri* sp. nov. – holotype MB.C.30539 (Neben & Krueger Coll.) from Werbellinsee (Brandenburg); previously figured by Neben & Krueger (1971: pl. 31 fig. 5); ventral and lateral views. Scale bar units = 1 mm.

## Description

Holotype MB.C.30539 (Fig. 63B) consists of the coiled part ( $dm = 33$  mm; innermost whorls are nearly in contact with the preceding, while the last whorl is detached and forms a gap 4.5 mm wide; coiling rates are  $WER_{dm} = 2.70$  and  $WER_{ah} = 2.00$ ; Fig. 64A–E) and a short part of the backcoiled part (length = 32 mm;  $wh = 11$  mm; EA ~1°). The ornament undergoes some ontogenetic change: shell is not preserved up to 16 mm diameter, but it appears that there are shallow annuli that are visible on the internal mould. Between 16 and 26 mm in diameter, the ornament consists of shallow annuli with distances of 0.5 mm, which are particularly well-developed on the inner and outer flank. They are accompanied by sharp growth lines, which are coarsest in the area of the ventrolateral projection. The annuli weaken at 26 mm diameter and are replaced by raised lirae produced by rhythmically strengthened growth lines. This type of ornament continues along the last part of the coiled part of the conch (33 mm diameter). The backcoiled part and the beginning of the straight part have then sharp growth lines, which are occasionally strengthened to form lirae. This part of the conch bears incipient annuli, which are most conspicuous in the ventrolateral area as semilunate, rounded elevations. The course of the growth lines is rather stable on the coiled and the uncoiled conch, but their direction changes from rectiradiate to prossiradiate. Generally, the growth lines extend nearly straight across the flank and form a moderately



**Fig. 64.** *Lituites kruegeri* sp. nov. and *Lituites* cf. *kruegeri*. A. *L. kruegeri* sp. nov., outline of coiled conch part of holotype MB.C.30539. B–E. *L. kruegeri* sp. nov., conch proportions and coiling rates of holotype MB.C.30539. F. *L. cf. kruegeri*, outline of coiled conch part of specimen MB.C.30540. G–J. *L. cf. kruegeri*, conch proportions and coiling rates of specimen MB.C.30540. Scale bar units = 1 mm.



**Fig. 65.** *Lituites kruegeri* sp. nov. from the Upper Grey Orthoceratite Limestone; lirae on the venter in holotype MB.C.30539 (Neben & Krueger Coll.) from Hohensaaten (Brandenburg, Germany), at wh = 11 mm. Scale bar units = 1 mm.

high ventrolateral projection. The shape of the ventral sinus changes: It is very deep and U-shaped in the coiled part and the beginning of the backcoiled part, where the growth lines touch the preceding and form a ventral band (Fig. 65). Along the backcoiled and the straight part, there occurs a shallowing of the ventral sinus. The chamber length ratio is ca 0.38, with lower values in the coiled part apically and higher values in the backcoiled part of the specimen.

### Remarks

*Lituites kruegeri* sp. nov. differs from *L. perfectus* in the more regular coiling of the conch and a more delicate shell ornament. *Lituites dewitzi* sp. nov. is similar in the type of coiling but has a coarser ornament and a greater expansion angle of the uncoiled part. *Lituites evolutus* (Late Ordovician strata of Hunan) is loosely coiled with a straight uncoiled part of the conch but some specimens have a curved uncoiled part (Fang *et al.* 2017: pl. 7 figs 2, 7); the whorl expansion rates are greater and the shell ornament is finer compared to *L. kruegeri* sp. nov.

Specimen MB.C.30540 (Figs 63A, 64F–J) might also belong to *L. kruegeri* sp. nov. because it has a similar geometry of the coiled part. However, the shell ornament has less prominent annuli, the ornament elements are less prorsiradiate and the interspace width is smaller. For these reasons, MB.C.30540 is classified as *Lituites cf. kruegeri* sp. nov.

## Genus *Trilacinoceras* Sweet, 1958

### Type species

*Lituites discors* Holm, 1891; designated by Sweet (1958).

### Species included

*Trilacinoceras aquaense* Lai & Wang in Wang, 1981; *Trilacinoceras costatum* Flower, 1975; *Lituites discors* Holm, 1891; *Trilacinoceras filix* sp. nov., *Trilacinoceras hunanense* Lai & Qi, 1977; *Trilacinoceras kalpinense* Lai & Wang in Wang, 1981; *Trilacinoceras knoeffleri* sp. nov., *Trilacinoceras norvegicum* Sweet, 1958; *Trilacinoceras reubeni* Flower, 1975; *Trilacinoceras undulatum* Flower, 1975; *Trilacinoceras xinjiangense* Lai & Wang in Wang, 1981.

### Diagnosis

Genus of the family Lituitidae with coiled part 18–40 mm in diameter; two to three open or tightly coiled volutions; whorl expansion rate 2.00–3.00. Whorl profile compressed throughout ontogeny. Uncoiled part straight to moderately curved, compressed, expansion angle up to 7°. Shell surface with narrow or prominent annulations and lirae, with conspicuously deep ventral sinus and five projections adapically, but only three projections (ventrolateral and dorsal) throughout most of the uncoiled part. Aperture with deep ventral sinus and three lappets: two incurving, tongue-shaped ventrolateral lappets and broad, low dorsal lappet; secondary dorsolateral lappet pair present in some species but this is not heralded in either

the growth-lines, or annulations at the extreme adoral end of the body chamber. Siphuncle dorsad of centre throughout the length of phragmocone (after Sweet 1958 and Aubrechtová & Turek 2018).

### Remarks

Flower (1975) attributed three newly described species to the genus *Trilacinoceras*, which are supposed to differ from all other species in the combination of a slightly depressed cross section (WWI = 1.10–1.25) and suture lines with broad and shallow ventral lobe. These characters would require an emendation of the genus diagnosis provided by Sweet (1958). However, the type specimens described by Flower (1975) are rather incomplete and the preservation raises doubts about the primary origin of the peculiarities of their conch morphology. Therefore, any emendation of the original diagnosis of the genus is avoided here.

### Geographic and stratigraphic occurrence

Nevada, Baltoscandia, northern Germany and Poland, Iberian Peninsula (?), central Bohemia and China; Middle to Late Ordovician.

*Trilacinoceras discors* (Holm, 1891)

Fig. 66A–B, Tables 12–13

*Lituites discors* Holm, 1891: 26, pl. 1 figs 5–7, pl. 3 figs 3–4.

*Ancistroceras discors* – Hyatt 1894: 508.

*Trilacinoceras discors* – Sweet 1958: 147, pl. 13 figs 1, 4, 6, pl. 15 fig. 5, pl. 16 figs 1, 3, 7–8, 10. —

Balashov 1962: pl. 7 fig. 6. — Dzik 1984: 138, text-fig. 55.12.

*Lituites discors* – Dzik 1984: 137, text-fig. 53b, e, pl. 40 figs 4–10.

### Diagnosis

Species of the genus *Trilacinoceras* with coiled conch 18–33 mm in diameter; 2–3 coiling open or whorls contiguous. Whorl profile slightly compressed through ontogeny, commonly ventrally flattened; whorl expansion rate ca 2.70. Expansion angle of uncoiled part 3–6°; whorl height at maturity about 23 mm. Shell surface with annuli and/or lirae, typically fine in the coiled part (less than 1 mm apart) and coarser in the uncoiled part (up to ca 3 mm apart) of the conch. Mature aperture with very shallow and broad lateral sinuses and a short and wide ventral sinus (after Holm 1891 and Sweet 1958; modified).

### Type material

Not available for study; Holm (1891) did not specify a type but he illustrated several specimens (Holm 1891: pl. 1 figs 5–7, pl. 3 figs 3–4); from Lerkaka (Island of Öland, Sweden), uppermost Red *Lituites* Limestone (Lasnamägi Regional Stage, late Darriwilian, Middle Ordovician).

### Material examined

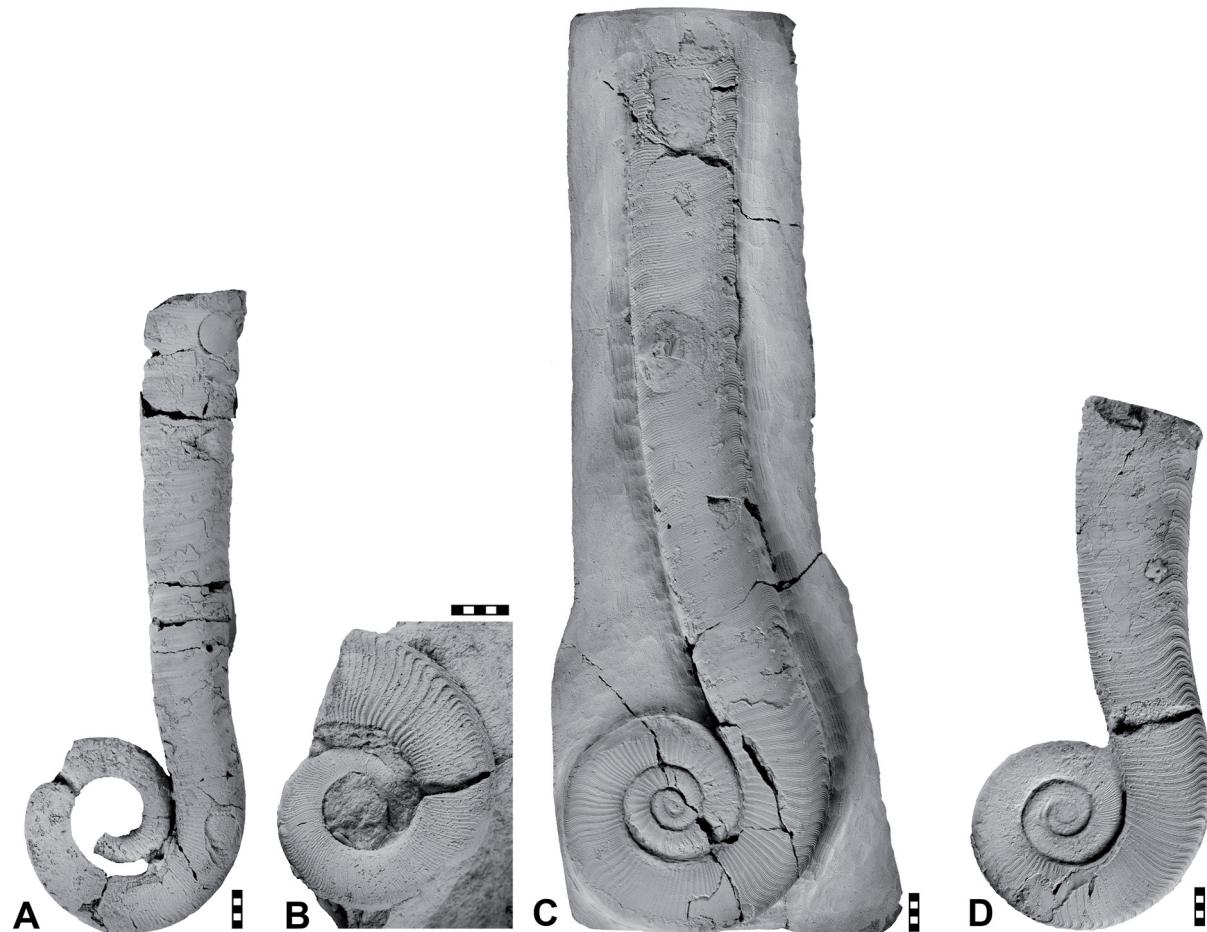
GERMANY • 1 spec.; Brandenburg, Niederfinow; Ordovician, Upper Red Orthoceratite Limestone; Neben and Krueger Coll.; MB.C.30552 • 1 spec.; Brandenburg, Schwedt; Ordovician, Upper Red Orthoceratite Limestone; MB.C.30553.

POLAND • 1 spec.; West Pomerania, Skowarcz (former Schönwarling), Gdańsk County; Ordovician, Upper Red Orthoceratite Limestone; MB.C.30554 • 2 specs; West Pomerania, Ustronie Morskie (former Henkengahen); Ordovician, Upper Red Orthoceratite Limestone; Krause Coll.; MB.C.11632.1, MB.C.11632.3.

COUNTRY UNKNOWN • 1 spec.; Ordovician, Upper Red Orthoceratite Limestone; MB.C.30555.

### Description

Specimen MB.C.30552 (Fig. 66A) is a fragment of a coiled part ( $dm = 30$  mm; 1.3 openly coiled whorls but the whorls get in contact just before uncoiling) and the almost straight backcoiled part (length = 60 mm;  $wh = 14$  mm; EA  $\sim 4^\circ$ ) of a conch. The whorl profile is compressed (WWI increases from 0.83–0.90 during the backcoiled stage). The shell ornament of the coiled part consists of rhythmically strengthened growth lines (0.10–0.15 mm apart), which ontogenetically transform into coarser lirae (up to 0.5 mm in distance); narrow annuli (ca 2.5 mm apart) appear after uncoiling. The ornament elements form a deep ventral sinus, a shallow to very shallow lateral sinus and a low dorsal projection; the ventral sinus is delineated by raised longitudinal lines in the coiled part, where the venter of the conch is slightly flattened. The ornament elements extend with a concavo-convex course; they are rectiradiate in the coiled part and prorsiradiate in the backcoiled part.



**Fig. 66.** Species of *Trilacinoceras* Sweet, 1958 from the Upper Grey Orthoceratite Limestone. **A.** *Trilacinoceras discors* (Holm, 1891), specimen MB.C.30552 (Neben & Krueger Coll.) from Niederfinow (Brandenburg); previously figured by Neben & Krueger (1971: pl. 21 fig. 1). **B.** *Trilacinoceras discors* (Holm, 1891), specimen MB.C.30553 from Schwedt (Brandenburg). **C.** *Trilacinoceras knoefleri* sp. nov., holotype MB.C.11658 (Knöfler Coll.) from Teschendorf near Löwenberg (Brandenburg). **D.** *Trilacinoceras knoefleri* sp. nov., paratype MB.C.30559 (Krueger Coll.) from Mukran (Sassnitz, Island of Rügen) (Mecklenburg-Vorpommern). Scale bar units = 1 mm.

Specimen MB.C.30553 (Fig. 66B) is a fragment of a coiled conch, 25 mm in diameter. The shell ornament consists of growth lines, which ontogenetically transform into transverse, slightly asymmetric lirae (0.8 mm distance) with fine growth lines in between them. The ornament elements form a very shallow lateral sinus and a deep ventral sinus; a low subangular ridge is present ventrally.

### Remarks

*Trilacinoceras discors* is most similar to *Lituites toernquisti* (described above), but differs in the possession of a three-lappeted aperture (instead of five-lappeted) and in being usually larger in conch dimensions (Holm 1891; Sweet 1958).

### Geographic and stratigraphic occurrence

Baltoscandia (in situ) and northern Germany and Poland (in erratics within Pleistocene gravels); late Aseri to Lasnamägi regional stages (late Darriwilian Middle Ordovician), possibly also early Kukruse Regional Stage (early Sandbian, early Late Ordovician).

*Trilacinoceras discors* has a relatively wide stratigraphic and palaeogeographic range of occurrence. It is characteristic for the early Lasnamägian *Lituites discors* Zone of Baltoscandia (Jaanusson & Mutvei 1953; Jaanusson 1960; Evans *et al.* 2014) but occurs also in the late Lasnamägian rocks of Germany (Pleistocene erratics) and possibly in the even younger, Uhakuan, strata of peri-Gondwana (Sá & Gutiérrez-Marco 2009; Aubrechtová & Turek 2018).

### *Trilacinoceras knöfleri* sp. nov.

urn:lsid:zoobank.org:act:F32CE3ED-2AF5-4959-9E5D-B97ECB7AB8B4

Figs 66C–D, 67–68, Tables 12–13

### Diagnosis

Species of the genus *Trilacinoceras* with coiled conch 38 mm in diameter; 2.50 to 3 tightly coiled volutions; whorl expansion rate ca 2.30. Whorl profile compressed in coiled part, weakly compressed or almost circular early after uncoiling. Backcoiled part moderately curved, expansion angle 2–5°; ventral side rounded. Shell surface with growth lines and raised lirae in the coiled part; wide, flat annuli and lirae present in the backcoiled part. Ornament elements slightly irregular in distance and thickness; in the coiled part rectiradiate, in the backcoiled part prorsiradiate. Lateral sinus shallow, located between the mid-flank and the ventrolateral projection. Ventral sinus wide and rounded.

### Etymology

After Hans-Rudolf Knöfler (Museum für Naturkunde, Berlin), preparator and collector of the holotype.

### Type material

#### Holotype

GERMANY • Brandenburg, Teschendorf (Löwenberg); Ordovician (late Lasnamägi Regional Stage, late Darriwilian), Upper Grey Orthoceratite Limestone; Knöfler Coll.; MB.C.11658 (illustrated here in Fig. 66C).

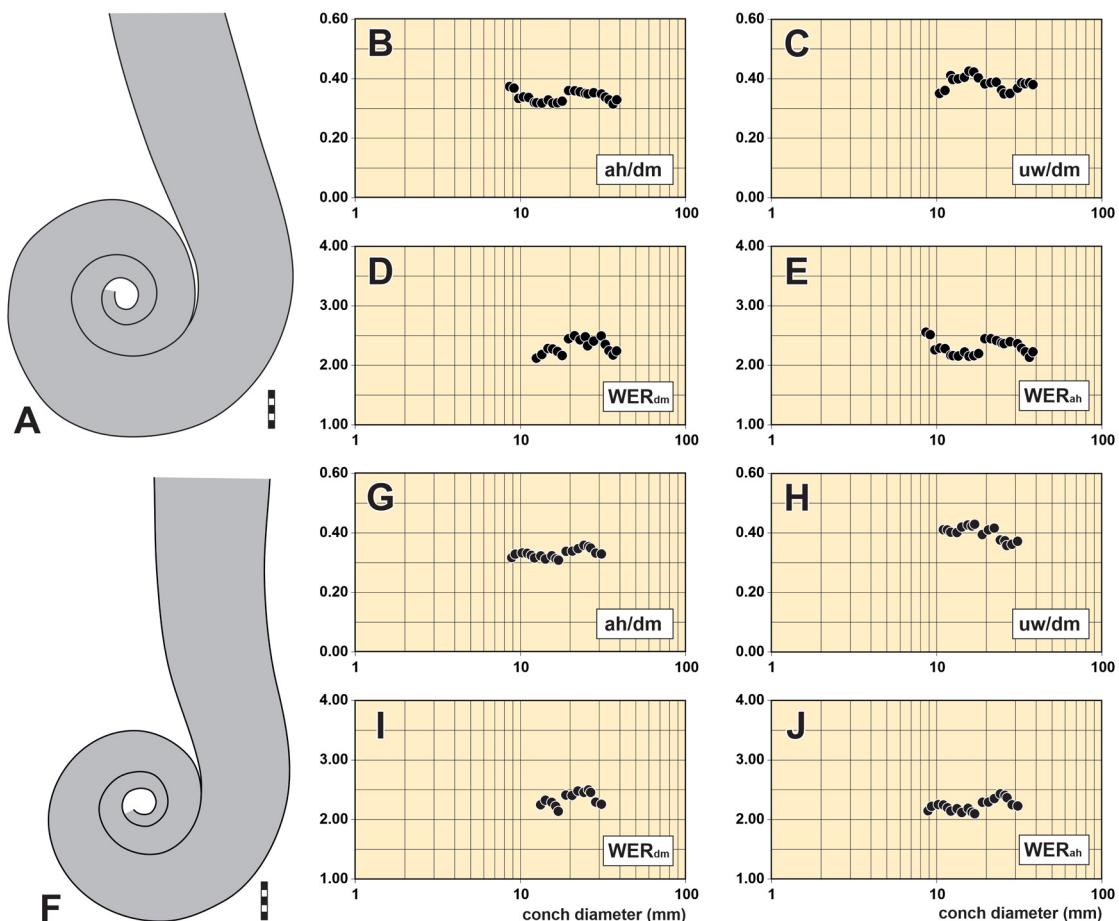
#### Paratype

GERMANY • Mecklenburg-Vorpommern, Mukran (Sassnitz, Island of Rügen); Ordovician, Upper Grey Orthoceratite Limestone; Krueger Coll.; MB.C.30559 (illustrated in Fig. 66D).

## Description

Holotype MB.C.11658 (Fig. 66C) consists of the almost complete coiled part ( $dm = 38$  mm; 2.75 tightly coiled whorls;  $WER = 2.20$ ; initial chamber does not appear to be preserved; Fig. 67A–E) and a portion of the uncoiled part (length = 87 mm;  $EA \sim 2^\circ$ ). The shell ornament is preserved along the whole length of the specimen. In the first 1.5 whorls, the ornament has fine growth lines and closely spaced annuli. In the rest of the coiled part, the shell bears growth lines (0.25–0.3 mm apart) and raised lirae (up to 1.7 mm apart) lirae. The lirae are rather irregularly developed, at conch diameters 24 mm and 28 mm, they are very fine and barely visible. In the backcoiled part of the specimen, wider and lower annuli (3 mm apart) appear; lirae are up to 0.5 mm apart. The distance of lirae increases during ontogeny, while the distance of annuli shows a decrease (up to about 7 mm wh) followed by an increase (Fig. 68B–C). In the coiled part, the ornament elements are rectiradiate with a lateral sinus between the mid-flank and the ventrolateral projection, while in the backcoiled part, the ornament elements change into prosriradiate and form a flat lateral sinus. Between coiled conch diameters 25 and 31 mm, the ornament elements are biconvex in shape.

Paratype MB.C.30559 (Fig. 66D) consists of a coiled part ( $dm = 30$  mm; 2.5 tightly coiled whorls;  $WER = 2.40$ ; Fig. 67F–J) and a portion of the moderately curved backcoiled part (length = 45 mm;  $EA \sim 4.5^\circ$ ); the whorl profile is almost circular at the beginning of uncoiling. The chamber length can



**Fig. 67.** *Trilacinoceras knoefleri* sp. nov. **A.** Coiling outline of holotype MB.C.11658. **B–E.** Conch proportions and coiling rates of holotype MB.C.11658. **F.** Coiling outline of paratype MB.C.30559. **G–J.** Conch proportions and coiling rates of paratype MB.C.30559. Scale bar units = 1 mm.

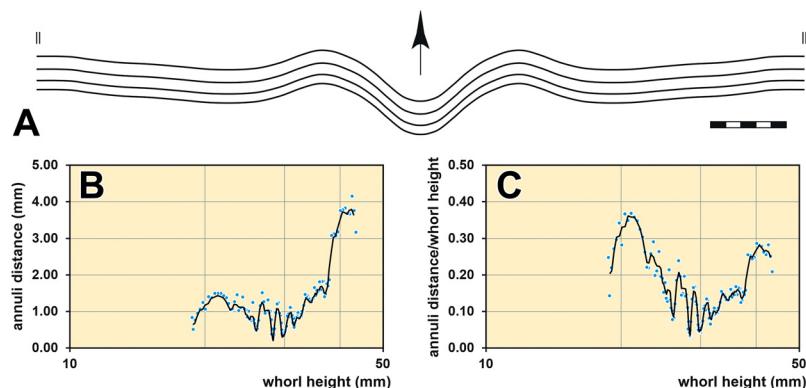
**Table 12.** Conch measurements (in mm), ratios and rates of coiled conch parts of *Trilacinoceras* Sweet, 1958.

taxon	catalogue nr	dm	wh	uw	ww	WERdm	WERah	UWI	WWI
<i>T. discors</i>	MB.C.30553	24.8	8.2	11.4	—	3.14	2.23	0.46	—
<i>T. discors</i>	MB.C.30555	29.0	10.6	—	26.7	2.48	2.48	—	0.92
<i>T. discors</i>	MB.C.30552	29.6	9.3	13.9	24.6	2.19	2.13	0.47	0.83
<i>T. filix</i>	MB.C.30557	28.0	8.4	13.4	—	2.47	2.04	0.48	—
<i>T. knoefleri</i>	MB.C.11658	38.3	12.6	16.1	—	2.22	2.22	0.42	—
<i>T. knoefleri</i>	MB.C.30559	29.8	10.6	13.1	25.3	2.41	2.41	0.44	0.85
<i>T. knoefleri</i>	MB.C.30558	30.9	10.2	13.6	—	2.25	2.23	0.44	—
<i>T. cf. hunanense</i>	MB.C.29655	36.3	11.4	15.6	—	2.09	2.13	0.43	—

be measured near the end of the specimen, where the CLR is 0.48. The shell ornament is preserved along the whole length of the specimen, except for the innermost whorls. In the coiled part of the conch, it consists of growth lines and more or less regularly raised lirae (up to 1 mm apart). After uncoiling, the lirae become wider and very flat annuli appear (ca 3 mm apart); the lirae are up to 1 mm apart. The ventral sinus of ornament elements is broad and rounded (Fig. 68A). The lateral sinus is shallow and located between the mid-flank and the ventrolateral projection. The dorsal sinus is very shallow.

### Remarks

The aperture is not preserved in the specimens but they are assigned to *Trilacinoceras* because of the combination of a large coiled portion consisting of almost three whorls, the slowly expanding and moderately curved backcoiled conch part and ornament that changes from narrow annuli/raised lirae to wider annuli during ontogeny. *Trilacinoceras knoefleri* sp. nov. differs from the type species *T. discors* in the larger size and lower expansion angle. Also, the ventral sinus of the ornament elements is broader and the whorl profile in the uncoiled part of the conch is less compressed and ventrally not flattened.



**Fig. 68.** *Trilacinoceras knoefleri* sp. nov. from the Upper Grey Orthoceratite Limestone. A. Lirae of paratype MB.C.30559 (Krueger Coll.) from Mukran (Sassnitz, Island of Rügen) (Mecklenburg-Vorpommern), at wh = 14 mm. B–C. Ontogenetic development of annuli distance (in mm) and annuli distance/whorl height of holotype MB.C.11658 (Knöfler Coll.) from Teschendorf near Löwenberg (Brandenburg). Blue dots = individual measurements, black lines = three data point averaged values. Scale bar units = 1 mm.

*Trilacinoceras knoefleri* sp. nov. is very similar to *T. cf. hunanense*, which is, however, more finely ornamented along the whole conch length and has a greater expansion angle of the uncoiled part; *T. hunanense* possesses a straight uncoiled part of the conch.

### Geographic and stratigraphic occurrence

Northern Germany (in erratics within Pleistocene gravels); late Lasnamägi Regional Stage, late Darriwilian, Middle Ordovician).

#### *Trilacinoceras filix* sp. nov.

urn:lsid:zoobank.org:act:76E53596-0229-4CB3-A62F-E12F3A296FEB

Figs 69A, 70, Tables 12–13

*Lituites* cf. *perfectus* – Neben & Krueger 1971: pl. 31 fig. 4.

*Lituites* sp. – Neben & Krueger 1971: pl. 31 fig. 6.

### Diagnosis

Species of *Trilacinoceras* with an openly coiled conch, 28 mm in diameter. Whorl profile slightly compressed throughout ontogeny. Backcoiled part of the conch moderately curved. Juvenile expansion angle <1°, later in ontogeny up to 5°. Shell ornament with narrow annuli (up to 4 mm in distance) and fine lirae in between; rectiradiate direction with low dorsal projection, deep ventral sinus and shallow lateral sinus.

### Etymology

From the Latin ‘*filix*’ = ‘fern’, referring to the shape of the holotype, which resembles the convoluted young leaves of some ferns.

### Type material

#### Holotype

GERMANY • Mecklenburg-Vorpommern, Rerik (Ostsee); Ordovician (Lasnamägi Regional Stage, late Darriwilian), Upper Grey Orthoceratite Limestone; Neben and Krueger 1961 Coll.; illustrated by Neben & Krueger (1971: pl. 31 fig. 4) and re-illustrated here in Fig. 69A; MB.C.30557.

#### Paratype

GERMANY • Brandenburg, Oderberg; Ordovician, Upper Grey Orthoceratite Limestone; Neben Coll.; MB.C.30556.

### Description

Holotype MB.C.30557 (Fig. 69A) consists of the coiled part ( $dm = 28$  mm; 1.25 openly coiled whorls;  $WER_{dm} = 2.50$ ,  $WER_{ah} = 2.00$ ) and a long portion of the almost straight backcoiled part and straight part (length = 250 mm; EA increases from ~1° to 4.6°). The whorl profile is compressed (WWI increases from 0.86–0.92). It can be estimated that about half of the original body chamber is preserved. The CLR is 0.40–0.50, without any apparent ontogenetic trend (Fig. 70). The shell ornament consists of annuli (1 to 3 mm in distance); fine lirae are locally preserved. The ornament elements form a deep ventral sinus and a low dorsal projection; on the flank, the elements are either straight or form a very shallow sinus.

Paratype MB.C.30556 is an incomplete, very slightly curved specimen of a body chamber with one chamber of the phragmocone preserved. The conch has similar proportions like the holotype but with better preserved shell ornament. The ornament consists of irregularly spaced annuli and lirae. The



**Fig. 69.** Species of *Trilacinoceras* Sweet, 1958. A. *Trilacinoceras filix* sp. nov., holotype MB.C.30557 (Neben & Krueger 1961 Coll.) from the Upper Grey Orthoceratite Limestone of Rerik (Ostsee) (Mecklenburg-Vorpommern); previously figured by Neben & Krueger (1971: pl. 31 fig. 4). B. *Trilacinoceras cf. hunanense* Lai & Qi, 1977, specimen MB.C.29655 (Bottke Coll.) from the Datianba Formation of Songtao County (Guizhou, South China). Scale bar units = 1 mm.

**Table 13.** Conch measurements (in mm), and expansion rates of uncoiled conch parts of *Trilacinoceras* Sweet, 1958.

taxon	catalogue nr	max. wh	max. ww	min. wh	min. ww	fragm. length	EA (°)
<i>T. discors</i>	MB.C.30552	14.0	—	10.0	8.5	61.9	3.7
<i>T. filix</i>	MB.C.30557	20.0	18.4	8.2	7.6	146.9	4.6
<i>T. filix</i>	MB.C.30556	20.0	18.8	15.0	13.7	57.3	5.0
<i>T. knoeffleri</i>	MB.C.11658	15.4	—	13.1	—	65.3	2.0
<i>T. knoeffleri</i>	MB.C.30559	16.2	15.5	13.0	11.9	40.7	4.5
<i>T. knoeffleri</i>	MB.C.30558	14.6	—	12.1	—	59.7	2.4
<i>T. cf. hunanense</i>	MB.C.29655	31.0	—	12.0	—	265.4	4.1

annuli are more strongly approximated behind the position of the last preserved septum (ca 1 mm apart) and have widest distances in the mid-length of the specimen (4 mm apart). The ornament elements form a deep ventral sinus, shallow lateral sinuses and a low dorsal projection. The single preserved phragmocone chamber has CLR of 0.32.

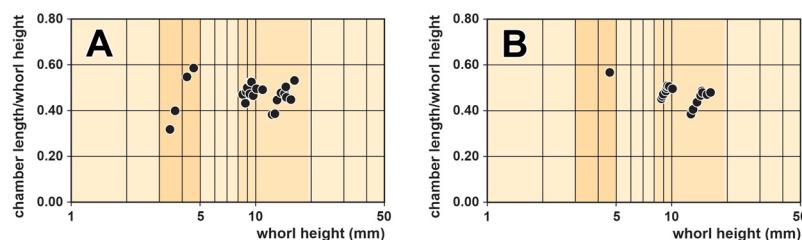
### Remarks

The new species is assigned to the genus *Trilacinoceras* because the conch has a conspicuously low expansion angle and the whorl profile remains compressed even in the apertural part of the conch (max. WWI 0.92 in the holotype and 0.94 in the paratype). The species is most similar to the type species *T. discors*, in which the conch has a higher expansion angle (3–6°), particularly after uncoiling. Furthermore, the ornament is different in both species. In *T. discors*, narrow but prominent annuli and lirae are developed in the coiled part and wider and flatter annuli in the uncoiled part. By contrast, the holotype of *T. filix* sp. nov. is decorated by rather widely spaced and strong annuli (1 mm apart) in the coiled part and comparatively narrower and widely spaced annuli (up to 4 mm apart) towards the apertural part.

*Trilacinoceras filix* sp. nov. is also rather similar to *Lituites nebeni* sp. nov. but the latter has a circular whorl profile, a more prominent shell ornament and a stronger curvature of the backcoiled part.

### Geographic and stratigraphic occurrence

Northern Germany (in erratics within Pleistocene gravels); late Lasnamägi Regional Stage, late Darriwilian, Middle Ordovician.



**Fig. 70.** *Trilacinoceras filix* sp. nov., chamber length/whorl height of holotype MB.C.30557 (Neben & Krueger Coll.) from Rerik (Ostsee) (Mecklenburg-Vorpommern). **A.** Empirical data. **B.** Three data point averaged.

*Trilacinoceras* cf. *hunanense* Lai & Qi, 1977  
Figs 69B, 71, Tables 12–13

### Material examined

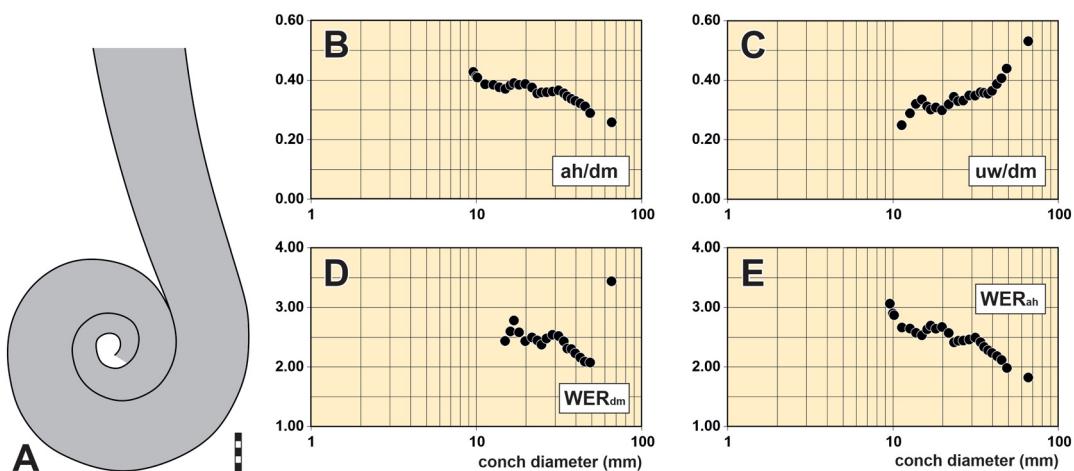
CHINA • 1 spec.; Guizhou, Songtao; Ordovician; Bottke Coll.; MB.C.29655.

### Description

Specimen MB.C.29655 (Fig. 69B) is a 326 mm long conch, which is partially embedded in the surrounding dark-brown limestone. The coiled part has a diameter of 36 mm and consists of at least 2.25 tightly coiled volutions (initial chamber is not preserved); the whorl expansion rate is 2.10 (Fig. 71). The uncoiled part is relatively strongly curved and expands with an angle of 4°. Ornament is preserved along the whole length of the specimen and is slightly irregular in distance. In the coiled part, the ornament consists of growth lines and raised lirae; in inner whorls, the ornament elements are straight, later, a shallow sinus is developed ventrolaterally. In the rest of the conch, narrow annuli (up to 2.7 mm in distance) and lirae (up to 0.3 mm apart) are present; the distance and thickness of the ornament elements is irregular; the conch is slightly constricted, where the ornament elements are the finest. The ornament elements in the backcoiled part have a rectiradiate direction but towards the straight part, they become rursiradiate; a marked dorsal projection and a sinus between the mid-flank and the ventrolateral projection is developed. The adapertural part of the specimen might represent the body chamber but terminal aperture is not preserved and suture lines are not visible.

### Remarks

*Trilacinoceras* cf. *hunanense* differs from *T. hunanense* in a smaller diameter of the coiled conch (36 mm vs 40 mm) and a more strongly curved (vs straight) uncoiled part (Xiang Fang, pers. com.). *Trilacinoceras knoeffleri* sp. nov. is distinguished by its smaller expansion angle and coarser, rectiradiate ornament of the backcoiled part. The rursiradiate direction of ornament elements in the straight conch part of *Trilacinoceras* cf. *hunanense* distinguishes the Chinese specimen from all specimens in the collection that come from European regions.



**Fig. 71.** *Trilacinoceras* cf. *hunanense* Lai & Qi, 1977. A. Coiling outline of specimen MB.C.29655. B–E. Conch proportions and coiling rates of specimen MB.C.29655. Scale bar units = 1 mm.

Genus *Cyclolituites* Remelé, 1886

**Type species**

*Lituites applanatus* Remelé, 1880; by original designation.

**Species included**

*Cyclolituites americanus* Hyatt, 1894; *Cyclolituites anhuiensis* Qi, 1980; *Lituites applanatus* Remelé, 1880; *Cyclolituites dazhubaensis* Chen in Gao *et al.*, 1982; *Cyclolituites hubeiensis* Xu & Liu, 1977; *Cyclolituites kjerulfi* Sweet, 1958; *Cyclolituites Lynceus* Holm, 1891; *Lituites Lynnensis* Kjerulff, 1865; *Cyclolituites trilobatus* Lai & Wang in Wang, 1981.

**Diagnosis**

Genus of the family Lituitidae with discoidally coiled conch, uncoiled conch part lacking. Inner whorls tightly coiled, last volution or only its apertural end detached from the preceding; umbilical window large, 2–5 mm wide; whorl expansion rate ca 3.10; increasingly prominent ventral ridge developed in apertural end of the conch. Shell surface faintly annulated or lirated. Siphuncle position subdorsal to subcentral. Aperture of mature conch five-lobed, characterised by a deep ventral sinus, a pair of asymmetric ventrolateral lappets, lateral sinuses and less pronounced dorsolateral and dorsal projections (after Sweet 1958 and Furnish & Glenister 1964; modified).

**Remarks**

*Cyclolituites americanus*, from the early or middle Darriwilian strata of Newfoundland, differs from all other species of the genus in a significantly larger coiled conch (over 40 mm diameter) and in the pronounced paired grooves flanking the ventral sinus of the ornament. In both characters, *C. americanus* is similar to *Angelinoceras latum* (Dzik 1984). However, *C. americanus* is known so far only from a single, fragmentary specimen (Flower 1975), in which adoral part of the conch are missing, and the species is thus tentatively retained in the genus *Cyclolituites*.

Dzik (1984) stated that *Cyclolituites applanatus*, *C. lynceus* and *C. lynnensis* cannot be recognised as separate species. In fact, however, the data presented herein show that the three species can be distinguished rather easily based on their maximum conch diameters, whorl expansion rates and shell ornament (see below). Dzik (1984) stated that *C. kjerulfi* appears to represent apical parts belonging to some species of the genus *Ancistroceras*. This interpretation is not possible to validate here without the study of the type specimens of *C. kjerulfi*, but from descriptions of the species by Sweet (1958), it is clear that the coiled conch has an umbilical window and a ventral keel. Both features are characteristic for species of the genus *Cyclolituites*.

**Geographic and stratigraphic occurrence**

Newfoundland (Canada), Norway, Sweden, northern Germany, Anhui and Hunan (China); Middle to Late Ordovician.

*Cyclolituites applanatus* (Remelé, 1880)  
Fig. 72

*Lituites applanatus* Remelé, 1880: 438.

*Cyclolituites applanatus* – Remelé 1886: 467; 1890: 101, pl. 1 fig. 6a–b.

*Lituites applanatus* – Remelé 1890: 30.

*Cyclolituites applanatum* – Holm 1891: 33.

*Cyclolituites applanata* – Neben & Krueger 1971: pl. 32 figs 19–20.

### Diagnosis

Species of the genus *Cyclolituites* with tightly coiled conch, only last whorl detached near mature aperture; whorl profile compressed ( $WWI = 0.60$ ). Shell surface with narrow annuli/raised lirae, adorally 0.5–1 mm apart, marked ventral sinus; lateral sinus weakly developed in inner whorls of the conch, shallow and asymmetric towards the aperture.

### Type material

#### Lectotype (designated herein)

GERMANY • Brandenburg, Eberswalde; Ordovician, Upper Grey Orthoceratite Limestone; Kgl. Forstakademie Eberswalde Coll.; illustrated by Remelé (1880: pl. 1 fig. 6; 1890: pl. 1 fig. 6), re-illustrated here in Fig. 72B; MB.C.11671.2.

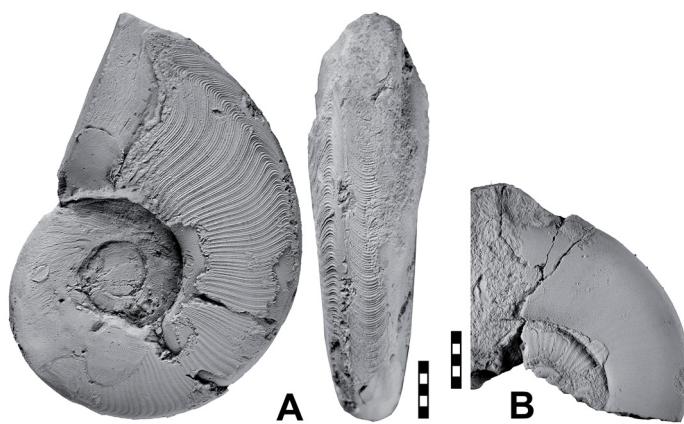
### Additional material

GERMANY • 1 spec.; Brandenburg, Oderberg; Ordovician, Upper Grey Orthoceratite Limestone; MB.C.30560.

### Description

Lectotype MB.C.11671.2 (Fig. 72B) consists of a part of the coiled conch ( $dm = 20$  mm; one and a half tightly coiled whorls;  $WWI = 0.60$ ;  $WER = 2.40$ ) with an incomplete body chamber. The shell ornament consists of narrow annuli/raised lirae (up to 0.5 mm apart) separated by very fine growth lines. The ornament elements form a deep ventral sinus and a shallow lateral sinus. The slightly flattened venter of the last whorl is raised and separated from the flanks by subangular ridges. The last quarter of the last whorl belongs to the body chamber.

Specimen MB.C.30560 (Fig. 72A) consists of the coiled part ( $dm = 33$  mm; one and a half tightly coiled whorls;  $WWI = 0.60$ ;  $WER_{dm} = 3.40$ ) with an almost complete body chamber. The shell is ornamented by narrow annuli/raised lirae (up to 0.50–1 mm apart) and very fine growth lines in between. The



**Fig. 72.** *Cyclolituites applanatus* (Remelé, 1880) from the Upper Grey Orthoceratite Limestone. **A.** Specimen MB.C.30560 (Neben & Krueger Coll.) from Oderberg (Brandenburg); previously figured by Neben & Krueger (1971: pl. 32 figs 19–20); lateral and ventral views. **B.** Lectotype MB.C.11671.2 (Kgl. Forstakademie Eberswalde Coll.) from Eberswalde (Brandenburg); previously figured by Remelé (1890: pl. 1 fig. 6); lateral view. Scale bar units = 1 mm.

**Table 14.** Conch measurements (in mm), ratios and rates of coiled conchs of *Cyclolituites* Remelé, 1886.

<b>taxon</b>	<b>catalogue nr</b>	<b>dm</b>	<b>wh</b>	<b>uw</b>	<b>ww</b>	<b>WERdm</b>	<b>WERah</b>	<b>UWI</b>	<b>WWI</b>
<i>C. applanatus</i>	MB.C.11671	20.3	7.3	12.0	8.5	2.44	2.44	0.42	0.59
<i>C. applanatus</i>	MB.C.30560	32.6	15.0	19.6	9.8	3.43	3.43	0.30	0.60
<i>C. lynceus</i>	MB.C.30562	32.4	13.3	22.7	12.0	2.94	2.88	0.37	0.70
<i>C. lynceus</i>	MB.C.30561	37.2	16.1	26.4	12.6	3.05	3.11	0.34	0.71

ornament elements form a ventral sinus and a lateral sinus. The lateral sinus is weakly developed and shallow, the point of its maximum backward curvature is located in the ventrolateral area. As in the lectotype, the ventral side of the last whorl is slightly raised and flattened and forms a subangular ridge. The body chamber has half the length of the last whorl.

### Remarks

The lectotype of *C. applanatus* differs from the below described specimens of *C. lynceus* because it has a smaller diameter of the conch (20 mm), a less compressed whorl profile (WWI = 0.60), a lower whorl expansion rate (WER 2.40) and a coarser ornament.

Specimen MB.C.30560 (also figured by Neben & Krueger 1971: pl. 32 figs 19–20) differs from the lectotype in the larger size and higher whorl expansion rate (WER = 3.40 vs 2.40 in the lectotype) and is thus similar to *Cyclolituites lynnensis* (late Middle or early Late Ordovician of Norway). It is possible, however, that the differences have the reason in an earlier ontogenetic growth stage of the lectotype. Since specimen MB.C.30560 has the same type of ornament and whorl profile shape (whorls are not impressed dorsally and lack a conspicuous keel ventrally) as the lectotype, it is retained in *C. applanatus* here.

### Geographic and stratigraphic occurrence

Northern Germany (in erratics within Pleistocene gravels); Upper Grey Orthoceratite Limestone, late Lasnamägi Regional Stage, late Darriwilian, Middle Ordovician.

*Cyclolituites lynceus* Holm, 1891  
Figs 73–74

*Cyclolituites Lynceus* Holm, 1891: 33, pl. 1 figs 8–9.

*Cyclolituites lynceus* – Sweet 1958: 21. — Neben & Krueger 1971: pl. 32 figs 17–18.

*Cyclolituites lycnus* – Flower 1975: 161.

### Diagnosis

Species of the genus *Cyclolituites* with conch diameters around 35 mm; tight coiling with only the apertural part of the body chamber detached from preceding volutions; whorl expansion rate ca 3.00; whorl profile compressed (WWI = 0.70). Shell surface with fine growth lines and raised pairs of lirae up to 0.4 mm apart.

### Type material

Not available for study; Holm (1891) did not specify a type but illustrated one specimen (Holm 1891: pl. 1 figs 8–9), which is reproduced here in Fig. 73C; it comes from Lerkaka (Island of Öland, Sweden),

Folkeslunda Limestone (Upper Grey Orthoceratite Limestone, late Lasnamägi Regional Stage, late Darriwilian, Middle Ordovician).

### Material examined

GERMANY • 1 spec.; Brandenburg, Oderberg; Ordovician; Neben and Krueger Coll.; MB.C.30561 • 1 spec.; Mecklenburg-Vorpommern, Boltenhagen (Gross Klütz Höved); Ordovician, Upper Grey Orthoceratite Limestone; Neben and Krueger 1962 Coll.; MB.C.30562.

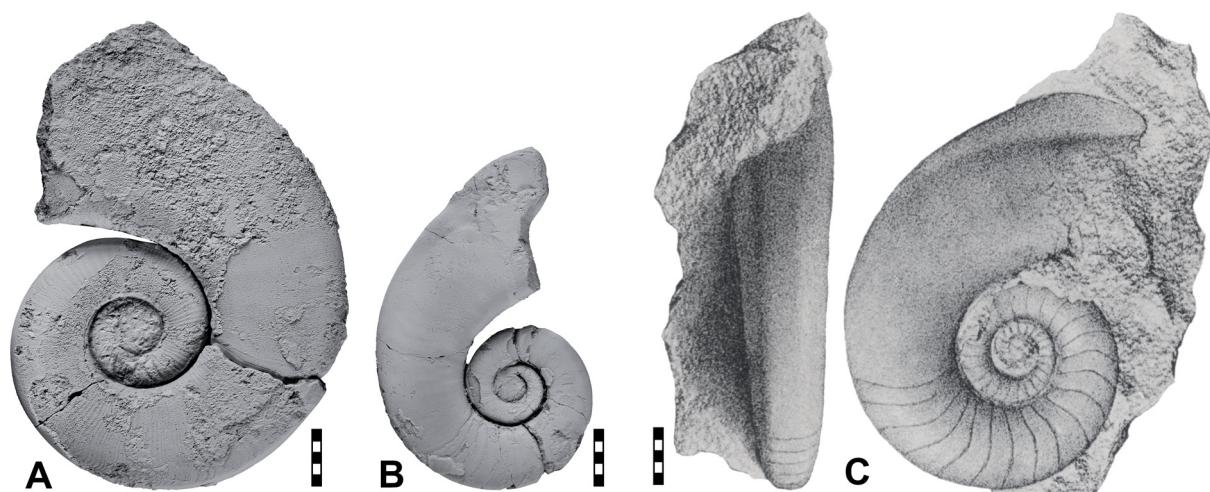
### Description

Specimen MB.C.30562 (Fig. 73B) is an almost complete, coiled conch with 32 mm diameter and consists nearly two tightly coiled whorls (WWI = 0.70; WER = 2.90; Fig. 74B–F), of which only the second half of the last whorl is detached from the preceding. The umbilical window is 4 mm wide. 135 degrees of the last whorl belongs to the body chamber. An increasingly pronounced ridge is raised on the venter at the apertural end of the specimen. The shell ornament is preserved only in the inner whorls and consists of raised pairs of lirae (up to 0.4 mm in distance) and very fine growth lines. The aperture is partly preserved; it has a deep ventral sinus, elongated ventrolateral lappets and a rather shallow lateral sinus (dorsal edge of the aperture is not preserved). The chamber length varies between CLR = 0.20 and 0.30.

Specimen MB.C.30561 (Fig. 73A) is an almost complete, coiled conch (dm = 37 mm, nearly two tightly coiled whorls with only the second half of the last whorl is detached; the umbilical window 5.3 mm wide; WWI = 0.71; WER = 3.10; Fig. 74A, C–F); 135 degrees of the last whorl belong to the body chamber. The shell ornament is preserved only locally and consists of slightly irregularly spaced, raised lirae (up to 0.2 mm in distance) and very fine growth lines in between; the lirae leave imprints on the internal mould. The aperture is incomplete, only a fragment of one ventrolateral lappet is preserved.

### Remarks

The two specimens under study are from the Neben & Krueger collection and one of them, MB.C.30562, was previously figured by Neben & Krueger (1971: pl. 32 figs 17–18). Both specimens closely resemble



**Fig. 73.** *Cyclolituites lynceus* Holm, 1891. **A.** Specimen MB.C.30561 (Neben & Krueger Coll.) from Oderberg (Brandenburg). **B.** Specimen MB.C.30562 (Neben & Krueger 1962 Coll.) from Boltenhagen, Groß Klütz (Mecklenburg); previously figured by Neben & Krueger (1971: pl. 32 figs 17–18). **C.** Reproduction of the illustration by Holm (1891: pl. 1 figs 8–9). Scale bar units = 1 mm.

**Table 15.** Siphuncular diameter ratio (SDR) and siphuncular distance ratio (SPR) at their corresponding whorl height in specimens of *Cyclolituites* Remelé, 1886.

taxon	catalogue nr	wh	SDR	wh	SPR
<i>C. applanatus</i>	MB.C.11671	6.0	0.25	6.0	0.08
<i>C. lynceus</i>	MB.C.30561	11.2	0.41	11.2	0.09

the lectotype of *Cyclolituites lynceus* described by Holm (1891: pl. 1 figs 8–9) and are thus confidently assigned to this species. Only specimen MB.C.30561 is slightly more compressed.

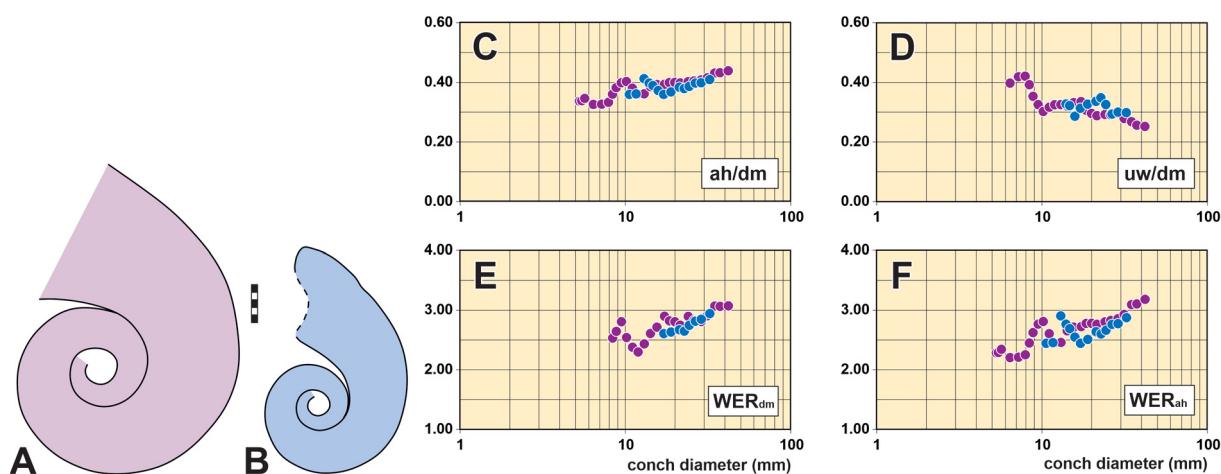
In contrast to *Cyclolituites applanatus*, the species *C. lynceus* has a larger diameter of the conch (ca 35 mm), a more compressed whorl profile (WWI = 0.70), a higher whorl expansion rate (WER ca 3.00) and a finer ornament. *Cyclolituites lynnensis* is smaller (conch diameter around 28 mm) than *C. lynceus* and has a coarser ornament. *Cyclolituites kjerulfi* differs from the other species of *Cyclolituites* in the smaller in diameter (20 mm); it uncoils much earlier (almost the whole last whorl is detached), has a narrower umbilical window and a much higher coiling rate (WER = 4.00–5.00).

#### Geographic and stratigraphic occurrence

Sweden (in situ) and northern Germany (in erratics within Pleistocene gravels); late Lasnamägi Regional Stage (late Darriwilian, Middle Ordovician).

#### Discussion

Cephalopods of the order Lituitida are among the most distinctive components of Ordovician fossil assemblages, especially from Northern Europe and China. At the same time, however, they are also one of those cephalopod groups where the clear identification and delimitation of species is a challenge. Most taxa were already described in the 19<sup>th</sup> century (e.g., Boll 1857; Angelin 1880; Dewitz 1880; Remelé 1880, 1882, 1890; Holm 1891; Hyatt 1894), but thereafter research interest declined and only



**Fig. 74.** *Cyclolituites lynceus* Holm, 1891. **A.** Coiling outline of specimen MB.C.30561. **B.** Coiling outline of specimen MB.C.30562. **C–F.** Conch proportions and coiling rates of the specimens MB.C.30561 and MB.C.30562. Scale bar units = 1 mm.

a few studies have dealt with the Baltoscandian lituitids in more detail during the 20<sup>th</sup> and 21<sup>st</sup> centuries (Foerste 1930; Balashov 1953; Sweet 1958; Furnish & Glenister 1964; Dzik 1984; King 1990, 1999; Aubrechtová & Meidla 2020; Fang *et al.* 2021). The insufficient knowledge of the type material and the extensive lack of detailed analyses of lituitid morphology and its changes in ontogeny have led to the fact that the classification of the Lituitida is unresolved; many taxa are only ambiguously delimited.

In this project, we studied a collection of the Baltoscandian Lituitida from Darriwilian (Middle Ordovician) erratics in Pleistocene glacio-fluvial sediments in Germany, Poland and the Kaliningrad Region of Russia and also specimens from in-situ limestones from Sweden (including the Island of Öland), Estonia and Norway. One additional specimen from the Datianba Formation (Middle or Late Ordovician) of the Songtao County (Guizhou, South China) was identified within the collection and added to the study because of its exceptionally complete preservation.

The studied material includes type specimens of several taxa, as well as later collected but unpublished material. This allowed the re-description of several poorly known and/or vaguely defined species, including *Lituites lituus* and *L. perfectus*. These two taxa were historically the first named lituitid species, but the lack of accurate descriptions as well as information on the type material made their subsequent use in the scientific literature inconsistent. Therefore, neotypes for these two species are proposed here. In addition, the following species are newly introduced: *Holmiceras havelense* sp. nov., *Lituites baculus* sp. nov., *L. bottkei* sp. nov., *L. clavis* sp. nov., *L. dewitzi* sp. nov., *L. kruegeri* sp. nov., *L. nebeni* sp. nov., *Rhynchorthoceras kranepuhlense* sp. nov., *R. rugium* sp. nov., *Trilacinoceras filix* sp. nov. and *T. knoefleri* sp. nov.

The new results update and clarify the classification and stratigraphic occurrence of lituitid cephalopods. To facilitate the taxa definition, we investigated the ontogenetic changes in coiling parameters, chamber length and ornament. Such an approach has previously proven effective in coiled cephalopods, particularly ammonoids (e.g., Klug *et al.* 2015 and references therein) but has been used rather rarely for early Palaeozoic nautiloid and orthoceratoid cephalopods.

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## Supplementary material

**Supp. file 1.** List of specimens investigated in this study. <https://doi.org/10.5852/ejt.2022.799.1681.6157>

**Supp. file 2.** Complete measurements table of the specimens investigated in this study.

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