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The coiled Middle Ordovician cephalopod genera *Trocholites* and *Curtoceras* (Tarphyceratida) from Baltoscandia and north-central Europe

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Abstract. The family Trocholitidae comprises a diverse group of Middle to Late Ordovician coiled cephalopods known from numerous finds in Baltoscandia and from glacial erratics in the Baltic Sea region. However, most descriptions of these forms date back more than a hundred years. Here we describe 83 specimens of the genera *Trocholites* and *Curtoceras* (family Trocholitidae). They were collected from boulders in Pleistocene glacio-fluvial sediments in Germany and Poland, as well as from in-situ strata in Sweden and Estonia. Sixteen species of *Trocholites* and two species of *Curtoceras* are identified; twelve species are new: *Trocholites baldri* sp. nov., *T. freyjae* sp. nov., *T. glacialis* sp. nov., *T. kadakaensis* sp. nov., *T. luna* sp. nov., *T. splendor* sp. nov., *T. triangulus* sp. nov., *T. tureki* sp. nov., *T. vodickai* sp. nov., *T. vortex* sp. nov., *T. zaryensis* sp. nov. and *Curtoceras meyeri* sp. nov. The diagnoses of previously described taxa are revised by incorporating information on ontogenetic changes, ontogenetic trajectories and variation of morphological characters. The three species of *Trocholites* established by Eichwald (1840), *T. odini*, *T. incongruus* and *T. depressus*, are synonymised and the latter name is retained based on priority. Neotypes are proposed for *Trocholites depressus*, *T. macrostoma* and *T. contractus*. *Curtoceras estonicum* Balashov, 1953 is synonymised with *C. teres*. *Trocholites macromphalus* Schröder, 1891 and *Trocholites scoticus* Blake, 1882 are transferred to *Curtoceras*. The species names *soraviensis* and *orbis* are considered valid but are still not used in this work because the original type collection was probably destroyed during World War II and no other specimens could be reliably assigned to any of these taxa.

Keywords. Tarphyceratida, *Trocholites*, *Curtoceras*, Orthoceratite Limestone, Ordovician.

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Introduction

The early Palaeozoic order Tarphyceratida Flower, 1950 (subclass Multiceratoidea Mutvei, 2013) includes the earliest coiled cephalopods. They are characterised by small to moderately large (~ 30–150 mm adult size) gyroconic to tightly coiled conchs with tubular siphuncles. The first representatives appeared already in the Tremadocian (earliest Ordovician) on the tropical carbonate platforms of Laurentia, where they rapidly evolved from their bassleroceratid predecessors (Kröger & Landing 2008). Tarphyceratids then diversified extensively and spread to other low- and mid-latitude palaeocontinents (Kröger & Zhang 2009; Kröger 2013). Rarely, they also occurred in high palaeolatitudes (Babin & Gutiérrez-Marco 1992; Babin *et al.* 1996; Manda 2008; Sá & Gutiérrez-Marco 2009; Aubrechtová *et al.* 2023). As a result, tarphyceratids became one of the most important faunal elements influencing the character of Ordovician tropical and subtropical marine environments. However, their numbers and diversity declined by the end-Ordovician extinctions and the group finally went extinct during the latest Silurian (Manda & Turek 2018) or Middle Devonian (King & Evans 2019).

Tarphyceratids appeared on Baltica in the early Darriwilian (Middle Ordovician) with members of the family Estonioceratidae Hyatt in Zittel, 1900 (King 1999) and a single representative of the family Tarphyceratidae Hyatt, 1894 (King 1999). From the middle to late Darriwilian onwards, a third tarphyceratid family, the Trocholitidae Chapman, 1857, became dominant on Baltica. In this paper, we revise two genera of this family: *Trocholites* Conrad, 1838 and *Curtoceras* Ulrich, Foerste, Miller & Furnish, 1942. Many of species of *Trocholites* and *Curtoceras* are poorly known and ambiguous, with type collections often inadequately documented or even lost; *Trocholites* in particular became a “wastebasket” taxon. Therefore, a revision is necessary and is carried out here based on a detailed analyses of ontogenetic trajectories and variation of morphological characters. This helped to properly define the range and distribution of the species of *Trocholites* and *Curtoceras* and to differentiate them from each other and from the rest of the family Trocholitidae, namely from *Discoceras* Barrande, 1867

Historical overview

The genus *Trocholites* was erected in the first half of the 19th century in North America for cephalopods with a tightly coiled, slowly expanding conch with a long body chamber, a widened aperture, depressed whorl profile, a dorsally shifted or dorsal siphuncle and a shallow imprint zone (Conrad 1838; Hall 1847). In the 19th century, coiled cephalopods were classified mainly on the basis of the external conch morphology, and many tightly coiled forms, including some collected from Baltoscandia or glacial erratics in north-central Europe, were included in *Trocholites*. Alternatively, the species were assigned to the genera *Clymenia* Münster, 1834 and *Nautilus* Linnaeus, 1758, and *Trocholites* was thought to be related to the latter two (e.g., Remelé 1880, 1890; Blake 1882).

Schröder (1891) summarised previous studies and discussed in detail the diagnostic characters, systematic position and relationships of *Trocholites*. He considered the variation in shell ornament and the shape of the whorl profile, suture line and aperture, but also recognised the structure of the siphuncle and initial chamber. In the end, Schröder (1891) concluded that *Trocholites* is not related to *Clymenia* or *Nautilus*, but is most closely related to *Discoceras* and to forms which later became included in *Curtoceras*. Selected illustrations from the monograph by Schröder (1891) are reproduced here for easier comparison with the material studied herein (Fig. 1).

Hyatt (1894) extended the work of Schröder (1891) by including even more details of early ontogeny; he expanded the family Trocholitidae to include three new genera; *Schroederoceras* Hyatt, 1894, *Trocholitoceras* Hyatt, 1894 and *Litoceras* Hyatt, 1894. However, *Schroederoceras* was later found to be heterogeneous and the species were placed in *Discoceras* or *Curtoceras* (Strand 1933; Ulrich *et al*. 1942; Flower & Kummel 1950; Sweet 1958).

During the 20th and 21st centuries, species of *Trocholites* have been described from many places around the world, including Ireland (Holland 1993; Evans 1994), China (Chen & Liu 1974, 1976; Lai 1981; Lai & Wang 1981; Chen 1982; Chen & Zou 1984; Zhang & Chen 2002), South Korea (Kobayashi 1934) and Australia (Stait *et al.* 1985), but also from central and southern Europe. Hence, it is now known that *Trocholites* had a wide palaeogeographical distribution during the Ordovician, not only in the middle

Fig. 1. Reproductions of lithographic illustrations published by Schröder (1891). **A**. *Trocholites macrostoma* Schröder, 1882 from "Ostpreußen"; illustrated by Schröder (1891: pl. 1 fig. 1). **B**. *Trocholites contractus* Schröder, 1891 from "Rosehnen in Ostpreußen"; illustrated by Schröder (1891: pl. 1 fig. 2). **C**. "*Trocholites orbis* Schröder, 1882" from "Nasser Garten bei Königsberg"; illustrated by Schröder (1891: pl. 1 fig. 3). **D**. *Trocholites depressus* (Eichwald, 1840) from Odinsholm; illustrated by Schröder (1891: pl. 1 fig. 4). **E**. *Trocholites macromphalus* Schröder, 1891 from Odinsholm; illustrated by Schröder (1891: pl. 1 fig. 5). **F**. *Trocholites soraviensis* Schröder, 1891 from Sorau; illustrated by Schröder (1891: pl. 2 fig. 1). **G**. *Trocholites hospes* (Remelé, 1880) from Memel; illustrated by Schröder (1891: pl. 1 fig. 8). **H**. *Trocholites hospes* (Remelé, 1880) from "Nasser Garten bei Königsberg"; illustrated by Schröder (1891: pl. 1 fig. 9). **I**. "*Trocholites incongruus* (Eichwald, 1840)" from Odinsholm; illustrated by Schröder (1891: pl. 2 fig. 2). **J**. "*Trocholites incongruus* (Eichwald, 1840)" from Odinsholm; illustrated by Schröder (1891: pl. 2 fig. 3). Scale bar units = 1 mm.

or low palaeolatitudes but also in the cool-water regions (Babin & Gutiérrez-Marco 1992; Babin *et al.* 1996; Manda 2008; Sá & Gutiérrez-Marco 2009; Aubrechtová *et al.* 2023).

Ulrich *et al.* (1942) defined the genus *Curtoceras* for cephalopods with evolute, slowly expanding and adaperturally uncoiled conchs with equidimensional, weakly impressed whorl profiles. *Curtoceras* included species previously assigned to *Lituites*, *Nautilus*, *Trocholites*, *Discoceras* or *Schroederoceras*. *Curtoceras* is not as widely distributed as *Trocholites*; it is unequivocally known only from North America, Baltoscandia and Russia (Ulrich *et al.* 1942; Balashov 1953; Kröger & Landing 2009; Kröger & Aubrechtová 2018), with a probable occurrence in Great Britain (Blake 1882), Argentina (Aceñolaza *et al.* 1977) and possibly southern Tibet (Chen 1975).

Material and methods

Studied material and taphonomy

This study includes 82 specimens. The vast majority of the material examined here comes from the middle and late Darriwilian part of the Orthoceratite Limestone at localities in northern Estonia and Sweden, and from erratic boulders embedded in Pleistocene glacio-fluviatile sediments in northern Germany and Poland (Figs 2–3; Table 1). “Orthoceratite Limestone” is an informal name for a succession of condensed, cool-water carbonates that developed between the Early and early Late Ordovician in a shallow epicontinental sea on the continental margin of Baltica (Lindskog & Eriksson 2017). For a summary and further references, see also Kröger (2004, 2012), Aubrechtová & Korn (2022) and Nielsen *et al.* (2023).

The stratigraphic age of each cephalopod specimen is determined based on information on the museum labels combined with previously published literature and references therein (Balashov 1953; Neben & Krueger 1971, 1973; Ebbestad & Högström 2007; Meidla *et al.* 2014, 2023; Nielsen *et al.* 2023). Information about the specimens from the Tallinn and Tartu collections is available in the Estonian Geoscience Data Portal eMaapõu (https://geoloogia.info), which contains verified and updated information on localities, stratigraphy and references; the database is also helpful in determining the stratigraphic age of non-Estonian material.

The specimens are mostly isolated fragments of subadult or adult conchs preserved as internal moulds or with remnants of the shell wall and ornament. The specimens are not deformed and usually not corroded, but the adapertural part of the conch, including the aperture, is usually broken off.

In some specimens, the initial part of the phragmocone is preserved, such as in MB.C.646 (*Curtoceras teres*) and GIT 145-1 (*Trocholites depressus*).

The two specimens MB.C.11556 and MB.C.32162 (*T. hospes*) preserve muscle attachment impressions at the base of the body chamber. The impressions are widest dorso-laterally, consistent with previously illustrated retractor attachments in *Trocholites* (Dzik 1984). The subventral, lateral or dorso-lateral retractor attachments in certain tarphyceratids arguably originated by the migration of ventral retractors (King & Evans 2019; Pohle *et al*. 2022).

Wavy structure at the base of the body chamber associated with regularly spaced longitudinal grooves on the flanks of the specimen FMNH HS.P31459 (*Curtoceras teres*) may also represent attachment impressions. As far as the present authors are aware, this would be the first record of these structures in *Curtoceras*.

With the exception of GIT 145-1 (*T. depressus*), which was previously recognised and described by Kröger & Keupp (2004), no specimens with traces of syn-vivo shell damage or injury were found.

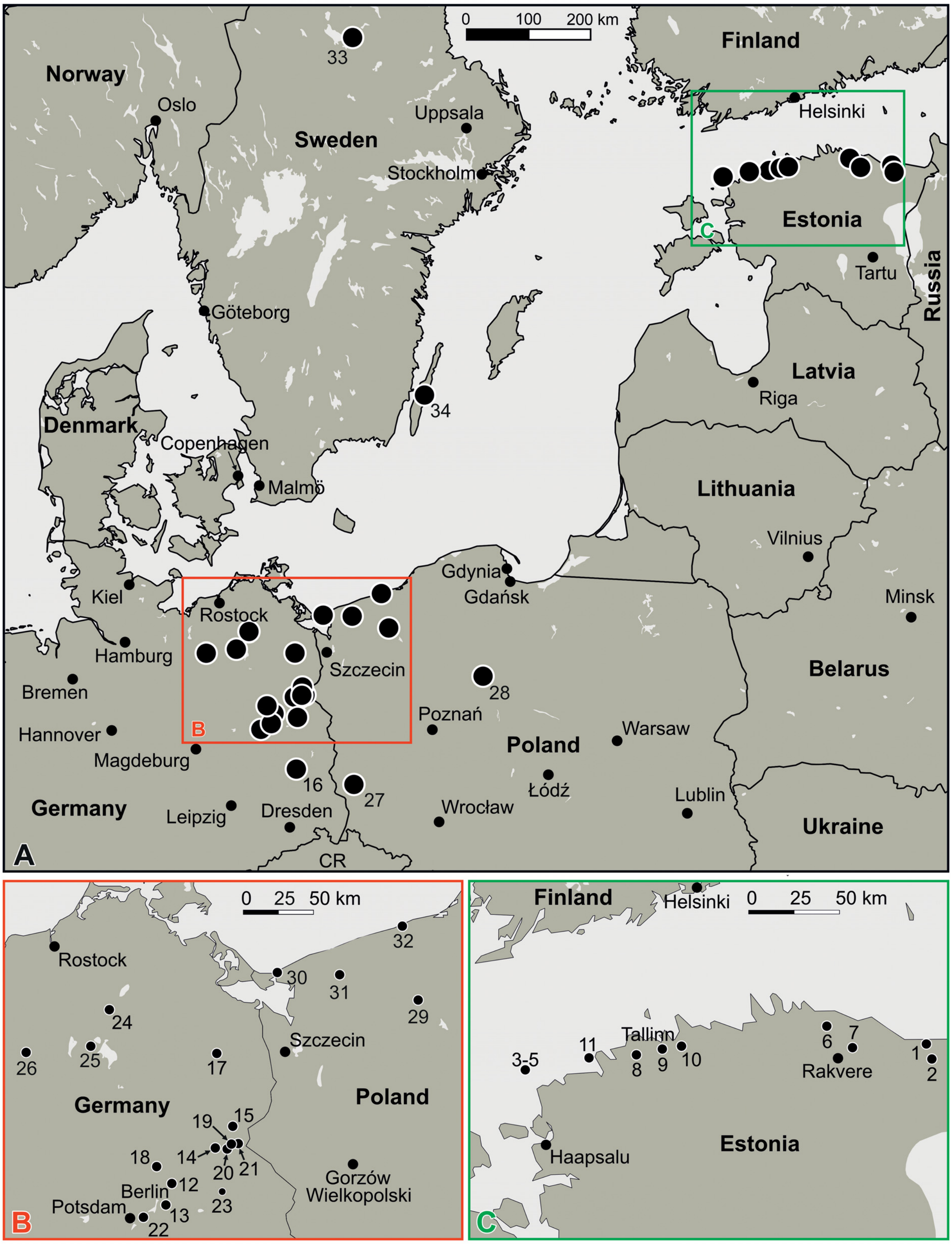

Fig. 2. **A**. Map showing localities from which the specimens studied herein originated. **B**. Localities in north-eastern Germany and western Poland. **C**. Localities in Estonia. Map prepared using the QGIS software (using the open-source World Map, OpenStreetMap and "WISE Large rivers and large lakes F1v1 geodatabase" of the European Environment Agency). Number coding of localities in Table 1.

On the flanks of the specimen GIT 362-721-2 (*T. tureki* sp. nov.), the shell has a shallow longitudinal groove or a light-coloured band that is paired on the inner whorls and wide and unpaired on the outer whorl; a similar but less well preserved structure is present also on the flanks of the specimen PMSPU 1-1128 (*T. depressus*). This structure is interpreted as the lateral furrow of Manda & Turek (2018). In addition, the specimen MB.C.32175 (*T. splendor* sp. nov.) has a thickening or ridge near the terminal aperture that we interpret as a shell growth anomaly.

Ichnofossils, epibionts and shell overgrowths are present in several specimens, such as:
GIT 145-1 (*T. depressus*), echinoderm holdfasts;
GIT 362-721-2 (*T. tureki* sp. nov.), microbioerosional trace fossil of the ichnofamily Dendrinidae Bromley *et al*., 2007;
MB.C.11550 (*C. meyeri* sp. nov.), bryozoan overgrowth;
GIT 697-328-1 (*T.* sp. indet.), ichnofossil *Oikobesalon coricaceum* Phillips, 1848;
MB.C.11563 (*T. kadakaensis* sp. nov.), borings of the ichnogenus *Trypanites* Mägdefrau, 1932 (Knaust *et al.* 2023; Vinn *et al.* 2023).

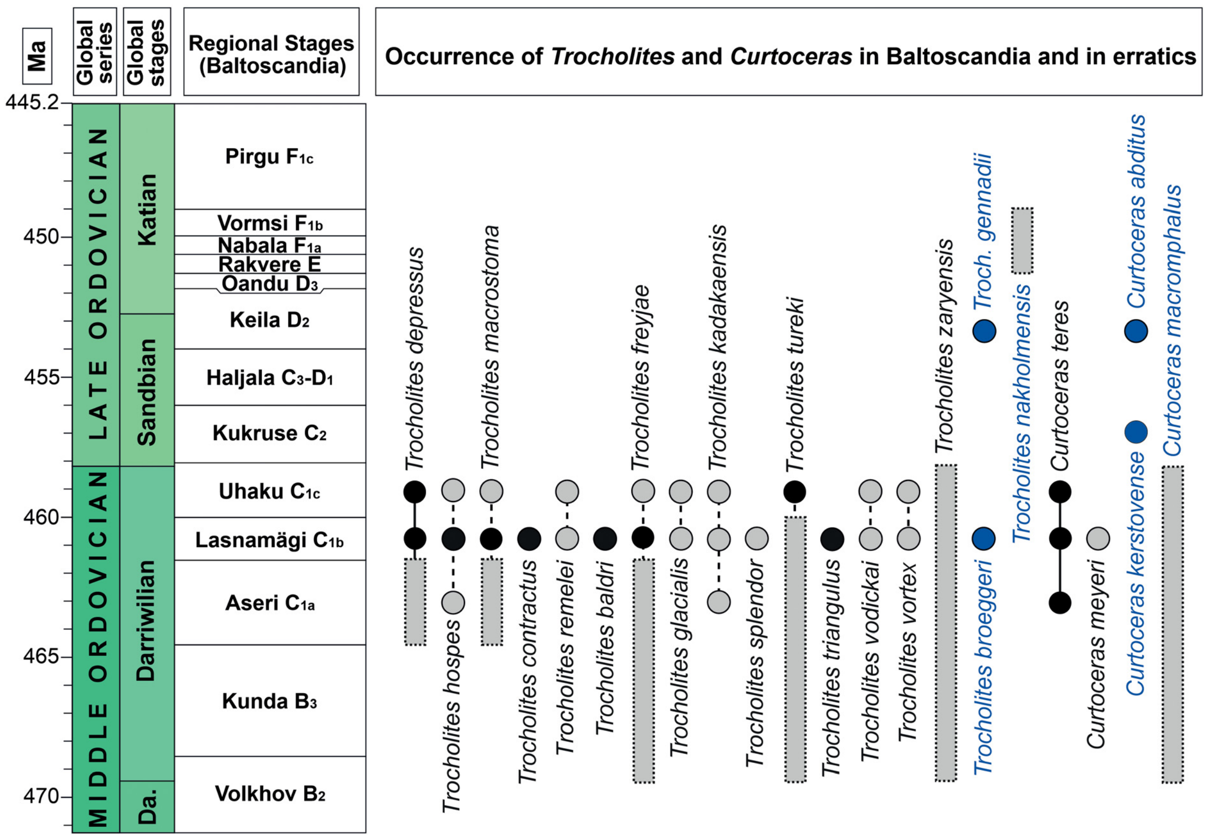

Fig. 3. Stratigraphic distribution of trocholitid taxa in Ordovician strata of Baltoscandia and in erratics; black circles indicate unambiguous presence, grey circles or rectangles indicate possible presence. Species not physically available for study here are marked in blue. Species with unknown stratigraphic occurrence are excluded from the scheme. Stratigraphic chart after Ebbestad & Högström (2007) and Meidla *et al.* (2014). Abbreviations: Da. = Dapingian; Troch. = *Trocholites*.

Table 1. Number coding of the localities shown in Fig. 2.

Coding	Country	Region	Locality
1	Estonia	Ida-Viru County	Aa
2	Estonia	Ida-Viru County	Kohtla-Nõmme
3	Estonia	Lääne County	Osmussaar 1
4	Estonia	Lääne County	Osmussaar 2
5	Estonia	Lääne County	Osmussaare cliff
6	Estonia	Lääne-Viru County	Aari quarry
7	Estonia	Lääne-Viru County	Ubja old quarry
8	Estonia	Harju County	Humala
9	Estonia	Harju County	Tallinn (Kadaka, Kadaka road)
10	Estonia	Harju County	Tallinn (Sõjamäe)
11	Estonia	Harju County	Väike-Pakri Island
12	Germany	Berlin	Lübars
13	Germany	Berlin	Schmargendorf
14	Germany	Brandenburg	Eberswalde
15	Germany	Brandenburg	Herzsprung (Uckermark)
16	Germany	Brandenburg	Hindenberg (near Calau)
17	Germany	Brandenburg	Karlstein (Neumark)
18	Germany	Brandenburg	Leegebruch (near Velten)
19	Germany	Brandenburg	Liepe
20	Germany	Brandenburg	Niederfinow
21	Germany	Brandenburg	Oderberg
22	Germany	Brandenburg	Potsdam
23	Germany	Brandenburg	Strausberg
24	Germany	Mecklenburg-Vorpommern	Basedow / Stöckersoll
25	Germany	Mecklenburg-Vorpommern	Göhren-Lebbin
26	Germany	Mecklenburg-Vorpommern	Parchim
27	Poland	Silesia	Żary
28	Poland	West Pomerania	Bydgoszcz
29	Poland	West Pomerania	Cieszeniewo
30	Poland	West Pomerania	Międzyzdroje
31	Poland	West Pomerania	Rybokarty (near Gryfice)
32	Poland	West Pomerania	Ustronie Morskie
33	Sweden	Dalarna	Altsarbyn
34	Sweden	Island of Öland	Lerkaka

Morphological terminology

The elementary morphological terminology used to describe cephalopod conchs is taken from Flower (1964) and Furnish & Glenister (1964); recently, Pohle *et al.* (2022) refined this terminology, which is followed here. In addition, to describe the suture line course and quantify the coiled conch geometry, we used parameters and ratios described in Korn & Klug (2003), Korn (2010) and Klug *et al.* (2015); these were originally defined for ammonoids but are increasingly used for non-ammonoid cephalopods. The terminology used is summarised in Fig. 4 and Table 2.

Chambers

Following Pohle *et al.* (2022), the distance of septa is expressed as the relative cameral length (RCL) and calculated as the ratio between cameral length (cl) and corresponding whorl height (wh):

$$\mathrm{RCL} = \mathrm{cl}/\mathrm{wh}$$

Siphuncle

The diameter of the siphuncle is described by the relative septal foramen height, RSH (Pohle *et al.* 2022), and calculated as the septal foramen height (fh) over the corresponding apertural height (ah):

$$\mathrm{RSH} = \mathrm{fh}/\mathrm{ah}$$

The position of the siphuncle is expressed as the relative septal foramen position, RSP (Pohle *et al.* 2022), and is calculated from the distance of the septal foramen from the ventral shell wall (sv), the apertural height (ah) and the septal foramen height (fh):

$$\mathrm{RSP} = \mathrm{sv}/(\mathrm{ah}-\mathrm{fh})$$

In contrast to Pohle *et al.* (2022), we use the apertural height (i.e., the distance between ventral sides of two successive whorls or smallest dorso-ventral height of the whorl profile) instead of the whorl height (i.e., the greatest dorso-ventral height of the whorl profile, Fig. 4) in the above formulae. The reason for this is that the use of whorl height results in an apparently narrower (i.e., artificially lower RSH) and more central (i.e., artificially lower RSP) siphuncle in specimens with a dorsal imprint zone, such as those of *Trocholites hospes*.

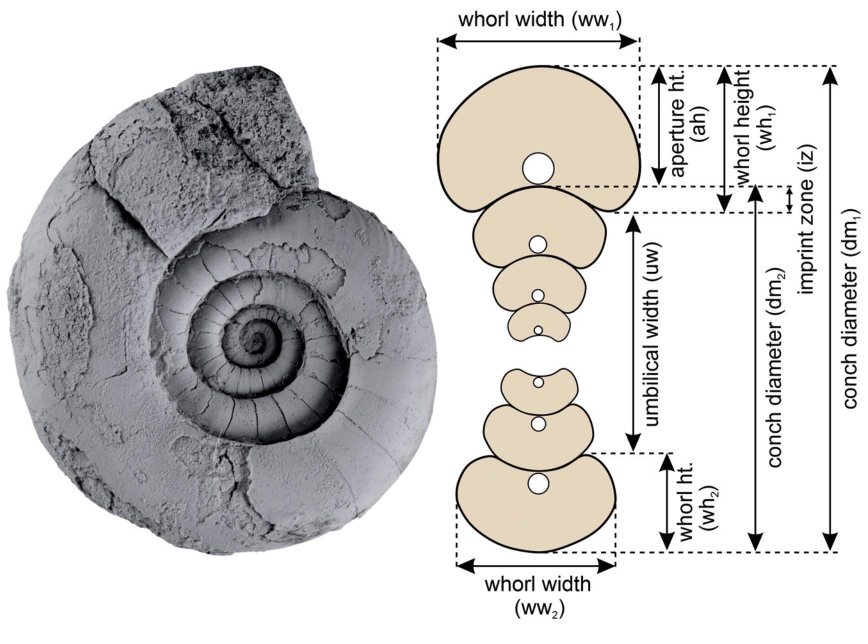

Fig. 4. Morphological terminology used in this study to describe trocholitid specimens (left: holotype of *Trocholites vortex* sp. nov., MB.C. 22574; right: cross-section reconstruction based on TUG 1351-14 of *T. depressus* Eichwald, 1840).

Table 2. Parameters and ratios used for the description of the tarphyceratid specimens studied herein.

Parameter [unit]	Abbrev.	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	dm_1-dm_2
imprint zone [mm]	iz	wh_1-ah
whorl expansion rate (outline)	WERdm	$(dm_1/dm_2)^2$
whorl expansion rate (apertural height)	WERah	$[dm_1/(dm_1-ah)]^2$
imprint zone rate	IZR	iz/wh
umbilical width index	UWI	uw/dm
conch width index	CWI	ww/dm
whorl width index	WWI	ww/wh

Ornament

The terminology of shell ornament follows (Kröger 2008), Klug *et al.* (2015) and Pohle *et al.* (2022). In the specimens examined here, the following ornamental elements are distinguished:

growth lines – represent the finest type of transverse ornament; formed by discontinuous shell secretion at the aperture (Klug *et al.* 2015);

lirae – transverse raised growth lines with transverse profile either symmetric or asymmetric, may be more or less narrowly undulated (frilled);

ribs – coarse transverse elements, which are limited to a certain part of conch circumference (typically flanks) and do not leave any traces on internal mould;

annuli – coarse transverse ornament elements, which are present around the whole circumference of the conch and are visible on internal mould; where annuli-like structures are visible on the internal mould but not on the shell surface, or where the shell surface is not present, the terms annular ridges or annular impressions are used;

spiral lines – longitudinal elements of ornament.

The general direction of transverse ornament elements is distinguished in the following manner:

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

Repositories

FMNH = Finnish Museum of Natural History, Helsinki, Finland
GIT = Tallinn University of Technology, Tallinn, Estonia
MB.C. = Museum für Naturkunde, Berlin, Germany
NM-S = National Museum, Prague, Czech Republic
NRM Mo = Swedish Museum of Natural History, Stockholm, Sweden
PMSPU = St Petersburg State University, St Petersburg, Russia
TAM = Estonian Museum of Natural History, Tallinn, Estonia
TUG = Museum of Natural History of the University of Tartu, Tartu, Estonia

Results

Class Cephalopoda Cuvier, 1797
Subclass Multiceratoidea Mutvei, 2013

Order **Tarphyceratida** Flower, 1950

Diagnosis (compiled after Furnish & Glenister 1964; Frey 1995; emended)

Multiceratoid cephalopods with coiled to gyroconic conchs of various whorl profile and simple transverse or slightly curved suture lines. Coiling planispiral, rarely torticonic; body chambers usually long, extending from a half to more than one complete whorl in length. Last whorl commonly slightly to greatly divergent from preceding coiled portions; terminal aperture commonly modified. Siphuncle varies in position; siphuncular segments more or less tubular, nautilosiphonate, with orthochoanitic or loxochoanitic septal necks and thick connecting rings in stratigraphically earlier forms, and cyrtochoanitic septal necks and thin homogeneous rings in stratigraphically later forms. Muscle attachment scars ventromyarian or sometimes pleuromyarian. Thin cameral deposits present in some taxa. Shell surface smooth or ornamented with transverse lirae, ribs or annuli, or spiral ornament elements.

Families included

Barrandeoceratidae Foerste, 1925; Estonioceratidae Hyatt in Zittel, 1900; Ophioceratidae Hyatt, 1894; Plectoceratidae Hyatt in Zittel, 1900; Tarphyceratidae Hyatt, 1894; Trocholitidae Chapman, 1857.

Remarks

The combined diagnosis of Furnish & Glenister (1964) and Frey (1995) is expanded here to include the presence of pleuromyarian muscle attachment scars (e.g., Dzik 1984; King & Evans 2019) and cameral deposits (Ulrich *et al*. 1942; Manda & Turek 2018) and the character of shell ornament.

Family **Trocholitidae** Chapman, 1857

Diagnosis (after Furnish & Glenister 1964; Frey 1995; emended)

Family of the order Tarphyceratida with subglobular to discoidal conchs consisting of three to five or more gradually expanding volutions; body chamber may uncoil from preceding volution. Terminal aperture of body chamber with flares in some taxa, aperture often modified with ventral sinus and lateral projections. Whorl profile usually impressed dorsally; usually depressed except for the adult growth stage that may have an equidimensional or compressed whorl profile; flanks and venter broadly rounded or flattened. Shell ornament varies during ontogeny, usually consisting of imbricating and / or frilled lirae, ribs or annuli, but taxa with smooth shell surface exist; ornament elements form ventral sinus. Conch in some taxa with periodic constrictions. Phragmocone chambers short (on average six phragmocone chambers relative to whorl height). Suture line simple with shallow ventral lobe or rarely saddle. Siphuncle subcentral, subdorsal or marginodorsal in position, ventral to central in initial volution; siphuncle segments tubular, weakly convex or weakly concavo-convex, narrow in diameter (usually less than 0.25 of apertural height); septal necks short (less than 0.20 of segment length), orthochoanitic or loxochoanitic; connecting rings usually thick, layered, but becoming thin and homogeneous in some taxa.

Genera included

Arkoceras Ulrich, Foerste, Miller & Furnish, 1942; *Crenuloceras* Flower, 1968; *Curtoceras* Ulrich, Foerste, Miller & Furnish 1942; *Discoceras* Barrande, 1867; *Hardmanoceras* Teichert & Glenister, 1952; *Jasperoceras* Ulrich, Foerste, Miller & Furnish, 1942; *Litoceras* Hyatt, 1884; *Paradiscoceras* Barskov, 1972; *Plectolites* Flower, 1968; *Trocholites* Conrad, 1838;

Trocholitoceras Hyatt, 1894; *Weberoceras* Barskov, 1972; *Wichitoceras* Ulrich, Foerste, Miller & Furnish, 1942; *Yushanoceras* Chen & Liu, 1976.

Remarks

Chapman (1857) must be regarded as the correct author of the family name. Trocholitidae Schröder, 1891 is an objective junior synonym.

The diagnosis compiled from Furnish & Glenister (1964) and Frey (1995) is rephrased and modified to reflect results of the revision of *Trocholites* and *Curtoceras* performed herein. The added details concern the shape of the terminal aperture, whorl profile, shape of connecting rings and shape of septal necks.

Genus ***Trocholites*** Conrad, 1838

Type species

Trocholites ammonius Conrad, 1838; by original designation.

Diagnosis (after Frey 1995; Kröger & Aubrechtová 2018; emended)

Genus of the family Trocholitidae with adult conch diameters of generally less than 100 mm, five or more volutions. Conch discoidal or pachyconic (CWI = 0.30–0.80) with moderately wide to very wide umbilicus (UWI = 0.30–0.60) and low or moderate whorl expansion (WER = 1.50–2.00). Body chamber 0.50–0.75 of a volution in length; not uncoiling from the preceding whorl. Whorl profile weakly to strongly depressed (WWI = 1.20–2.20), broadly reniform, weakly to strongly impressed dorsally (IZR up to 0.45), broadly rounded across venter and flanks. Aperture commonly flared with ventral sinus and ventrolateral extensions. Siphuncular diameter 0.16–0.30 of the whorl height, marginodorsal or subdorsal in position in all growth stages; septal necks short (< 0.20 of chamber height), orthochoanitic and / or loxochoanitic in shape. Ornament composed of growth lines and lirae, less commonly of narrow annuli or ribs; ornament elements extended into ventral sinus. Suture line straight or with shallow lobes.

Species included

North America (Conrad 1838; Miller & Dyer 1878; Hyatt 1894; Ruedemann 1926; Foerste 1930; Flower 1943): *Trocholites ammonius* Conrad, 1838; *T. canadensis* Hyatt, 1894; *T. circularis* Miller & Dyer, 1878; *T. dyeri* Hyatt, 1894; *T. faberi* Foerste, 1930; *T. gracilis* Flower, 1943; *T. major* Ruedemann, 1926; *T. minusculus* Miller & Dyer, 1878; *T. planorbiformis* Conrad, 1838; *T. ruedemanni* Flower, 1943.

Great Britain (Hyatt 1894): *Trocholites blakei* Hyatt, 1894.

North Europe and St Petersburg Region of Russia (Eichwald 1840; Kjerulf 1865; Remelé 1880; Schröder 1882, 1891; Foerste 1932; Kröger & Aubrechtová 2018; this paper): *Trocholites baldri* sp. nov.; *Palaeonautilus broeggeri* Foerste, 1932; *T. contractus* Schröder, 1891; *Nautilus depressus* Eichwald, 1840; *T. freyjae* sp. nov.; *T. gennadii* Kröger & Aubrechtová, 2018; *T. glacialis* sp. nov.; *P. hospes* Remelé, 1880; *T. kadakaensis* sp. nov.; *T. luna* sp. nov.; *T. macrostoma* Schröder, 1882; *Lituites nakholmensis* Kjerulf, 1865; *T. remélei* Schröder, 1891; *T. splendor* sp. nov.; *T. tureki* sp. nov.; *T. triangulus* sp. nov.; *T. vodickai* sp. nov.; *T. vortex* sp. nov.; *T. zaryensis* sp. nov.

South and Central Europe (Babin & Gutiérrez-Marco 1992; Aubrechtová *et al.* 2023): *Trocholites fugax* Babin & Gutiérrez Marco, 1992; *T. chaloupkai* Aubrechtová *et al*., 2023.

South Korea (Kobayashi 1934): *Trocholites ammonioides* Kobayashi, 1934.

China (Frech 1911; Chen & Liu 1974, 1976; Lai 1981; Lai & Wang 1981; Gao *et al.* 1982; Chen & Zou 1984; Guo 1998): *Palaeonautilus hubeiensis* Chen & Liu, 1974; *Trocholites huanxianese* Chen in Gao, Lai & Wen, 1982; *T. jiangxiense* Lai, 1981; *T. lativentrosus* Lai & Wang, 1981; *T. mirabilis* Lai & Wang, 1981; *T. wuhaiensis* Chen in Chen & Zou, 1984; *T. xiazhenensis* Chen & Liu, 1976; *T. yushanensis* Lai, 1981; *T. yunnanensis* Reed, 1917; *T. zhejiangense* Lai, 1981.

Australia (Stait *et al.* 1985): *Trocholites costatum* Stait *et al.*1985.

Remarks

Representatives of the genus *Trocholites* are usually rather small with only 20 to 60 mm conch diameter in the terminal growth stage. They possess evolute or subevolute conchs and have a distinctly depressed whorl profile; the whorl profile possesses a small dorsal imprint zone. The terminal body chamber does not deviate from the preceding whorl, but often has an aperture with ventral and lateral flares.

Trocholites is similar to *Curtoceras* and both genera may be confused under certain circumstances. The conch in *Curtoceras* is more discoidal (CWI = 0.30–0.40) and the whorl profile is weakly depressed or nearly equidimensional (WWI = 1.00–1.50). The terminal body chamber uncoils from the preceding whorl at least in some species of *Curtoceras*. However, there are species with transitional morphology that are difficult to assign to one genus or the other, especially if the adult growth stage is not known.

Discoceras is distinguished from *Trocholites* by the much greater adult conch size (usually exceeding 100 mm) and coarser shell ornament with elements that are characteristically frilled and imbricate; the siphuncle in the species of *Discoceras* is usually not marginal in position. In adult growth stages of *Discoceras*, the conch is more discoidal (CWI < 0.35) and the whorls are usually only weakly embracing. The whorl profile in *Discoceras* is very variable between species and during ontogeny. It is usually weakly depressed in earlier stages of growth (WWI = 1.00–1.50), but becomes equidimensional or compressed during ontogeny (WWI = 0.50–1.00). In some species of *Discoceras*, the whorl profile is oval or circular, while in others it is subrectangular, subquadratic, trapezoidal or heart-shaped. In many species of *Discoceras*, the last volution uncoils from the preceding whorl to varying degrees.

Schröder (1882, 1891) discussed or established several species of *Trocholites*, most of which could be reliably identified in the collection currently studied. Only three species remain problematic: *T. orbis*, *T. macromphalus* and *T. soraviensis*.

Trocholites orbis, according to its original description, is very similar to *T. depressus* and differs from this species only in being somewhat more discoidal and lacking strong ribs on the shell surface. Unfortunately, *T. orbis* is only known from the original description and illustration of the holotype (Schröder 1891: pl. 1(24) fig. 3; see also Fig. 1C herein). This specimen originated from an Ordovician erratic boulder at "Nasser Garten bei Königsberg" (present day Portowoje, south of Kaliningrad, Russia) and belonged to the collection of the "Provinzial-Museum zu Königsberg i. Pr." (Regional Museum of Königsberg in Prussia), which was most probably destroyed during World War II (pers. com. D. Weyer, Berlin, 2022). The species has never been revised and the only two other specimens assigned to it by Neben & Krueger (1971) and Dzik (1984) probably belong to *T. depressus*. From the collection at hand, we could not unequivocally assign any specimens to the species *T. orbis*. The available information on the (probably lost) type material do not permit further comparison of *T. orbis* with *T. depressus* or any other species of the genus.

Trocholites macromphalus is known only from the holotype (Schröder 1891: pl. 1(24) fig. 5; see also Fig. 1E herein). It originated from Darriwilian strata of the Estonian island of Osmussaar and was said to be deposited at the "Museum der Akademie der Wissenschaften zu St. Petersburg" (Museum of the

Academy of Sciences of St Petersburg). The holotype was never re-examined and its current location and status could not be confirmed. In the currently examined collection, some specimens of *Curtoceras teres* are most similar based on the original description and illustration. However, since Schröder (1891) noted that the holotype had a dorsal siphuncle and ribs on internal whorls, the species is transferred to *Curtoceras* but not synonymised with *C. teres*.

The holotype of *Trocholites soraviensis* originated from an Ordovician erratic boulder at Żory (Poland) and was included in the "Sammlung der Kgl. geologischen Landesanstalt und Bergakademie zu Berlin" (Collection of the Royal Geological Survey and Mining Academy of Berlin). After its description by Schröder (1891), it has never been restudied and remains the only unequivocal representative of the species. The holotype (Schröder 1891: pl. 2 fig. 1; see also Fig. 1F herein) is most similar to specimens herein assigned to *Trocholites freyjae* sp. nov., *T. baldri* sp. nov. and *T. glacialis* sp. nov. However, reliable comparison is not possible based on the available information. The present location of the holotype is unknown and it is possible that it was destroyed during World War II. This cannot be confirmed, though, and thus, neotype designation and comparison to representatives of other species of *Trocholites* is avoided.

Some species of *Trocholites* recorded from various regions of China, especially *T. huanxianese*, *T. yunnanensis* and *T. xiazhenensis*, may in fact belong to *Curtoceras* or *Discoceras*, but the currently available data do not allow a reliable taxonomic assignment.

The holotype of the Ordovician species *Trocholites zhuozishanensis* described by Guo (1998) from Inner Mongolia (northern China) has ventrally shifted siphuncle and thus should not be assigned to *Trocholites* or any other genus of the family Trocholitidae.

Trocholites lativentrosus from the Sandbian Kanling Formation of the Tarim Basin of north-west China appears to resemble some species studied here (*Trocholites freyjae* sp. nov., *T. baldri* sp. nov. and *T. glacialis* sp. nov.) in conch geometry, especially whorl profile shape and impression rate, but information available on the type material is not sufficient to make reliable comparisons and draw conclusions regarding possible synonymy.

Myagkova (1955) reported the occurrence of the type species *Trocholites ammonius* from Middle Ordovician strata of the Middle Urals of Russia. However, the illustration and description suggest that the specimen should rather be assigned to a species of *Curtoceras* or possibly *Discoceras*; the type species is thus only unequivocally known from North America.

The late Darriwilian species *Trocholites scoticus* from Great Britain is transferred to *Curtoceras* because the two type specimens of Blake (1882) reportedly have only weakly depressed whorl profile and the body chamber in the holotype is adaperturally uncoiled.

Geographic and stratigraphic occurrence

North America, Europe, St Petersburg Region of Russia, China, South Korea, Australia, Middle–Late Ordovician; Great Britain, Llandovery Series (early Silurian).

Trocholites depressus (Eichwald, 1840)
Figs 1D, I, 5–7; Table 3

Nautilus depressus Eichwald, 1840: 106.
Clymenia incongrua Eichwald, 1840: 108.
Clymenia Odini Eichwald, 1840: 107.

Clymenia depressa – Eichwald 1860: 1305, pl. 50 fig. 5.
Clymenia incongrua – Eichwald 1860: 1306, pl. 50 fig. 7.
Clymenia Odini – Eichwald 1860: 1304, pl. 51 fig. 27.
Palaeonautilus depressus – Remelé 1880: 246; 1890: 37.
Palaeonautilus incongruus – Remelé 1880: 247.
? *Trocholites depressus* – Rüdiger 1889: 48. — Sweet 1958: 93, pl. 7 figs 3–7, text-fig. 12. — Chen 1987: 173, pl. 7 figs 7–9, text-fig. 35.
Trocholites depressus – Schröder 1891: 13(151), pl. 1(24) figs 4, 7. — Balashov 1953: 242, pl. 7 fig. 2. — Kröger & Keupp 2004: text-fig. 1.
? *Trocholites incongruus* – Schröder 1891: 154, pl. 2(25) figs 3–4.
Trocholites incongruus – Schröder 1891: 153, pl. 2(25) fig. 2. — Balashov 1953: 240, pl. 7 fig. 1; 1962: pl. 9 fig. 6; 1974: pl. 9 fig. 6.
Trocholites cf. *orbis* – Schröder 1891: 13(151), pl. 1(24) fig. 6.
Trocholites Odini – Foord 1891: 50. — Schröder 1891: 13(151). — Balashov 1953: 243, pl. 7 fig. 3.
Trocholites orbis – Neben & Krueger 1971: pl. 32 figs 10–11. — Dzik 1984: pl. 6 fig. 3.
? *Trocholites* cf. *incongruus* – Neben & Krueger 1971: pl. 32 figs 8–9.
? *Trocholites soraviensis* – Neben & Krueger 1973: pl. 81 figs 10–11.
? *Trocholites orbis* – Dzik 1984: pl. 6 fig. 2.
? *Trocholites* cf. *depressus* – Babin & Gutiérrez-Marco 1992: 524, 534, text-fig. 4g.

non *Trocholites incongruus* – Angelin 1880: 11, pl. 9 figs 15–18.
non *Trocholites* cf. *incongruus* – Rüdiger 1889: 48.

Diagnosis

Species of the genus *Trocholites* with an adult conch diameter of 30–40 mm. Conch in the last whorl thinly discoidal (CWI = 0.35–0.40) and evolute (UWI ~ 0.50) with low coiling rate (WER ~ 1.65). Whorl profile weakly to moderately depressed (WWI = 1.25–1.60) with rounded flanks and slightly flattened venter in the adult stage. Whorl width slightly increasing, whorl height slightly decreasing in last quarter volution. Phragmocone chambers moderately long (RCL = 0.30–0.40). Suture line nearly straight. Ornament on inner whorls with lirae and narrow or distinct ribs, and on outer whorl with raised lirae, sometimes with annular ridges visible on the internal mould.

Type material

Neotype (designated here)
ESTONIA • Odinsholm (= Osmussaar); Lasnamägi Regional Stage, late Darriwilian; Eichwald Coll.; illustrated by Eichwald (1860: pl. 50 fig. 5), Schröder (1891: pl. 1(24) fig. 4) and Balashov (1953: pl. 7 fig. 2), re-illustrated here in Fig. 5A; PMSPU 1-1128.

Additional material

ESTONIA • 1 spec.; Osmussaar; Darriwilian Stage; 1876; Dames Coll.; illustrated by Schröder (1891: pl. 1 fig. 7), re-illustrated here in Fig. 6F; MB.C.9719 • 1 spec.; Osmussaar 1; Lasnamägi Regional Stage; illustrated in Fig. 5B; TUG 1351-14 • 1 spec.; Osmussaar; Lasnamägi Regional Stage; Schmidt Coll.; illustrated in Fig. 6G; GIT 225-1074 • 1 spec.; Osmussaar 1; Uhaku Regional Stage; illustrated in Fig. 6A; GIT 697-129 • 2 specs; Osmussaar 2; Uhaku Regional Stage; Männil Coll.; illustrated in Fig. 6C; GIT 697-410 • 1 spec.; Osmussaar 2; Uhaku Regional Stage; Männil Coll.; GIT 697-404-1 • 1 spec.; Osmussaar; probably Darriwilian Stage; TAM G432:787 • 1 spec.; Osmussaar cliff; probably Darriwilian Stage; 1985; Männil Coll.; illustrated in Fig. 6B; GIT 697-535 • 1 spec.; Väike-Pakri Island; Lasnamägi Regional Stage; Orviku Coll.; illustrated in Fig. 5C; GIT 145-1 • 1 spec.; Tallinn; Lasnamägi Regional Stage; TUG 2-721 • 1 spec.; Odinsholm (= Osmussaar); Lasnamägi Regional

Stage, late Darriwilian; Eichwald Coll.; illustrated by Eichwald (1860: pl. 51 fig. 27), Schröder (1891: pl. 1(24) fig. 6) and Balashov (1953: pl. 7 fig. 3), re-illustrated here in Fig. 5D; PMSPU 1-1127 • 1 spec.; Odinsholm (= Osmussaar); Lasnamägi Regional Stage, late Darriwilian; Eichwald Coll.; illustrated by Eichwald (1860: pl. 50 fig. 7a), Schröder (1891: pl. 2(25) fig. 2) and Balashov (1953: pl. 7 fig. 1a, c); PMSPU 1-1129 • 1 spec.; Odinsholm (= Osmussaar); Lasnamägi Regional Stage, late Darriwilian; Eichwald Coll.; illustrated by Balashov (1953: pl. 7 fig. 1b); PMSPU 1-2622.

GERMANY – **Brandenburg** • 1 spec.; Niederfinow; Ordovician; Neben and Krueger Coll.; illustrated in Fig. 6D; MB.C.32160. – **Mecklenburg-Vorpommern** • 1 spec.; Lebbin; Lasnamägi Regional Stage; Neben and Krueger Coll.; illustrated by Neben & Krueger (1971: pl. 32 figs 10–11), re-illustrated here in Fig. 6E; MB.C.32161.

Description

Neotype PMSPU 1-1128 (Fig. 5A) is a nearly complete conch with 3.5 volutions preserved. The diameter of the conch is 36 mm; the body chamber is 240 degrees long and the aperture has a ventral sinus, ventrolateral extension and dorsolateral sinus. In the last 90 degrees, the conch is discoidal (CWI ~ 0.40) and widely umbilicate (UWI increases slightly from 0.46 to 0.48); the whorl profile is evenly convex from the venter to the flanks and increasingly depressed (WWI increases from 1.36 to 1.48). Ornament is only locally preserved; it consists of fine lirae, which are accompanied by narrow but distinct ribs on inner whorls. The phragmocone chambers are moderately long (RCL = 0.31); the suture line is straight.

Specimen MB.C.32160 (Fig. 6D) is an almost complete adult specimen with a conch diameter of 29 mm. The length of the body chamber is half a volution; its terminal apertural end has a ventral extension and thus produces a pronounced ventral sinus. Within the last half volution, the conch becomes progressively discoidal (CWI decreases from 0.44 to 0.38) and remains evolute (UWI rises weakly from 0.50 to 0.52) with a low coiling rate (WER = 1.64). The largest whorl is moderately depressed (WWI = 1.58) and weakly embracing (IZR = 0.09). The shell is only preserved in inner whorls, where there are distinct, smooth ribs and lirae; the internal mould of the adult body chamber has annular grooves that extend with a ventral sinus and a single more prominent impression near the beginning of the body chamber. The phragmocone chambers are moderately long (RCL = 0.30); the suture line is more or less straight.

Specimen MB.C.32161 (Fig. 6E) is an almost complete, well-preserved conch of an adult individual with 29 mm conch diameter. The length of the body chamber is half a volution; the terminal aperture extends into a ventral sinus. In the last half volution, the conch is increasingly discoidal (CWI decreases from 0.41 to 0.33), increasingly evolute (UWI increases slightly from 0.44 to 0.48) and moderately expanding (WER = 1.77). The whorl profile is weakly depressed (WWI decreases from 1.31 to 1.21) and weakly impressed dorsally (IZR = 0.10) with a broadly rounded venter and rounded flanks. The shell wall of the inner whorls is ornamented with unevenly spaced thin ribs and lirae; in the outer whorl, the ribs fade out and are replaced by raised lirae. There are annular impressions present on the internal mould of the terminal body chamber. The ornament elements extend straight across the flank and turn to form a deep ventral sinus. In the outer whorl, the phragmocone chambers are short or moderately long (RCL varies between 0.17 and 0.23). The suture line is nearly straight.

Specimen PMSPU 1-1127 (Fig. 5D) is a conch of 31 mm diameter, consisting of nearly five whorls; the last ~ 35 degrees of the conch belong to the body chamber. The initial volution of the phragmocone is preserved, the initial chamber is present, the umbilical window is ~ 0.25 mm across. In the last 90 degrees of the last whorl, the conch is widely umbilicate (UWI ~ 0.46). Ornament is poorly preserved but transverse elements are indicated locally on the surface. Phragmocone chambers are moderately long (RCL up to ~ 0.40); suture line is almost straight.

Specimen GIT 697-129 (Fig. 6A) has a conch diameter of 34 mm; the specimen possesses 5.25 whorls and is nearly complete. Only the aperture of the body chamber is missing. At a diameter of 30 mm, the conch is thinly discoidal (CWI = 0.39) and evolute (UWI = 0.49). The whorl profile is weakly depressed in the last whorl (WWI decreases from 1.43 to 1.35) with broadly rounded flanks and venter. The ornament consists of evenly spaced lirae, which are irregularly raised and form groups of more widely spaced, rib-like elements (0.5–1.0 mm apart in inner whorls). The phragmocone chambers are rather long (RCL = 0.40 at wh = 7 mm); the suture line is almost straight.

Specimen GIT 145-1 (Fig. 5C) is a median longitudinal section of an essentially complete conch with a maximum diameter of 40 mm, consisting of six volutions. During ontogeny, the coiling rate generally decreases from WER = 2.70 to WER = 1.70. The siphuncle remains marginodorsal (RSP = 1.00) and is relatively wide (RSH between 0.26 and 0.32). The septal necks are short and loxochoanitic, sometimes the brims are thickened. The connecting rings are thin with a deposit-like structure on the side facing the

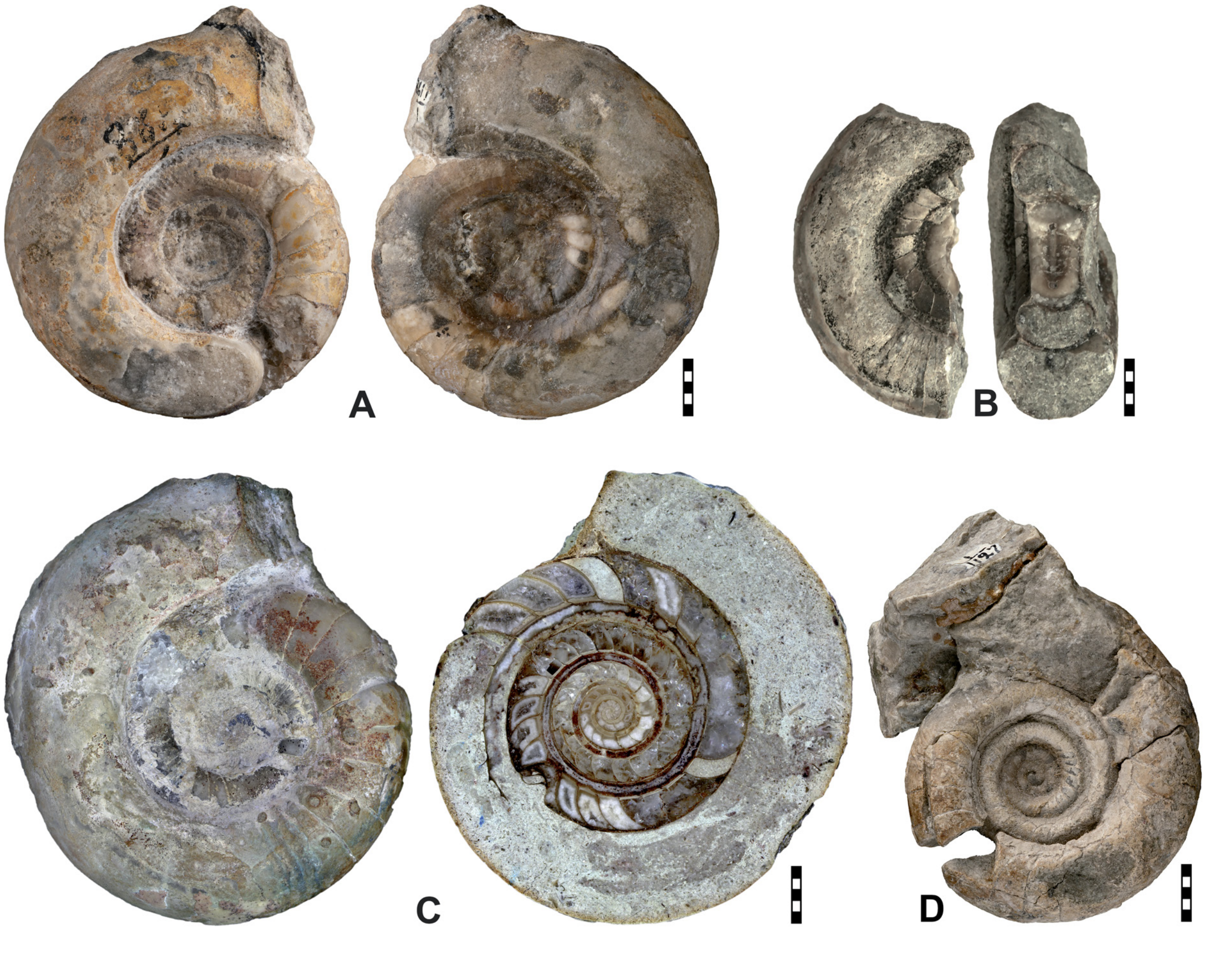

Fig. 5. *Trocholites depressus* (Eichwald, 1840). **A**. Neotype PMSPU 1-1128 (Eichwald Coll.) from “Odinsholm” (= Osmussaar) (Estonia); previously figured by Eichwald (1860: pl. 50 fig. 5), Schröder (1891: pl. 1(24) fig. 4) and Balashov (1953: pl. 7 fig. 2); lateral views. **B**. Specimen TUG 1351-14 from Osmussaar (Estonia); lateral and cross sectional views. **C**. Specimen GIT 145-1 (Orviku Coll.) from Väike-Pakri Island (Estonia); lateral and sagittal sectional views. **D**. Specimen PMSPU 1-1127 (Eichwald Coll.) from “Odinsholm” (= Osmussaar) (Estonia); previously figured by Eichwald (1860: pl. 51 fig. 27), Schröder (1891: pl. 1(24) fig. 6) and Balashov (1953: pl. 7 fig. 3); lateral views. Scale bar units = 1 mm.

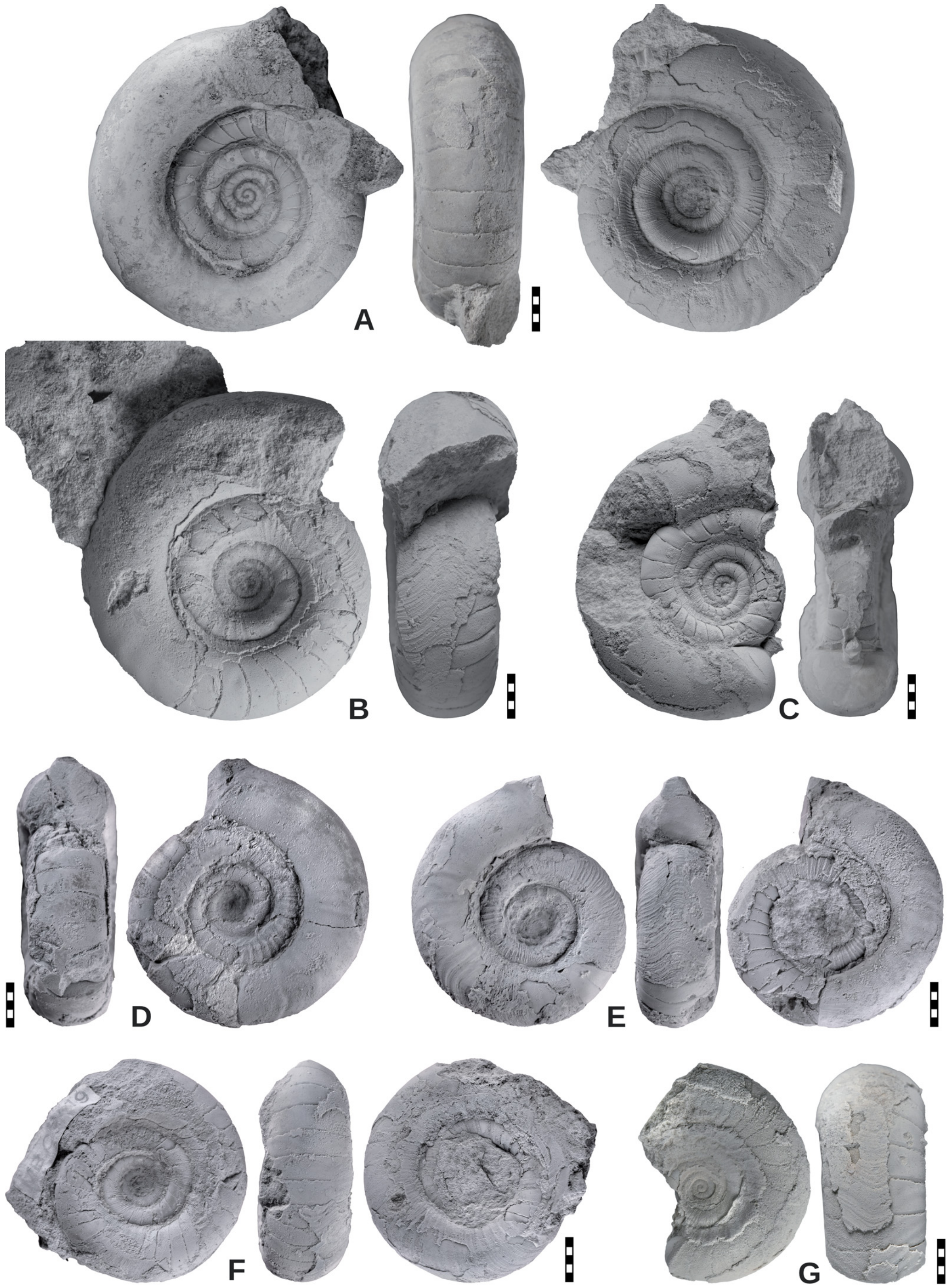

Fig. 6. *Trocholites depressus* (Eichwald, 1840). **A**. Specimen GIT 697-129 from Osmussaar 1 (Estonia); lateral and ventral views. **B**. Specimen GIT 697-535 (Männil Coll. 1985) from Osmussaar cliff (Estonia); lateral and dorsal views. **C**. Specimen GIT 697-410 from Osmussaar 2 (Estonia); lateral and cross sectional views. **D**. Specimen MB.C.32160 (Neben and Krueger Coll.) from Niederfinow (Brandenburg); dorsal and lateral views. **E**. Specimen MB.C.32161 (Neben and Krueger Coll.) from Lebbin (Mecklenburg-Vorpommern); previously figured by Neben & Krueger (1971: pl. 32 figs 10–11); lateral and dorsal views. **F**. Specimen MB.C.9719 (Dames Coll. 1876), Osmussaar (Estonia); previously figured by by Schröder (1891: pl. 1 fig. 7); lateral and ventral views. **G**. Specimen GIT 225-1074 (Schmidt Coll.), Osmussaar (Estonia); lateral and ventral views. Scale bar units = 1 mm.

chamber, which extends also on the adapical side of septum. The phragmocone chambers are rather long especially in the early volutions (RCL 0.70–0.30); the suture line is straight. Ornament is preserved in small area on penultimate whorl and consists from lirae and low ribs; two annular ridges are present on the internal mould at about the beginning of the body chamber.

Specimen PMSPU 1-1129 represents a juvenile growth stage of a conch in which four whorls are preserved; traces of at least one more volution are visible. The maximum diameter of the conch is 22 mm; at this size the conch has UWI of 0.41 and RCL of ~ 0.25. The suture line is straight. Fine transverse ornament is visible on the shell surface.

Specimen PMSPU 1-2622 is a median transverse section of a conch in the juvenile growth stage, consisting of four volutions and 22 mm in diameter. In the last 1.5 volutions, the conch changes from thickly to thinly discoidal (CWI = 0.52–0.45) and is evolute (UWI = 0.48–0.50); coiling rate is moderate to low (WER = 1.82–1.70). Whorl profile of the outer volution is rounded from ventral and lateral sides but inner whorl profiles appear to be slightly ventrally flattened; the whorls are moderately depressed (WWI = 1.64–1.67) and moderately to weakly impressed (IZR = 0.19–0.14). The siphuncle is marginodorsal (RSP = 1.00) and rather wide (RSH ~ 0.30).

Specimen MB.C.9719 (Fig. 6F) is a subadult phragmocone with 26 mm diameter; the body chamber is missing. At this diameter, the conch is thinly discoidal (CWI = 0.41) and evolute (UWI = 0.45). In the last three quarters volution, the whorl profile has broadly rounded flanks and venter and changes from moderately to weakly depressed (WWI decreases from 1.67 to 1.38). The shell wall is ornamented with fine lirae with symmetric crests, but low ribs are locally visible on one side of the specimen. The phragmocone chambers increase in length in the last three quarters of the terminal volution (RCL changes from 0.24 to 0.37); the suture line is almost straight.

The other specimens are in a subadult or adult growth stage and range from 31 to 43 mm in conch diameter. In the last whorl, these conchs become more discoidal (CWI decreases from 0.45 to 0.36) and more widely umbilicate (UWI increases from 0.44 to 0.50) (Fig. 7A–B). The whorl profile in the last whorl is rounded, moderately to weakly impressed and becomes less depressed (WWI decreases from 1.61 to 1.20) during ontogeny (Fig. 7C). In some specimens, the WWI increases in the last half of the body chamber (e.g., GIT 697-535). The siphuncle has a marginodorsal position (RSP = 1.00) and the RSH decreases from 0.35 to 0.26 (n = 5). The complete body chamber is preserved in GIT 697-410 (Fig. 6C), where it is about half a volution long and the aperture extends into a ventral sinus. In the specimens TUG 2-271 and TUG 1351-14 (Fig. 5B), the latest phragmocone chambers are significantly shortened (down to RCL = 0.10).

Remarks

Three late Darriwilian species of *Trocholites* have been described from the Estonian islet of Osmussaar (formerly Odinsholm or Odensholm): *T. depressus*, *T. incongruus* and *T. odini*. These species were established by Eichwald (1840), who gave short descriptions but no illustrations of any type material. One specimen of each species was illustrated later by him (Eichwald 1860), but he did not explicitly state that these belonged to the respective type collections. The originals of Eichwald (1860) were studied and re-illustrated by Schröder (1891) and Balashov (1953); the latter author regarded them as holotypes (see discussion below). *Trocholites incongruus* and *T. odini* were not properly revised and are unequivocally known only from the probable type material. New material was assigned only to *Trocholites depressus* by Kröger & Keupp (2004). Other assignments to *T. depressus* are more or less questionable (e.g., Sweet 1958; Chen 1987).

Table 3 (continued on next page). Conch measurements, ratios and rates of *Trocholites depressus* (Eichwald, 1860).

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
GIT 697-410	32.6	12.9	9.8	14.6	–	0.40	1.32	0.45	–	–
minus 180°	–	10.9	8.3	11.3	–	–	1.32	–	–	–
MB.C.32160	29.3	11.1	7.1	15.1	6.4	0.38	1.58	0.52	1.64	0.09
minus 90°	26.6	10.7	7.5	12.6	–	0.40	1.43	0.47	–	–
minus 180°	22.9	10.1	6.6	11.5	–	0.44	1.54	0.50	–	–
TUG 1351-14	29.3	11.4	–	–	–	0.39	–	–	–	–
minus 90	24.5	10.5	7.3	12.0	6.2	0.43	1.44	0.49	1.79	0.16
minus 270	18.3	7.8	5.2	8.7	–	0.43	1.49	0.47	–	–
MB.C.32161	28.6	9.6	7.9	13.8	7.1	0.33	1.21	0.48	1.77	0.10
minus 90°	23.9	9.4	7.7	11.1	–	0.39	1.22	0.46	–	–
minus 180°	21.3	8.8	6.7	9.5	–	0.41	1.31	0.44	–	–
MB.C.9719	25.6	10.5	7.6	11.5	–	0.41	1.38	0.45	–	–
minus 90°	22.2	10.3	6.4	10.4	–	0.46	1.61	0.47	–	–
GIT 145-1	39.6	–	10.2	19.3	8.7	–	–	0.49	1.64	0.14
minus 90°	35.0	–	–	–	8.1	–	–	–	1.70	–
minus 180°	30.9	–	9.5	–	7.8	–	–	–	1.75	0.20
minus 270°	26.8	–	–	–	6.4	–	–	–	1.72	–
minus 360°	23.3	–	–	–	5.5	–	–	–	1.71	–
GIT 697-535	31.4	–	9.7	14.1	–	–	–	0.45	–	–
minus 90°	27.5	12.0	8.2	12.6	–	0.44	1.47	0.46	–	–
minus 180°	–	10.0	7.7	9.6	–	–	1.31	–	–	–
minus 270°	–	9.2	6.8	8.6	–	–	1.36	–	–	–
TUG 2-721	41.6	15.0	11.8	20.8	–	0.36	1.27	0.50	–	–
minus 90°	36.3	–	10.6	18.0	–	–	–	0.50	–	–
minus 180°	–	12.7	9.0	16.5	–	–	1.40	–	–	–
minus 270°	–	–	7.7	14.3	–	–	–	–	–	–
GIT 225-1074	27.0	–	–	–	–	–	–	–	–	–
minus 180°	19.5	8.8	7.0	–	–	0.45	1.26	–	–	–
GIT 697-404-1	28.0	12.0	10.0	–	–	0.43	1.20	–	–	–
minus 90°	24.0	9.6	7.0	–	5.5	0.40	1.37	–	–	–
GIT 697-129	–	–	–	–	–	–	–	–	–	–
minus 90°	33.4	–	8.6	17.6	–	–	–	0.53	–	–
minus 180°	30.1	11.7	8.7	14.8	–	0.39	1:35	0.49	–	–
minus 270°	–	10.1	7.3	13.5	–	–	1.39	–	–	–
TAM G432:787	33.4	–	10.8	14.5	–	–	–	0.43	–	–
minus 90°	28.5	–	10	11.6	–	–	–	0.41	–	–
minus 180°	–	–	8.2	–	–	–	–	–	–	–
minus 270°	–	10.4	6.9	–	–	–	1.51	–	–	–

Table 3 (continued). Conch measurements, ratios and rates of *Trocholites depressus* (Eichwald, 1860).

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
PMSPU 1-1129	21.8	–	7.3	9.0	–	–	–	0.41	–	–
minus 90°	19.9	–	6.7	7.5	–	–	–	0.38	–	–
minus 180°	–	–	5.6	6.6	–	–	–	–	–	–
minus 270°	–	–	5.2	5.8	–	–	–	–	–	–
PMSPU 1-2622	21.3	9.6	5.7	10.8	4.9	0.45	1.67	0.50	1.70	0.14
minus 180°	16.4	8.0	4.8	7.3	4.0	0.49	1.64	0.45	1.74	0.18
minus 360°	12.4	–	–	–	–	–	–	–	–	–
minus 540°	9.0	4.7	2.9	4.3	2.3	0.52	1.64	0.48	1.82	0.19
minus 720°	6.7	–	2.3	–	–	–	–	–	–	–
PMSPU 1-1127	29.3	–	8.6	13.5	–	–	–	0.46	–	–
minus 90°	25.8	–	7.6	12.1	–	–	–	0.47	–	–
minus 180°	–	–	7.1	10.5	–	–	–	–	–	–
minus 270°	–	–	6.1	–	–	–	–	–	–	–
PMSPU 1-1128	34.9	–	10.5	16.7	–	0.39	1.48	0.48	–	–
minus 90°	30.6	–	9.6	14.0	–	0.41	1.36	0.46	–	–
minus 180°	–	–	7.8	11.8	–	–	–	–	–	–
minus 270°	–	–	7.1	9.6	–	–	–	–	–	–

High-resolution photographs of the originals of Eichwald (1860) are accessible for our study. These, along with the historical descriptions and illustrations, suggest that these specimens differ only slightly in conch geometry and shell ornament. Furthermore, the original specimens of *T. incongruus* appear to only represent an earlier ontogenetic stage of representatives of the other two species.

Among the material currently examined from northern Germany and Estonia, there are over a dozen specimens that appear to closely resemble the probable types of the three species discussed above. These specimens are all discoidal, slowly expanding with a wide umbilicus and weakly depressed, weakly impressed and laterally broadly rounded whorl profile. The siphuncle is marginodorsal (RSP = 1.00) and rather wide; the shell ornament consists of lirae raised at irregular intervals. The variation concerns the ww / wh ratio (WWI = 1.58 in specimen MB.C.32160 but 1.21 in specimen MB.C.32161 in the adult growth stage; Fig. 7C) and the dorsal impression (IZR = 0.09 in specimen MB.C.32160 and 0.16 in specimen GIT 697-404-1). At least some of these differences may be due to the variation in adult conch size (between 30 mm and 40 mm) resulting in the comparison of non-corresponding growth stages. Ribs are developed on the shell surface in most specimens but these ribs are of variable thickness (GIT 697-129 and MB.C.32160). Therefore, the results of our investigation conclude that the differences between *Trocholites depressus*, *T. incongruus* and *T. odini* are likely attributable to intraspecific variation and based on ontogenetic differences. The three taxa are consequently synonymized herein; the species name *depressus* has priority.

Eichwald (1840) did not figure any specimens and later (Eichwald 1860) he did not indicate whether the illustrated specimen was part of the type collection. Therefore, the specimen of Eichwald (1860), later re-illustrated by Balashov (1953: pl. 7 fig. 2), cannot be considered the holotype of "*Nautilus depressus*". Nevertheless, we refer to it here as a neotype. This is justified by the following reasons: Eichwald (1860) clearly regarded the specimen as a representative of his earlier described species *Nautilus depressus*

Eichwald, 1840; Balashov (1953) physically examined and re-photographed the specimen; photographs of the specimen were available for the present study, confirming that it corresponds to the original as well as to the currently understood range of the species. The neotype is deposited in the Natural History Collections of St Petersburg State University under collection number PMSP-1-1128.

It is important to note that there is some inconsistency in the scientific literature regarding the use of the species name *odini*. The confusion occurred after Verneuil (1845: 360, pl. 25 fig. 8) included a specimen with a nearly circular whorl profile and an uncoiled terminal body chamber in the species and used for this the combination *Lituites odini*. This contradicts the original description by Eichwald (1840). Consequently, Eichwald (1860) and others (Remelé 1890; Foord 1891) correctly assigned that specimen to *Curtoceras teres*. However, many authors confused the two species and used the names *odini* and *teres* as synonyms; both Eichwald and Verneuil were sometimes stated as authors of the name *odini*. The fact that the probable holotype of *T. odini* was first figured by Eichwald as late as in 1860 possibly contributed to this ambiguity. Nevertheless, the material examined by us confirms that they are clearly two separate species but also represent two different genera, *Trocholites* and *Curtoceras* (see under *C. teres* below).

Specimen GIT 145-1 (Fig. 5C) is extraordinary as it has a healed perforation of the phragmocone, which was previously discussed in detail by Kröger & Keupp (2004). This specimen is shortly re-described and re-figured here for completeness.

Representatives of *Trocholites depressus* are similar to specimen MB.C.32182 of *T.* sp. 4 and the type specimens NRM Mo 152354 and GIT 362-721-2 of *T. tureki* sp. nov. in conch width and whorl profile shape. However, specimen MB.C.32182 has a narrower siphuncle shifted from the dorsal shell wall and its inner volutions are not flattened ventrally; both specimens NRM Mo 152354 and GIT 362-721-2 have a more regularly developed ornament with low ribs / annuli present also on the surface of the outer whorl.

The subadult holotype of *Trocholites chaloupkai* from the early Katian part of the Zahořany Formation of the Prague Basin is also similar to the representatives of *T. depressus*, particularly in conch geometry

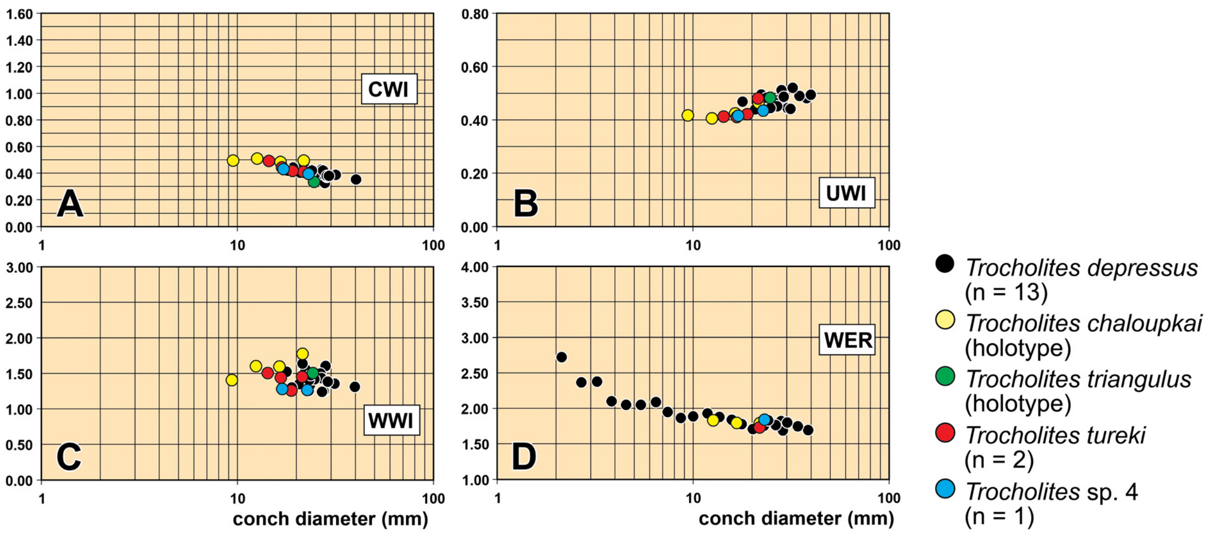

Fig. 7. A–D. Ontogenetic development of the conch width index (CWI), umbilical width index (UWI), whorl width index (WWI) and whorl expansion rate (WER) of *Trocholites depressus* (Eichwald, 1840) and some other species of *Trocholites* Conrad, 1838.

and siphuncular position and diameter (Aubrechtová *et al.* 2023). However, the Bohemian specimen differs by a more significant ventral flattening of the conch, presence of deep ventral lobe of suture line and a unique, web-like shell ornament.

Compared to the species of *Curtoceras*, *T. depressus* is most similar to *C. teres*; the similarities concern especially the umbilical width (UWI) and conch width (CWI). The specimens of *C. teres* differ from the specimens of *T. depressus*, however, in the much higher and much more rapidly decreasing coiling rate (particularly in early and mid-ontogeny; WER = 9.9–1.9 vs 2.7–1.6), the whorl profile is less depressed, equidimensional or even slightly compressed (WWI = 1.66–0.82 vs 1.67–1.2 in ontogeny) and the siphuncle is much narrower (RSH ~ 0.16 vs 0.30) with some distance from the dorsal shell wall; also, the shell ornament in *C. teres* lacks strong ribs on inner whorls.

Geographic and stratigraphic occurrence

Northern Estonia, northern Germany, north-west Poland, Sweden, ?Norway and ?Tibet; Darriwilian, Middle Ordovician.

Trocholites hospes (Remelé, 1880)
Figs 1G–H, 8–12; Table 4

Palaeonautilus hospes Remelé, 1880: 249, pl. 2 fig. 3.
? *Palaeonautilus hospes* Remelé, 1880: 249, pl. 2 fig. 4.

Palaeonautilus hospes – Remelé 1881: 2, 13, text-fig.1. — Foerste 1930: 286, pl. 43 fig. 2, pl. 44 figs 4–5. — Balashov 1962: pl. 9 fig. 5.
Palaeonautilus (*Trocholites*) *hospes* – Remelé 1890: 40, pl. 2 fig. 3.
? *Palaeonautilus* (*Trocholites*) *hospes* – Remelé 1890: pl. 2 fig. 4, pl. 5 fig. 8.
? *Trocholites hospes* – Schröder 1891: 17(155), pl. 1(24) figs 8–9.
? *Palaeonautilus hospes* – Schindewolf 1939: 60, text-fig. 14, pl. 4 fig. 7.
Trocholites hospes – Balashov 1953: 244, pl. 5 fig. 3. — Sweet 1958: 96, pl. 8 figs 3, 5. — Neben & Krueger 1971: pl. 32 figs 12–14.

Diagnosis

Species of the genus *Trocholites* with an adult conch diameter of 43–60 mm. Conch in the last whorl thickly discoidal (CWI = 0.52–0.60) and subevolute (UWI = 0.30–0.40) with moderately high coiling rate (WER = 1.75–1.90). Whorl profile weakly to moderately depressed (WWI = 1.40–1.80), rounded, venter sometimes slightly flattened, usually moderately embracing (IZR = 0.20–0.30). Whorl width and whorl height stagnant or slightly increasing in last quarter volution. Terminal aperture with ventral and lateral flares. Shell ornament with fine lirae extending with rather deep, rounded ventral sinus. Phragmocone chambers moderately long (RCL = 0.20–0.24). Suture line straight.

Material examined

BALTIC REGION • 1 spec.; locality unknown; Aseri or Lasnamägi or Uhaku regional stages; Deubel Coll.; illustrated in Fig. 10A; MB.C.7638.

GERMANY – **Brandenburg** • 1 spec.; Herzsprung (Uckermark); upper Lasnamägi Regional Stage; illustrated by Foerste (1930: pl. 44 fig. 4), re-illustrated here in Fig. 8A; MB.C.11557 • 1 spec.; Oderberg; Lasnamägi or Uhaku Regional Stage; Neben Coll.; illustrated by Neben & Krueger (1971: pl. 32 fig. 14), re-illustrated here in Fig. 8C; MB.C.32162 • 1 spec.; Karlstein (Neumark); probably Darriwilian; Neben and Krueger Coll.; illustrated in Fig. 9A; MB.C.32163 • 1 spec.; Oderberg; upper Lasnamägi Regional Stage; 1936: Neben Coll.; illustrated by Neben & Krueger (1971: pl. 32 figs 12–13), re-illustrated here in Fig. 9B; MB.C.11556 • 1 spec.; Eberswalde; Lasnamägi or Uhaku Regional Stage; Remelé Coll.; illustrated by Neben & Krueger (1971: pl. 32 figs 1–2), re-illustrated here in Fig. 8D; MB.C.11555.2 • 1 spec.; Oderberg; upper Lasnamägi Regional Stage; Neben and Krueger Coll.; illustrated in Fig. 9C; MB.C.32164.

POLAND – **West Pomerania** • 1 spec.; Cieszeniewo; upper Lasnamägi Regional Stage; 1890; Dorow Coll.; illustrated by Foerste (1930: pl. 43 fig. 2, pl. 44 fig. 5), re-illustrated here in Fig. 8B; MB.C.11558 • 1 spec.; Ustronie Morskie (West Pomerania); Lasnamägi or Uhaku Regional Stage; Müldner Coll.; illustrated in Fig. 9D; MB.C.32165 • 1 spec.; Ustronie Morskie (West Pomerania); Lasnamägi or Uhaku Regional Stage; Neben and Krueger Coll.; MB.C.32166.

Description

Specimen MB.C.11557 (Fig. 8A) is a conch in the terminal stage of growth and has a diameter of about 56 mm. The conch is thickly discoidal (CWI = 0.56) and subevolute (UWI = 0.38). The last whorl is moderately depressed; the WWI decreases from 1.64 to 1.58 during the last quarter volution of the conch. The length of the terminal body chamber is 270 degrees; its venter is slightly flattened. Its aperture possesses ventral and lateral flares producing a deep ventral sinus and prominent ventrolateral lappets. The shell ornament is preserved only in the penultimate whorl and in a very small area at the ventral margin of the aperture; it consists of irregularly spaced, coarse lirae. The internal mould has very low annuli on the venter and in the ventrolateral area. The phragmocone chambers are rather long (RCL = 0.40). The suture line is almost straight and extends with a very broad and shallow external lobe.

Specimen MB.C.11558 (Fig. 8B) is an almost complete conch of a fully grown individual with a conch diameter of 51 mm. The conch is thickly discoidal (CWI = 0.58) and subevolute (UWI = 0.37). The whorl profile is moderately depressed; the WWI increases from 1.73 to 1.83 in the last 90 degrees of the volutions. The body chamber has a length of about 220 degrees and possesses ventral and ventrolateral flares; a ventral sinus is developed at the aperture. Small remains of the shell ornament are preserved only in the ventrolateral area near the aperture and in the inner volutions; they consist of fine and irregularly developed lirae. The phragmocone chambers are moderately long (RCL = 0.23). The suture line is almost straight with the exception of a very shallow and broad external lobe. At the beginning of the last whorl, the moderately wide siphuncle has a subdorsal position (RSH = 0.24; RSP = 0.84).

Specimen MB.C.32162 (Fig. 8C) is an almost complete adult conch with a conch diameter of 51 mm and has nearly five whorls preserved. The conch is thickly discoidal (CWI = 0.57) and subevolute (UWI = 0.42); the coiling rate is moderate (WER = 1.77). The whorl profile is moderately depressed (WWI = 1.75) and moderately embracing (IZR = 0.24). The specimen is almost completely exfoliated; small remains of the shell ornament are preserved only in the inner whorls, where fine and regularly spaced lirae are present. The phragmocone chambers are moderately long (RCL = 0.22). The suture line is almost straight, but extends with a very shallow and broad external lobe. At about half of the last whorl, the rather thin siphuncle has a subdorsal position (RSH = 0.18; RSP = 0.80). At the base of the body chamber, traces of muscle scar imprints are preserved.

Specimen MB.C.32163 (Fig. 9A) is an almost complete, well-preserved adult conch with a diameter of 50 mm. The conch is thickly discoidal (CWI = 0.58) and subevolute (UWI = 0.33) with a moderately high coiling rate (WER = 1.82). The whorl profile is weakly depressed (WWI = 1.50) and strongly impressed dorsally (IZR = 0.33) in the terminal half volution of the conch. The terminal body chamber is slightly longer than half of a volution; its aperture possesses ventral and lateral flares; a ventral sinus is indicated. Remain of the shell are preserved only in small areas; the ornament consists of rather regular, fine lirae.

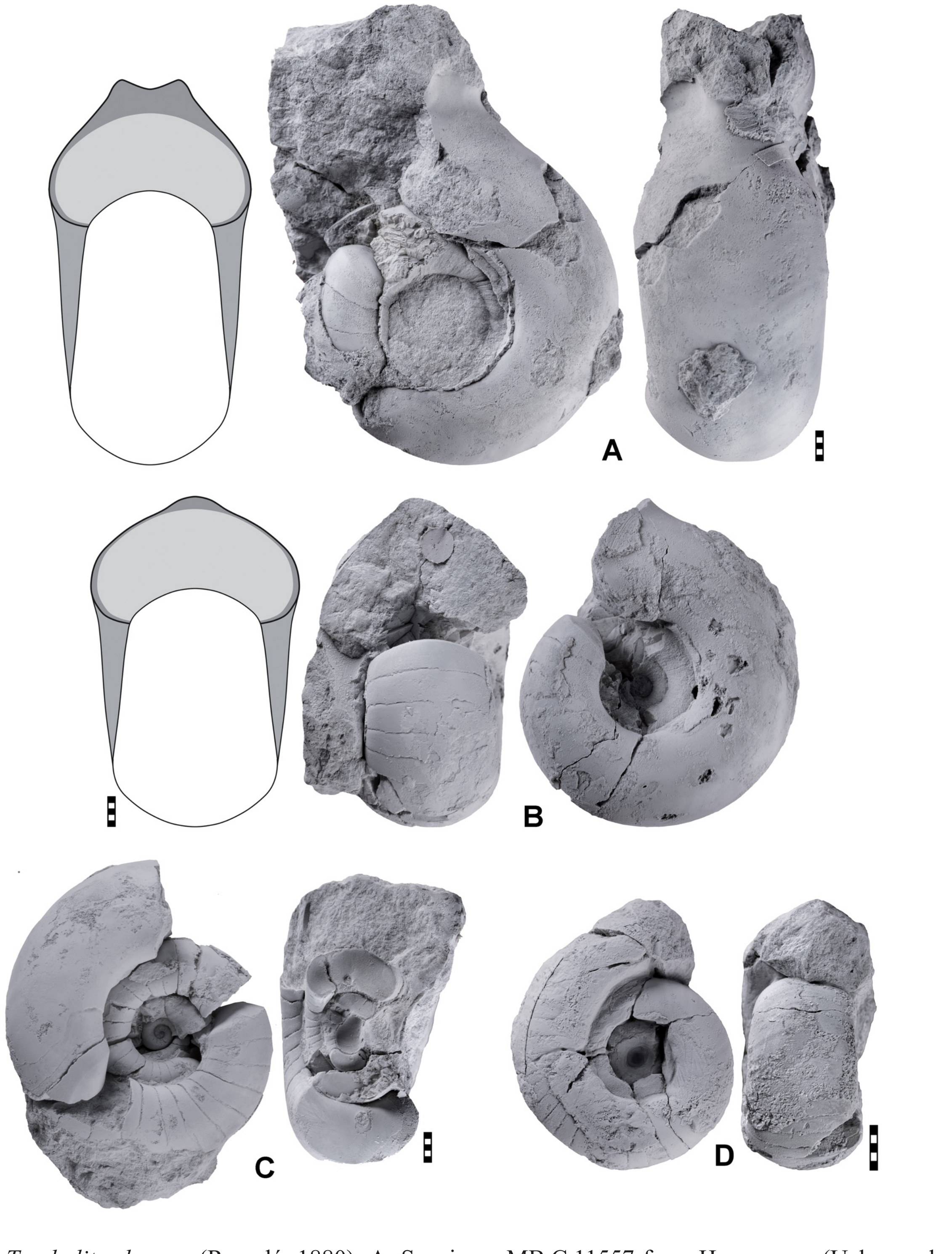

Fig. 8. *Trocholites hospes* (Remelé, 1880). **A**. Specimen MB.C.11557 from Herzsprung (Uckermark, Brandenburg); previously figured by Foerste (1930: pl. 44 fig. 4); reconstruction of apertural view, lateral and ventral views. **B**. Specimen MB.C.11558 (Dorow Coll., 1890) from Cieszeniewo (West Pomerania, Poland); previously figured by Foerste (1930: pl. 43 fig. 2, pl. 44 fig. 5); reconstruction of apertural view, dorsal and lateral views. **C**. Specimen MB.C.32162 (Neben Coll.) from Oderberg (Brandenburg); previously figured by Neben & Krueger (1971: pl. 32 fig. 14); lateral view and broken surface. **D**. Specimen MB.C.11555.2 from Herzsprung (Uckermark, Brandenburg); previously figured by Remelé (1880: pl. 2 fig. 4); lateral and dorsal views. Scale bar units = 1 mm.

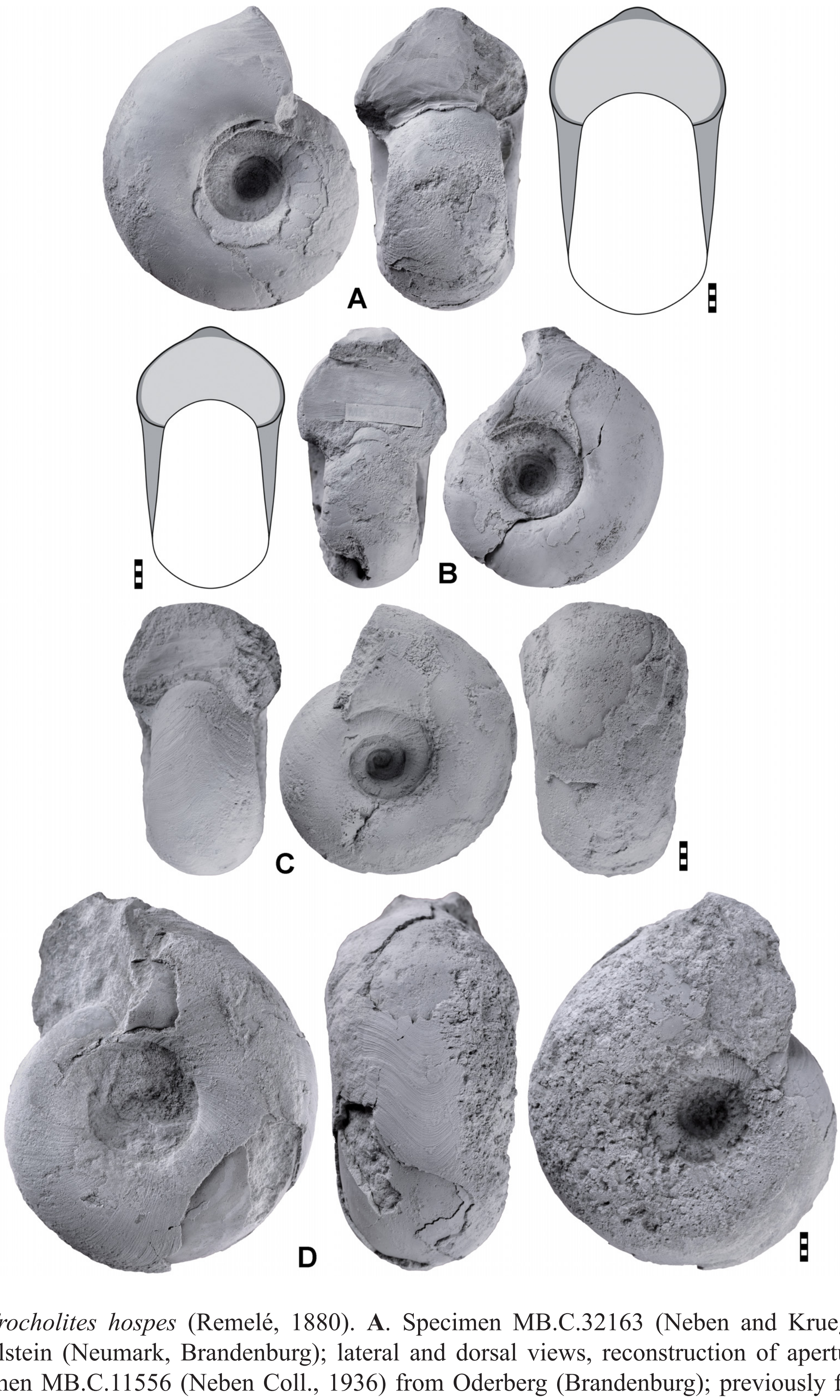

Fig. 9. *Trocholites hospes* (Remelé, 1880). **A**. Specimen MB.C.32163 (Neben and Krueger Coll.) from Karlstein (Neumark, Brandenburg); lateral and dorsal views, reconstruction of apertural view. **B**. Specimen MB.C.11556 (Neben Coll., 1936) from Oderberg (Brandenburg); previously figured by Neben & Krueger (1971: pl. 32 figs 12–13); reconstruction of apertural view, dorsal and lateral views. **C**. Specimen MB.C.32164 (Neben and Krueger Coll.) from Oderberg (Brandenburg); dorsal, lateral and ventral views. **D**. Specimen MB.C.32165 (Müldner Coll.) from Ustronie Morskie (West Pomerania, Poland); lateral and ventral views. Scale bar units = 1 mm.

Specimen MB.C.11556 (Fig. 9B) is a well-preserved, almost complete conch, which already represents the final stage of growth with a diameter of 43 mm. In this stage of growth, the conch is thickly discoidal (CWI = 0.56), subevolute (UWI = 0.37) and moderately expanding (WER = 1.83); the whorl profile in the last half volution is rounded, moderately depressed (WWI = 1.59) and moderately impressed dorsally (IZR = 0.27). The length of the terminal body chamber is 250 degrees; its aperture possesses ventral and lateral flares. The shell ornament is preserved only near the aperture and consists of irregularly thick lirae, which turn back already from the umbilical seam and form a rather deep, blunt V-shaped ventral sinus. The phragmocone chambers are moderately long (RCL = 0.24). The suture line extends almost straight across the flank and form a very broad and shallow external lobe. Faint traces of muscle scar imprints are preserved in the rear part of the body chamber.

Specimen MB.C.32164 (Fig. 9C) is a well-preserved, subadult individual with 47 mm conch diameter; the conch is thinly discoidal (CWI = 0.52) and subevolute (UWI = 0.35) and the profile of the last whorl is moderately depressed (WWI = 1.53). The whorl profile is crescent-shaped with broadly rounded venter and flanks; an umbilical margin is not discernible. The shell ornament is well-preserved in large areas; it consists of irregularly spaced, fine and slightly thickened lirae. They are directed backwardly right from the umbilical seam and form a deep, blunt V-shaped ventral sinus.

Specimen MB.C.32165 (Fig. 9D) is, with a conch diameter of 64 mm, the largest specimen of *Trocholites* in our collection. The last ~ 0.50 a whorl corresponds to the body chamber. The specimen has a well-preserved shell ornament that consists of fine and almost equally spaced lirae. On the body chamber, the lirae are fine on the flanks, but on the venter they become more prominent and form a rounded, nearly rectangular sinus.

Specimen MB.C.7638 (Fig, 10A) is an incomplete conch in the early growth stage with 26.5 mm diameter and was sectioned. During ontogeny (between 4.0 mm and 26.5 mm conch diameter), the conch changes from thickly pachyconic to thinly pachyconic (CWI decreases from 0.82 to 0.71) and from involute to subinvolute (UWI increases from 0.15 to 0.29); the coiling rate decreases markedly (WER drops from 2.60 to 1.67). The whorl profile changes only slightly and remains moderately depressed

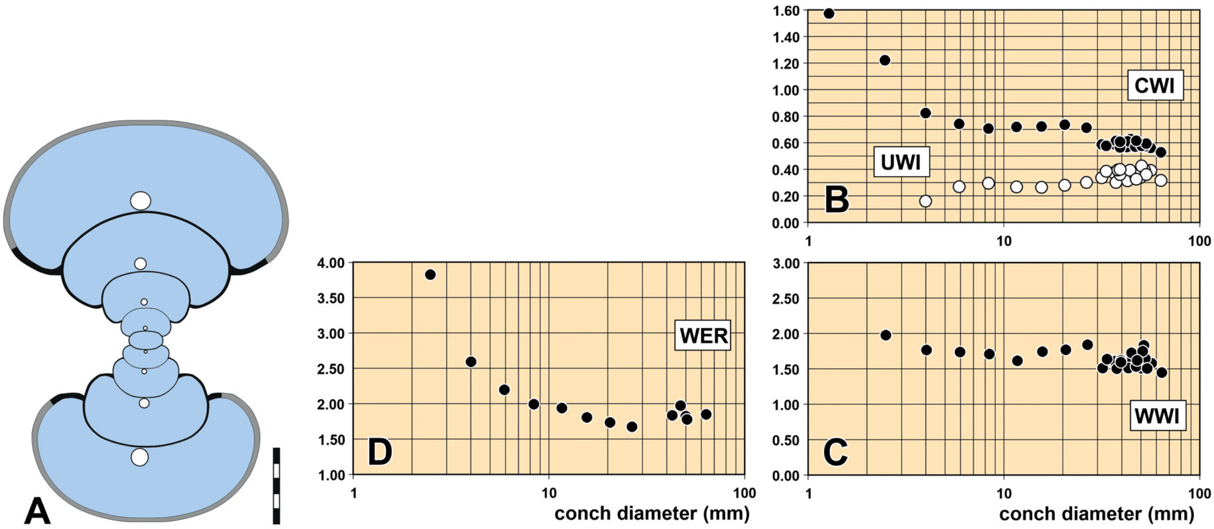

Fig. 10. *Trocholites hospes* (Remelé, 1880). **A**. Specimen MB.C.7638 (Deubel Coll.) from an unknown locality; cross section. **B–D**. Ontogenetic development of the conch width index (CWI), umbilical width index (UWI), whorl width index (WWI) and whorl expansion rate (WER) of selected specimens. Scale bar units = 1 mm.

Table 4. Conch measurements, ratios and rates of *Trocholites hospes* (Remelé, 1880).

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.32165	63.5	33.1	22.9	19.5	16.7	0.52	1.44	0.31	1.84	0.27
minus 90°	53.5	31.5	21.0	18.9	–	0.59	1.50	0.35	–	–
minus 180°	47.5	29.0	18.0	15.1	–	0.61	1.62	0.32	–	–
MB.C.11557	56.4	31.4	19.9	21.6	–	0.56	1.58	0.38	–	–
minus 90°	52.3	29.7	18.1	20.3	–	0.57	1.64	0.39	–	–
MB.C.11558	51.4	29.8	16.3	19.0	–	0.58	1.83	0.37	–	–
minus 90°	44.5	27.7	16.1	16.3	–	0.62	1.73	0.37	–	–
MB.C.32162	50.7	28.9	16.6	21.2	12.6	0.57	1.75	0.42	1.77	0.24
MB.C.32163	50.0	28.9	19.2	16.5	12.9	0.58	1.50	0.33	1.82	0.33
minus 90°	42.9	26.0	17.3	13.1	–	0.61	1.51	0.31	–	–
minus 180°	37.5	22.8	15.2	11.0	–	0.61	1.50	0.29	–	–
MB.C.32164	47.0	26.6	17.4	16.3	13.0	0.57	1.53	0.35	1.91	0.25
minus 90°	39.3	22.0	13.6	13.9	–	0.56	1.62	0.35	–	–
MB.C.11556	42.6	24.0	15.1	15.6	11.1	0.56	1.59	0.37	1.83	0.27
minus 90°	36.5	21.3	13.3	13.4	–	0.58	1.60	0.37	–	–
minus 180°	31.7	18.5	12.3	10.4	–	0.58	1.51	0.33	–	–
MB.C.32166	39.3	23.7	14.9	15.4	–	0.60	1.59	0.39	–	–
minus 90°	33.4	19.1	11.7	12.6	–	0.57	1.63	0.38	–	–
MB.C.7638	26.5	18.8	10.2	7.8	6.0	0.71	1.84	0.29	1.67	0.42
minus 180°	20.6	15.1	8.5	5.6	4.9	0.73	1.77	0.27	1.73	0.42
minus 360°	15.6	11.3	6.5	4.0	4.0	0.72	1.74	0.26	1.80	0.38
minus 540°	11.7	8.4	5.2	3.0	3.3	0.72	1.61	0.26	1.93	0.37
minus 720°	8.4	5.9	3.5	2.4	2.4	0.70	1.71	0.29	1.99	0.29
minus 900°	5.9	4.4	2.5	1.5	1.9	0.74	1.73	0.26	2.20	0.24
minus 1080°	4.0	3.3	1.9	0.6	1.5	0.82	1.76	0.15	2.60	0.19
minus 1260°	2.5	3.1	1.5	–	1.3	1.22	1.98	–	4.10	0.18

(WWI = 1.98–1.84), but changes from moderately to strongly impressed (IZR increases from 0.18 to 0.42) (Fig. 10B–D). The shell ornament is not well-discernible; it appears to consist of thin ribs or raised lirae in the internal whorl and only lirae in the outer whorl. The phragmocone chambers are rather long (RCL = 0.39 in the external volution). The siphuncle remains close or in contact with the dorsal shell wall and changes from RSH 0.15 to 0.20 in ontogeny.

Remarks

Remelé (1880) described and figured two specimens of "*Palaeonautilus hospes*" from late Darriwilian erratics near Heegermühle (Brandenburg, Germany); subsequently these specimens were re-described and re-figured by him (Remelé 1881, 1890). Only one of these two specimens (MB.C.11555.2) is available for study; it was also illustrated by Neben & Krueger (1971: pl. 32 figs 1–2) and is re-illustrated here in Fig. 8D. However, this syntype was assigned to *Trocholites remelei* by Neben & Krueger (1971). Its internal mould shows some annular ridges in the outermost preserved whorl, but the shell surface is ornamented only with fine lirae, not clusters of raised lirae as in the lectotype of *T. remelei* (see below).

Alternatively, it is possible that the specimen MB.C.11555.2 (Fig. 8D) belongs to *T. contractus*, but the corresponding growth stage (dm = 26 mm) of that species has a wider conch (CWI ~ 0.65 in the neotype of *T. contractus*, but only ~ 0.55 in specimen MB.C.11555.2) with a more depressed whorl

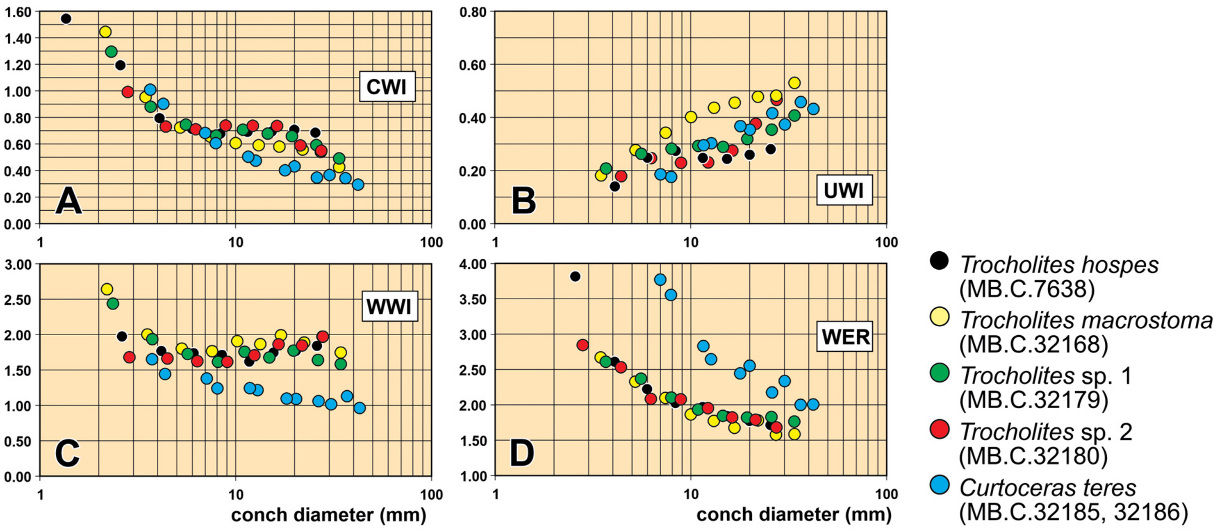

Fig. 11. A–D. Ontogenetic development of the conch width index (CWI), umbilical width index (UWI), whorl width index (WWI) and whorl expansion rate (WER) of some species of *Trocholites* Conrad, 1838 and *Curtoceras* Ulrich, Foerste, Miller & Furnish, 1942.

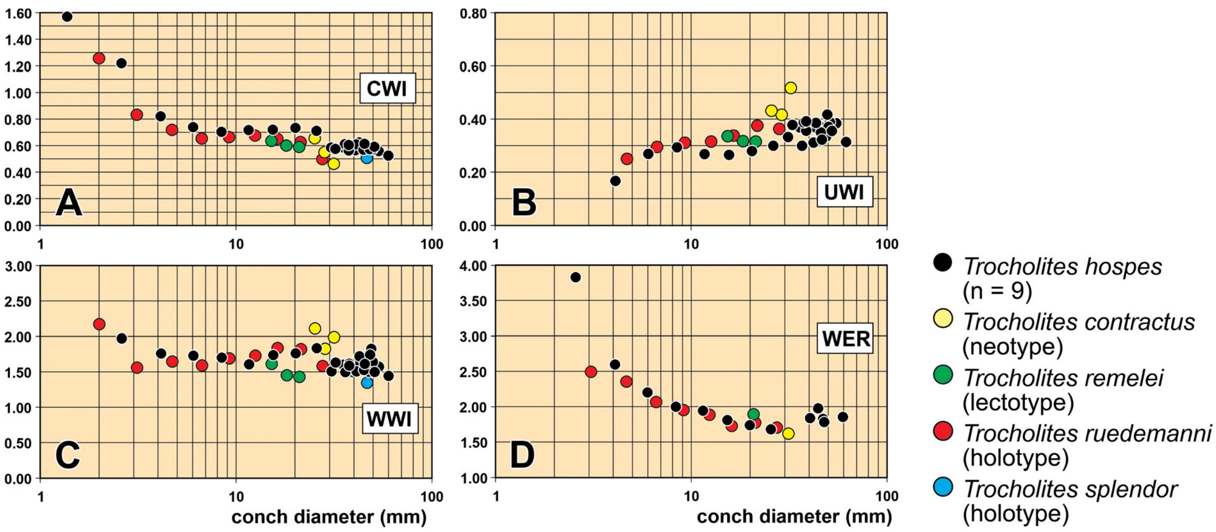

Fig. 12. A–D. Ontogenetic development of the conch width index (CWI), umbilical width index (UWI), whorl width index (WWI) and whorl expansion rate (WER) of *Trocholites hospes* (Remelé, 1880) and some other species of *Trocholites* Conrad, 1838.

profile (WWI ~ 2.12 vs ~ 2.00). The unprofessional preparation of specimen MB.C.11555.2 by previous researchers makes it difficult to decide whether this syntype belongs to *T. hospes* or another species of *Trocholites* such as *T. contractus*. For this reason, this syntype is not considered here.

The other syntype presented by Remelé (1880, 1881, 1890) was not available for study, but according to original descriptions, as well as figures, it can be reliably assigned to *T. hospes*.

Some specimens of *Trocholites hospes* have a more depressed whorl profile (WWI = 1.83 at 52 mm diameter in MB.C.11558; WWI = 1.75 at 51 mm diameter in MB.C.32162) than others (WWI = 1.50 at dm at 50 mm diameter in MB.C.32163) in the terminal growth stage (Fig. 12). These differences probably result from size variations of fully adult conchs, which range in their diameters between 43 mm and 60 mm.

Trocholites hospes is easily recognised among the species of *Trocholites* by its rather large and stout conch, the deep and moderately wide umbilicus, the fine lirae on the shell surface and the terminal body chamber with apertural flares. Most similar to *T. hospes* is *T. splendor* sp. nov., which differs by its more slender conch (CWI = 0.50 at dm = 49 mm), a less strongly depressed whorl profile (WWI = 1.34 at dm = 49 mm) (Fig. 12) and the presence of thin ribs or raised lirae on the shell surface of the inner whorls.

The lectotype of the Darriwilian *Trocholites remelei* from Sweden also resembles specimens of *T. hospes*, but the shell in *T. remelei* possesses annuli or groups of raised lirae, which are visible not only on the internal mould but also on the shell surface. Furthermore, *T. remelei*, which is known only from a single specimen, has more strongly expanding, less depressed and narrower whorl than corresponding growth stages of *T. hospes* (Fig. 12).

Another species that could be confused with juvenile growth stages of *Trocholites hospes* is *T. contractus* (Fig. 12); specimens of both species have similarly stout conchs (CWI ~ 0.60) with a deep umbilicus, distinctly depressed whorl profiles (WWI ~ 2.00), similar whorl overlap (IZR ~ 0.30) and lirae on the shell surface. However, *T. contractus* reaches a much smaller terminal conch diameter (about 33 mm) and its body chamber markedly decreases in height, width and imprint zone rate toward the aperture.

Among the non-Baltic trocholitid species, the specimens of *Trocholites hospes* resemble the holotype of *T. hubeiensis* (Kuniutan (Guniutan) Formation, Darriwilian, Hubei Province of China). It is difficult to make an accurate measurement of the holotype from the only figure and description available, but it appears that the holotype has a similar conch geometry, including a high expansion rate, a narrow umbilicus, a moderately depressed and continuously rounded whorl profile and a subdorsal, comparatively thin siphuncle. On the other hand, the phragmocone chambers appear to be shorter in the holotype of *T. hubeiensis*. Nothing is known of the adult conch size. However, the similarity is rather high and it may thus be possible that *T. hubeiensis* is a junior synonym of *T. hospes*. This would be another species of coiled cephalopods that occurs in both Baltica and South China; the other species include the tarphyceratid *Discoceras rarospira* (Eichwald, 1860) from Middle–Late Ordovician strata of Baltoscandia and the Kuniutan (Guniutan) Formation (Middle Ordovician) of Yunnan (Zhang & Chen 2002), and the lituitid *Cyclolituites lynnensis* Kjerulf, 1865 that is known from the late Darriwilian / early Sandbian boundary strata of Norway (Kjerulf 1865; Sweet 1958) and the Sandbian of the Hunan Province of China (Fang *et al.* 2017, 2021). Chen (1987) also reported an occurrence of *T. depressus* in Ordovician strata of northern Tibet.

Similar in conch geometry to the specimens of *Trocholites hospes* is also the holotype of *T. ruedemanni* (Fig. 12) from early Sandbian (?) strata of New York (USA), except that the adult conch size in the latter is considerably smaller (29 mm vs 43–60 mm), the terminal body chamber is slightly uncoiled and the shell ornament on the umbilical wall in the last two whorls has nodes and fine costae (Flower 1943).

Geographic and stratigraphic occurrence

Norway, Sweden (Island of Öland), northern Germany, northern Poland, St Petersburg Region of Russia; Darriwilian (Middle Ordovician).

Trocholites macrostoma Schröder, 1882

Figs 1A, 13–14; Table 5

Trocholites macrostoma Schröder, 1882: 99.

Trocholites macrostoma – Schröder 1891: 149, pl. 1(24) fig. 1. — Neben & Krueger 1971: pl. 32 figs 15–16.

Diagnosis

Species of the genus *Trocholites* with an adult conch diameter of about 42 mm. Conch in the last whorl thinly discoidal (CWI ~ 0.43) and evolute (UWI ~ 0.53) with very low coiling rate (WER ~ 1.52). Whorl profile moderately depressed (WWI ~ 1.73) with rounded venter and flanks, moderately embracing (IZR = 0.18–0.28). Aperture with ventral flares. Shell ornament with irregularly thick, rursiradiate lirae, accumulations of lirae and growth lines, with shallow but relatively sharp ventral sinus; surface of internal mould with low and wide annular ridges.

Type material

Neotype (designated here)

GERMANY – **Brandenburg** • Oderberg; Darriwilian; Neben and Krueger Coll.; figured by Neben & Krueger (1971: pl. 32 figs 15–16), re-illustrated here in Fig. 13; MB.C.32167.

Additional material

GERMANY – **Brandenburg** • 1 spec.; Niederfinow; Lasnamägi Regional Stage; Neben and Krueger Coll.; illustrated in Fig. 14A; MB.C.32168.

Description

Neotype MB.C.32167 (Fig. 13) is a well-preserved, nearly complete adult specimen with a conch diameter of 40 mm. The terminal body chamber is slightly longer than half a volution and possesses a ventral flare at the aperture. In the last half volution, the conch becomes more discoidal (CWI decreases from 0.48 to 0.43) and more evolute (UWI increases from 0.46 to 0.53); the terminal whorl is moderately depressed (WWI decreases from 1.81 to 1.72) and moderately embracing (IZR = 0.28). The coiling rate of the conch is very low (WER = 1.48). Shell ornament is well-preserved in the inner whorls and part of the last whorl; it consists of distinct and irregularly thick lirae or clusters of lirae; the internal mould has very low and widely spaced annular ridges. The elements of the ornament are rursiradiate in their direction and form a shallow, subangular ventral sinus.

Specimen MB.C.32168 (Fig. 14A) is a conch with 35 mm diameter; the specimen was sectioned and displays five whorls. Conch width and coiling rate generally decrease during ontogeny between 3.4 mm

Fig. 13. *Trocholites macrostoma* Schröder, 1882; neotype MB.C.32167 (Neben and Krueger Coll.) from Oderberg (Brandenburg); previously figured by Neben & Krueger (1971: pl. 32 figs 15–16); reconstruction of apertural view, dorsal and lateral views. Scale bar units = 1 mm.

and 35 mm conch diameter (CWI changes from 0.96 to 0.43 and the WER from 2.66 to 1.56), while the umbilicus becomes wider (UWI increases significantly from 0.18 to 0.53). The whorl profile shows rounded flanks and a slightly flattened venter only in some inner whorls; it is always weakly impressed and strongly or moderately depressed (WWI decreases from 2.65 to 1.74). Whorl height and whorl width increase during growth but in the last half volution, the width appears to decrease slightly (ww changes from 15.4 to 15.1 mm). The siphuncle has a subdorsal position and a relative diameter (RSH) of about 0.20, however, both distance and diameter cannot be accurately measured due to the insufficient preservation of the specimen.

Remarks

A single specimen of *Trocholites macrostoma* was described by Schröder (1882) and subsequently illustrated by him (Schröder 1891: pl. 1(24) fig. 1; see also Fig. 1A herein). This holotype originated from the *Echinosphaerites* Limestone (Darriwilian Stage, Middle Ordovician) of an unspecified locality in "Ostpreußen" (present day Kaliningrad Region of Russia). Schröder (1891) stated that the holotype was kept in the Mineralogical Museum of the University of Königsberg (now Kaliningrad). However, this collection was most probably destroyed in World War II (pers. com. D. Weyer, Berlin, 2022). Therefore, we propose here specimen MB.C.32167 as the neotype for *T. macrostoma*. This specimen is nearly identical in size and dimensions to the holotype. The only difference is that the last whorl in the holotype is slightly less impressed (IZR ~ 0.23 vs ~ 0.28) and that the last whorl of the holotype appears to have had an even lower coiling rate than that calculated for neotype MB.C.32167. However, the precise value cannot be determined reliably from the illustration of the holotype. The two specimens come probably from the same stratigraphic horizon (Darriwilian, Middle Ordovician).

The neotype of *Trocholites macrostoma* closely resembles the specimens of *T. vodickai* sp. nov., but it is separated from these by the slowly expanding, moderately impressed and moderately depressed last whorl and by the presence of distinct, rursiradiate lirae on the shell surface.

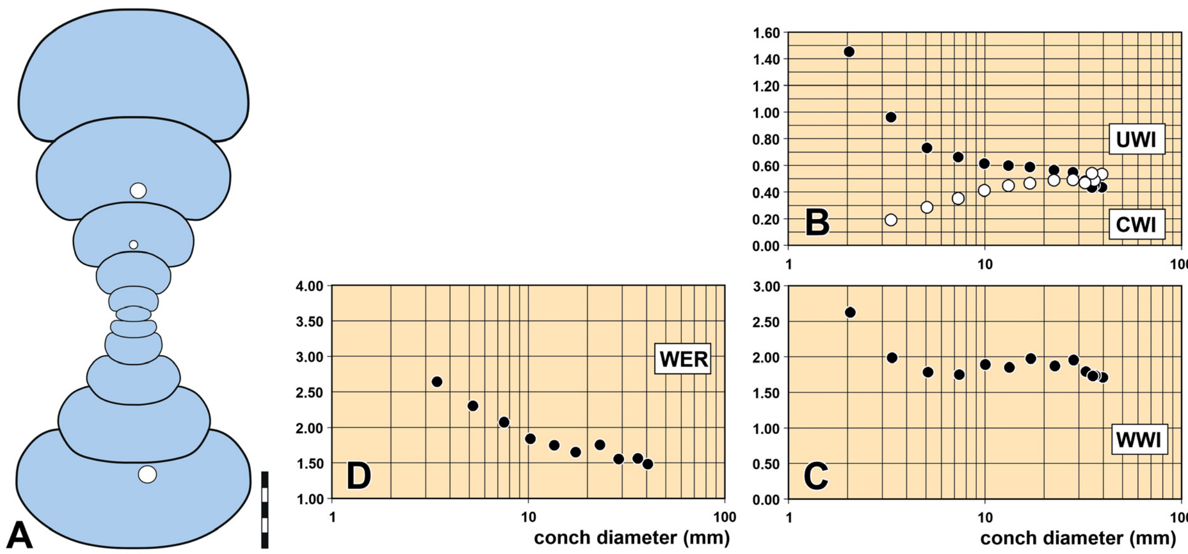

Fig. 14. *Trocholites macrostoma* Schröder, 1882. **A**. Specimen MB.C.32168 (Neben and Krueger Coll.) from Niederfinow (Brandenburg); cross section. **B–D**. Ontogenetic development of the conch width index (CWI), umbilical width index (UWI), whorl width index (WWI) and whorl expansion rate (WER). Scale bar units = 1 mm.

Table 5. Conch measurements, ratios and rates of *Trocholites macrostoma* Schröder, 1882.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.32167	39.8	17.0	9.9	21.1	7.1	0.43	1.72	0.53	1.48	0.28
minus 90°	36.5	16.2	9.3	17.5	–	0.44	1.75	0.48	–	–
minus 180°	32.7	15.7	8.7	15.1	–	0.48	1.81	0.46	–	–
MB.C.32168	35.44	15.11	8.67	18.95	7.09	0.43	1.74	0.53	1.56	0.18
minus 180°	28.36	15.39	7.82	13.78	5.61	0.54	1.97	0.49	1.55	0.28
minus 360°	22.74	12.74	6.76	10.96	5.59	0.56	1.88	0.48	1.76	0.17
minus 540°	17.15	9.99	5.02	7.88	3.81	0.58	1.99	0.46	1.65	0.24
minus 720°	13.34	7.92	4.25	5.87	3.26	0.59	1.86	0.44	1.75	0.23
minus 900°	10.08	6.14	3.23	4.08	2.66	0.61	1.90	0.40	1.84	0.18
minus 1080°	7.43	4.89	2.78	2.56	2.28	0.66	1.76	0.34	2.08	0.18
minus 1260°	5.15	3.75	2.09	1.43	1.76	0.73	1.80	0.28	2.31	0.16
minus 1440°	3.39	3.26	1.63	0.61	1.31	0.96	2.00	0.18	2.66	0.20
minus 1620°	2.08	3.03	1.15	–	1.08	1.46	2.65	–	4.30	0.06

The other specimen (MB.C.32168) assigned here to *T. macrostoma* differs from the neotype only by the small decrease in absolute whorl width in the latest ontogeny. Specimen MB.C.32168 additionally differs from *T. freyjae* sp. nov., *T. baldri* sp. nov., *T. glacialis* sp. nov., *T.* sp. 1, *T.* sp. 2 and *T.* sp. 3 in the ontogenetic trajectories of several characters between conch diameters of 5 to 25 mm. In this growth interval, the CWI decreases and UWI increases significantly in MB.C.32168; the WWI is higher than in the other species (Fig. 11). In addition, the whorl width (but not whorl height) of the terminal body chamber appears to decrease close to the aperture.

In *Trocholites depressus*, the last whorl tends to be more discoidal (CWI as low as 0.33 vs over 0.40 in *T. macrostoma*) and more rapidly expanding (WER ~ 1.65 vs 1.52) with a less depressed (WWI = 1.25–1.60 vs ~1.73) whorl profile; the shell ornament has ribs (vs irregularly thick lirae in *T. macrostoma*). The specimens of *Trocholites macrostoma* differ from the holotype of *T. luna* sp. nov. in that the last whorl of the conch is less expanded (WER ~ 1.52 vs 1.60), the whorl profile is more depressed (WWI ~ 1.73 vs 1.55; the venter of body chamber lacks annuli, only lirae are present.

Trocholites contractus Schröder, 1891
Figs 1B, 15; Table 6

Trocholites contractus Schröder, 1891: 19(157), pl. 1(24) fig. 2.

Trocholites contractus – Sweet 1958: 95, pl. 7, figs 1–2. — Neben & Krueger 1971: pl. 32 figs 6–7. — Dzik 1984: 43, text-figs 11, 12.52, pl. 5 fig. 4, pl. 6 fig. 1.
? *Trocholites contractus* – Dzik 1984: pl. 5 fig. 4, pl. 6 fig. 1.

Diagnosis

Species of the genus *Trocholites* with an adult conch diameter of about 33 mm. Conch in the last whorl thickly discoidal (CWI ~ 0.46) and evolute (UWI ~ 0.53) with low coiling rate (WER ~ 1.60). Whorl profile moderately depressed (WWI ~ 1.95) with rounded venter and flanks. Whorl width and whorl height decreasing in last half volution (CWI ~ 0.70–0.50; wh / dm ~ 0.30–0.20). Siphuncle marginodorsal in position.

Table 6. Conch measurements, ratios and rates of *Trocholites contractus* Schröder, 1882.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.32169	32.8	15.0	7.5	17.3	6.9	0.46	1.99	0.53	1.61	0.08
minus 90°	29.3	16.0	8.8	12.3	–	0.55	1.83	0.42	–	–
minus 180°	26.0	17.0	8.0	11.3	–	0.65	2.12	0.43	–	–

Type material

Neotype (designated here)

GERMANY – **Berlin** • Lübars; Lasnamägi Regional Stage; Neben and Krueger Coll.; figured by Neben and Krueger (1971: pl. 32 figs 6–7), re-illustrated here in Fig. 15; MB.C.32169.

Description

Neotype MB.C.32169 (Fig. 15) is an adult, well-preserved internal mould with a conch diameter of 33 mm; almost 3 whorls are preserved. The last half volution shows conspicuous changes in the shape of the conch morphology, where the terminal body chamber undergoes a significant reduction of width and height. During the last half whorl, in which the conch diameter increases from 26 mm to 33 mm, the general morphology changes from thinly pachyconic to discoidal (CWI decreases from 0.65 to 0.46) and from subevolute to evolute (umbilicus widens, UWI increases from 0.43 to 0.53); the last half whorl becomes less strongly depressed (WWI decreases from 2.12 to 1.99), the coiling rate is low (WER = 1.61) and the last whorl is weakly embracing (IZR = 0.08) at the mature aperture. The body chamber clearly decreases in width starting from its beginning (from about 17 mm to 15 mm), and also in height starting at about its mid-length (from 8.8 mm to 7.5 mm; wh/dm = 0.30–0.23). The phragmocone chambers are moderately long (RCL = 0.23).

Remarks

Trocholites contractus was described by Schröder (1891: 19(157), pl. 1(24) fig. 2; see also Fig. 1B herein) on the basis of a single specimen from the locality "Rosehnen in Samlande", present day Priboi on the Samland Peninsula, Kaliningrad Region of Russia. The specimen came from a block of the *Echinosphaerites* Limestone (Darriwilian, Middle Ordovician) and Schröder (1891) stated that it had been kept in the "Regional Museum of Königsberg" (Kaliningrad). Since that collection was most probably destroyed during World War II (pers. com. D. Weyer, Berlin, 2022), a neotype has been

Fig. 15. *Trocholites contractus* Schröder, 1891; neotype MB.C.32169 (Neben and Krueger Coll.) from Lübars near Berlin; previously figured by Neben & Krueger (1971: pl. 32 figs 6–7); ventral, lateral and dorsal views; reconstruction of apertural view. Scale bar units = 1 mm.

selected and described here. The proposed neotype corresponds stratigraphically to the holotype. Both specimens do not differ significantly from each other morphologically.

Trocholites contractus differs from other species of the genus in the whorl profile; its whorls are wider, more depressed and more strongly embracing. In these aspects, the neotype of *T. contractus* resembles the preadult growth stage of *T. hospes* (Fig. 12). However, individuals of *T. hospes* attain a much larger adult size (up to 60 mm in diameter), while in *T. contractus* the size of the conch in the terminal stage is only about 33 mm. Furthermore, a characteristic feature that readily distinguishes *T. contractus* from *T. hospes* and any other trocholitid species is the marked and rapid decrease in whorl width, whorl height and impression rate of the terminal body chamber.

Geographic and stratigraphic occurrence

Kaliningrad Region of Russia, northern Germany, Poland, Norway, Estonia; Darriwilian, Middle Ordovician.

Trocholites remelei Schröder, 1891
Fig. 16; Table 7

Trocholites Remeléi Schröder, 1891: 18(156).

Trocholites remeléi – Neben & Krueger 1971: pl. 32 figs 4–5.

non *Trocholites incongruus* – Angelin 1880: 11, pl. 9 figs 15–18.
non *Trocholites remeléi* – Neben & Krueger 1971: pl. 32 figs 1–3.

Diagnosis

Species of the genus *Trocholites* with conch at dm 22 mm thinly pachyconic (CWI ~ 0.60) and subevolute (UWI ~ 0.30). Whorl profile weakly depressed (WWI ~ 1.43) and moderately impressed (IZR ~ 0.34), rounded from lateral sides and slightly flattened from ventral side. Coiling rate is moderate (WER ~ 1.88). Shell ornament with low, regularly spaced clusters of raised lirae manifested on internal mould as annular ridges.

Fig. 16. *Trocholites remelei* Schröder, 1891; lectotype MB.C.11562 (Dames Coll., 1881) from Lerkaka (Öland); previously figured by Neben & Krueger (1971: pl. 32 figs 4–5); ventral and lateral views; reconstruction of apertural view. Scale bar units = 1 mm.

Table 7. Conch measurements, ratios and rates of *Trocholites remelei* Schröder, 1891.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.11562	21.5	12.6	8.8	6.7	5.8	0.59	1.43	0.31	1.88	0.34
minus 90°	18.4	11.0	7.6	5.7	–	0.60	1.45	0.31	–	–
minus 180°	15.4	9.7	6.0	5.1	–	0.63	1.61	0.33	–	–

Type material

Lectotype

SWEDEN – **Öland** • 1 spec.; Lerkaka; Lasnamägi or Uhaku regional stages; 1881; Dames Coll.; illustrated by Neben & Krueger (1971: pl. 32 figs 4–5), re-illustrated here in Fig. 16; MB.C.11562.

Description

Lectotype MB.C.11562 (Fig. 16) is a conch with 22 mm diameter. At least three whorls are visible; the last half whorl belongs to the body chamber. In the last half volution, the conch becomes slightly more slender (CWI decreases from 0.63 to 0.59) and remains subevolute (UWI ~ 0.32) with a moderate coiling rate (WER = 1.88). The body chamber is moderately embracing the preceding whorl (IZR = 0.34) and less depressed (WWI decreases from 1.61 to 1.43). The shell is ornamented with low, regularly spaced clusters of raised lirae, which are visible on the internal mould as annular ridges; the lirae extend with a sinus across the venter.

Remarks

Angelin (1880: pl. 9 figs 15–18) illustrated two specimens of *Trocholites incongruus* from Darriwilian strata of Sweden. Remelé (1880) stated that these specimens do not belong to *T. incongruus* and subsequently Schröder (1891) established the new species *Trocholites remelei* based on these specimens. Schröder also assigned a small late Darriwilian trocholitid (MB.C.11562; Fig. 16) from the Island of Öland (Sweden) to *T. remelei*. This was illustrated by Neben & Krueger (1971) and is chosen here as lectotype. Examination of the two specimens NRM Mo 152355 and NRM Mo 152354 of Angelin (1880) revealed that they are more discoidal (CWI = 0.50 and 0.41 vs 0.59), with a wider umbilicus and less impressed whorls. They possess a different type of ornament than the lectotype and each is assigned to a different species below (*Trocholites tureki* sp. nov. and *T. freyjae* sp. nov.).

It has to be noted that Neben & Krueger (1971) also included syntype MB.C.11555.2 of *T. hospes* (Remelé 1890: pl. 2 fig. 4) in *T. remelei*; however, this is not accepted here since no annular ornament elements are present on the shell surface or internal mould surface of this specimen (Fig. 8D).

Lectotype MB.C.11562 is unique among specimens of *Trocholites* because of the relatively stout conch (Fig. 12C) combined with narrow umbilicus and prominent annuli that are visible on the shell surface as well as on internal mould.

Trocholites baldri sp. nov.
urn:lsid:zoobank.org:act:EE665BAD-AF26-4024-A9C5-8A558A5D376F
Fig. 17; Table 8

Diagnosis

Species of the genus *Trocholites* with an adult conch diameter of more than 30 mm. Conch in the last whorl thickly discoidal (CWI ~ 0.50) and evolute (UWI ~ 0.45) with moderately high coiling rate (WER ~ 1.75). Whorl profile moderately depressed (WWI ~ 1.80) with rounded flanks and venter,

Table 8. Conch measurements, ratios and rates of *Trocholites baldri* sp. nov.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.32170	30.9	15.5	8.6	14.1	7.6	0.50	1.80	0.46	1.76	0.12
minus 90°	28.7	15.8	9.2	11.6	–	0.55	1.72	0.40	–	–
minus 180°	24.1	14.8	8.1	8.9	–	0.61	1.83	0.37	–	–

weakly embracing (IZR ~ 0.14). Whorl width and whorl height slightly decreasing in last quarter volution. Phragmocone chambers moderately long (RCL ~ 0.28). Suture line nearly straight.

Etymology

After Baldr, the Norse god of light, beauty and purity.

Type material

Holotype

GERMANY – **Mecklenburg-Vorpommern** • Göhren (Isle of Rügen); Lasnamägi Regional Stage; illustrated in Fig. 17; MB.C.32170.

Description

Holotype MB.C.32170 (Fig. 17) is a specimen with a conch diameter of 31 mm; the specimen is largely an internal mould with few shell remnants. The body chamber is preserved for a little more than half a volution in length and decreases slightly in width and height; the whorl width is reduced from 9.2 mm to 8.6 mm and the whorl height from 15.8 mm to 15.5 mm. This means that during the last half volution the conch becomes markedly narrower (CWI decreases from 0.61 to 0.50) and increasingly umbilicate (UWI increases from 0.37 to 0.46) with a terminal coiling rate of WER = 1.76. During this growth interval, the whorl profile is depressed (WWI decreases from 1.83 to 1.72) and weakly impressed dorsally (IZR = 0.12 at the maximum whorl height) with broadly rounded flanks and venter. Fine traces of transverse ornament elements are locally preserved on the shell surface. The phragmocone chambers are moderately long (RCL = 0.28) in the last volution; the suture line is almost straight.

Remarks

Trocholites baldri sp. nov. is most similar to the species *T. macrostoma*, *T. freyjae* sp. nov., *T. glacialis* sp. nov., *T.* sp. 1 and *T.* sp. 3 but differs in the decrease of both whorl width and whorl height of the terminal body chamber.

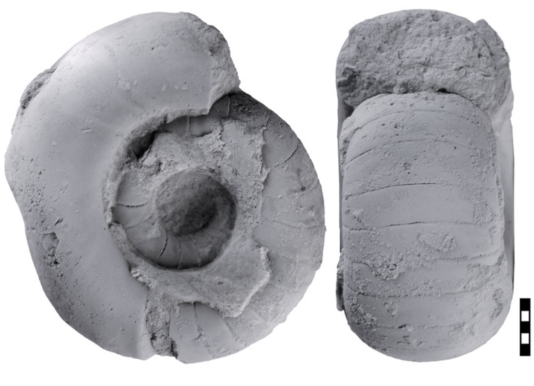

Fig. 17. *Trocholites baldri* sp. nov.; holotype MB.C.32170 from Göhren (Isle of Rügen, Mecklenburg-Vorpommern); lateral and dorsal views. Scale bar units = 1 mm.

Compared to the specimens of *Trocholites depressus*, the holotype of *T. baldri* sp. nov. is stouter (CWI ~ 0.50 vs 0.35–0.40), expands more rapidly (WER ~ 1.75 vs 1.65) and the whorl profile is more depressed (WWI ~ 1.80 vs 1.25–1.60).

Rather similar in conch geometry to the holotype of *T. baldri* sp. nov. is the neotype of *T. contractus*; however, in *T. contractus*, the decrease of body chamber width and height is much greater, the phragmocone chambers are slightly shorter and the suture line has a deeper ventral lobe.

Trocholites freyjae sp. nov.
urn:lsid:zoobank.org:act:7EC4E3F9-662D-4F88-BC4F-81779A9EB017
Fig. 18; Table 9

Trocholites incongruus – Angelin 1880: 11, pl. 9 fig. 17.

Diagnosis

Species of the genus *Trocholites* with an adult conch diameter of 30–40 mm. Conch in the last whorl thickly discoidal (CWI = 0.45–0.50) and evolute (UWI ~ 0.46). Whorl profile moderately depressed (WWI = 1.60–1.80) with trumpet-shaped aperture (ventral and lateral flares). Whorl width slightly increasing, whorl height slightly decreasing in last quarter volution. Phragmocone chambers moderately long to long (RCL = 0.20–0.40). Suture line straight or with shallow ventral lobe. Siphuncle subdorsal in position with relative diameter of ~ 0.20.

Etymology

After Freyja, the Norse goddess of love, beauty, fertility and war.

Type material

Holotype

GERMANY • probably Brandenburg; Neben and Krueger Coll.; illustrated in Fig. 18A; MB.C.32171.

Paratypes

ESTONIA • 1 spec.; Osmussaar; Lasnamägi Regional Stage; illustrated in Fig. 18C; TUG 46-167.

GERMANY – **Brandenburg** • 1 spec.; Niederfinow; Lasnamägi Regional Stage; Neben and Krueger Coll.; illustrated in Fig. 18B; MB.C.32172.

SWEDEN • 1 spec.; Altsarbyn (earlier spelling Alsarbyn, Dalarna); Darriwilian Stage; Angelin Coll.; figured by Angelin (1880: pl. 9 fig. 17), re-illustrated here in Fig. 18D; NRM Mo 152355.

Description

Holotype MB.C.32171 (Fig. 18A) is a specimen in the terminal growth stage with 31 mm conch diameter. With a diameter of 31 mm, the conch is discoidal (CWI = 0.48) and evolute (UWI = 0.46). The whorl profile is moderately depressed (WWI = 1.85) and impressed dorsally; it possesses broadly rounded flanks and venter. The body chamber is almost complete at about 220 degrees in length. In the last quarter, it slightly decreases in height from 8.4 mm to 8.0 mm. The aperture possesses conspicuous lateral and ventral flares, which give the aperture a trumpet-like appearance. Since the body chamber is exfoliated, the shell ornament is visible only on the chambered part of the conch, where it consists of rather sharp, densely spaced rursiradiate lirae; the internal mould of the body chamber shows faint impressions of raised lirae or narrow annuli.

Paratype MB.C.32172 (Fig. 18B) is a conch with 34 mm diameter and consists of 3.25 volutions; more than the last half whorl belongs to the incomplete body chamber. In the last half volution, the conch is thinly discoidal (CWI = 0.43) and evolute (UWI = 0.49). The whorl height decreases from 8.8 mm at the beginning of the body chamber to 8.2 mm in its apertural end; the whorl width of the body chamber increases slightly in this interval from 13.8 mm to14.3 mm. The whorl profile becomes increasingly depressed in the last half a whorl (WWI changes from 1.58 to 1.74); it has rounded flanks and a very slightly flattened venter. The shell is ornamented with irregularly spaced, rursiradiate lirae, which are occasionally approximated and raised. The phragmocone chambers are moderately long (RCL ranges between 0.20 and 0.35) in the last half of the phragmocone.

Paratype TUG 46-167 (Fig. 18C) is a preadult specimen with 28 mm conch diameter; one third of the last volution is occupied by the body chamber. At its maximum diameter, the conch is discoidal (CWI = 0.44) and widely umbilicate (UWI = 0.52). The whorl profile shows broadly rounded flanks and a slightly flattened venter; it is moderately depressed (WWI = 1.80). Both the whorl width and whorl height increase gradually, but it appears that the whorl height in the last quarter whorl starts to decrease slightly. The phragmocone chambers are moderately long (RCL = 0.30–0.40) in the last whorl; the suture line is almost straight with a very shallow external lobe.

Paratype NRM Mo 152355 (Fig. 18D) is a preadult conch with 26 mm diameter with two whorls preserved; the body chamber is not present. At the maximum diameter, the conch is thickly discoidal

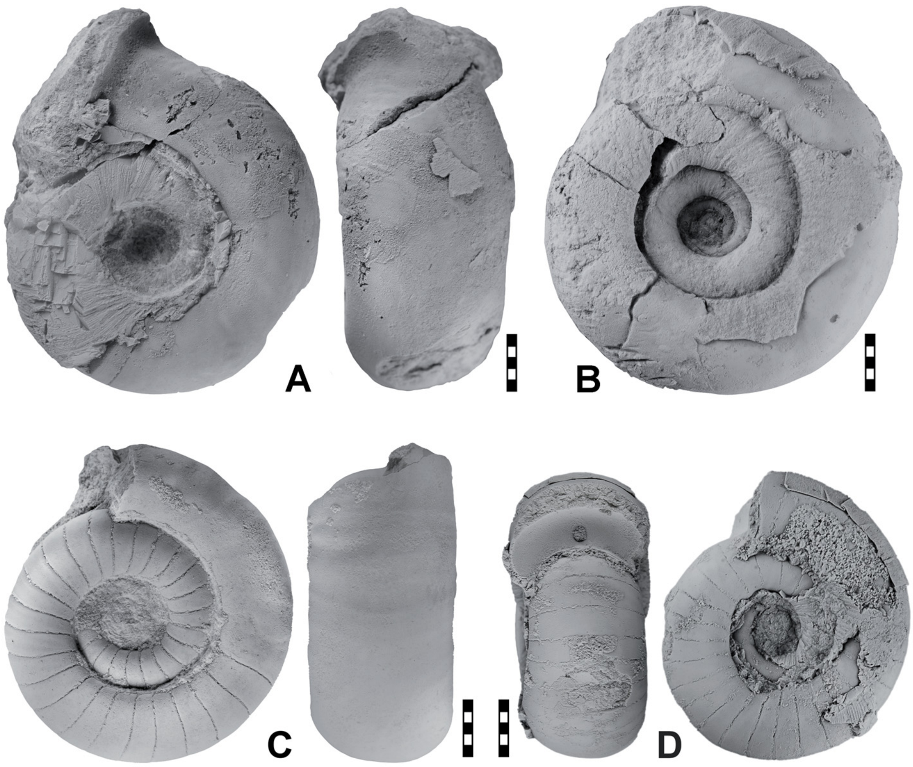

Fig. 18. *Trocholites freyjae* sp. nov. **A**. Holotype MB.C.32171 (Neben and Krueger Coll.), probably from Brandenburg; lateral and ventral views. **B**. Paratype MB.C.32172 (Neben and Krueger Coll.) from Niederfinow (Brandenburg); lateral view. **C**. Paratype TUG 46-167 from Osmussaar (Estonia); lateral and ventral views. **D**. Paratype NRM Mo 152355 (Angelin Coll.) from Altsarbyn (earlier spelling Alsarbyn, Dalarna, Sweden); previously figured by Angelin (1880: pl. 9 fig. 17); dorsal and lateral views. Scale bar units = 1 mm.

Table 9. Conch measurements, ratios and rates of *Trocholites freyjae* sp. nov.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.32172	33.6	14.3	8.2	16.6	–	0.43	1.74	0.49	–	–
minus 90°	31.0	13.9	8.7	13.4	–	0.45	1.60	0.43	–	–
MB.C.32171	30.8	14.8	8.0	14.3	–	0.48	1.85	0.46	–	–
minus 90°	27.0	13.7	8.4	10.4	–	0.51	1.63	0.39	–	–
TUG 46-167	27.3	12.0	6.7	14.3	–	0.44	1.80	0.52	–	–
minus 90°	24.5	11.8	6.7	11.7	–	0.48	1.76	0.48	–	–
NRM Mo 152355	25.6	13.0	7.4	–	5.70	0.50	1.76	–	1.65	–
minus 90°	22.0	–	6.6	–	–	–	–	–	–	–
minus 180°	–	12.0	–	–	–	–	–	–	–	–

(CWI = 0.50); the latest whorl profile is moderately impressed (IZR = 0.23) and moderately depressed (WWI = 1.76) with rounded flanks and venter. The coiling rate is low (WER = 1.65). The ornament is preserved only in small shell relicts; it consists of sharp, regularly spaced lirae and does not leave any traces on the internal mould. The phragmocone chambers are moderately long (RCL = 0.25 in the external volution); the latest two chambers appear to be shortened. The suture line is almost straight with a very shallow and wide external lobe. At the maximum diameter, the siphuncle has a subdorsal position (RSP = 0.86) and a relative diameter (RSH) of about 0.20.

Remarks

Trocholites freyjae sp. nov. differs from *T. macrostoma*, *T. contractus*, *T. baldri* sp. nov., *T. glacialis* sp. nov., *T.* sp. 1 and *T.* sp. 3 in the combination of whorl width increase and whorl height decrease in the terminal body chamber.

In *Trocholites depressus*, the whorl height may slightly decrease in last quarter volution, as in *T. freyjae* sp. nov. However, *T. depressus* differs in that the last whorl is more discoidal (CWI up to 0.40 vs up to 0.50), the whorl profile tends to be less depressed (WWI = 1.25–1.60 vs 1.60–1.80) and the siphuncle is marginodorsal (vs subdorsal) in position and relatively wider in diameter (RSH ~ 0.30 vs 0.20 in the last whorl).

Paratype NRM Mo 152355 was previously figured by Angelin (1880) and used by Schröder (1891) as a syntype of *Trocholites remelei*. The type collection of that species consisting of three specimens (NRM Mo 152355, NRM Mo 152354, MB.C.11562) is revised herein and all three were found to represent different species.

Paratype NRM Mo 152355 differs from MB.C.11562 (lectotype of *T. remelei*) by being more discoidal (CWI = 0.50 at dm 26 mm vs 0.59 at dm 22 mm) with less rapidly expanding whorls (WER = 1.65 at dm 26 mm vs 1.87 at dm 22 mm); its whorl profile is more depressed (WWI = 1.76 at dm 26 mm vs 1.43 at dm 22 mm) and less impressed (IZR = 0.23 at dm 26 mm vs 0.34 at dm 22 mm).

Paratype NRM Mo 152355 is additionally distinguished from NRM Mo 152354 (holotype of *Trocholites tureki* sp. nov.) because it is stouter (CWI = 0.50 at dm 26 mm vs 0.41 at dm 22 mm) with more strongly depressed whorls (WWI = 1.76 at dm 26 mm vs 1.46 at dm 22 mm). Most remarkably, the shell surface of NRM Mo 152355 is ornamented only by sharp lirae and lacks any annuli or ribs, unlike in the representatives of *T. remelei* and *T. tureki*.

Trocholites glacialis sp. nov.
urn:lsid:zoobank.org:act:09A65391-6E39-4073-8C94-89570D4005DC
Fig. 19; Table 10

Diagnosis

Species of the genus *Trocholites* with an adult conch diameter of 35 mm. Conch in the last whorl thickly discoidal (CWI ~ 0.52) and evolute (UWI ~ 0.45). Whorl profile moderately depressed (WWI ~ 1.80) with rounded flanks and venter. Whorl width and whorl height slightly increasing in last quarter volution. Shell ornament with irregularly thick, rursiradiate lirae, adaperturally raised; sharp lirae on inner whorls. Phragmocone chambers moderately long (RCL ~ 0.25). Suture line straight.

Etymology

From the Latin '*glacialis*' (adjective), meaning 'glacial' or 'frozen'.

Type material

Holotype

POLAND – **West Pomerania** • Ustronie Morskie; Lasnamägi or Uhaku Regional Stage; Müldner Coll.; illustrated in Fig. 19A; MB.C.32173.

Paratype

GERMANY – **Berlin** • 1 spec.; Schmargendorf; Ordovician; 1906; Schmidt Coll.; illustrated in Fig. 19B; MB.C.11561.

Description

Holotype MB.C.32173 (Fig. 19A) is an incomplete specimen with a conch diameter of 35 mm and shows about 3.5 whorls. At maximum diameter, the conch is discoidal and evolute (CWI = 0.52; UWI = 0.45); the last whorl is moderately depressed (WWI = 1.81). Both whorl height and whorl width slowly gradually increase in the last preserved whorl. The ornament is only preserved in small areas and consists of irregularly coarse, rursiradiate lirae, which are raised near the aperture. Sharp lirae are present in the inner whorls. The length of the body chamber and shape and distance of suture lines cannot be determined.

Fig. 19. *Trocholites glacialis* sp. nov. **A**. Holotype MB.C.32173 (Müldner Coll.) from Ustronie Morskie (West Pomerania); lateral and ventral views. **B**. Paratype MB.C.11561 (Schmidt Coll., 1906) from Schmargendorf (Berlin); dorsal and lateral views. Scale bar units = 1 mm.

Table 10. Conch measurements, ratios and rates of *Trocholites glacialis* sp. nov.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.11561	34.6	17.6	9.8	15.4	–	0.51	1.80	0.44	–	–
MB.C.32173	34.5	17.9	9.9	15.6	–	0.52	1.81	0.45	–	–

Paratype MB.C.11561 (Fig. 19B) with nearly identical dimensions and ratios shows that the body chamber occupies a little more than half of the last volution. The phragmocone chambers are moderately long (RCL ~ 0.25); the suture line is nearly straight.

Remarks

Trocholites glacialis sp. nov. differs from *T. contractus*, *T. freyjae* sp. nov., *T. baldri* sp. nov., *T*. sp. 1 and *T*. sp. 3 in the increase of both whorl width and whorl height in the terminal body chamber.

Trocholites macrostoma has a greater adult conch diameter (42 vs 35 mm) and in the last whorl, the conch is more discoidal (CWI ~ 0.43 vs 0.52) and more evolute (UWI ~ 0.53 vs 0.45).

In the last whorl of *Trocholites depressus*, the conch is much more discoidal (CWI up to 0.40 vs ~ 0.52), the whorl profile is much less depressed (WWI 1.25–1.60 vs ~ 1.80) and the whorl height may slightly decrease adaperturally; phragmocone chambers tend to be longer (RCL = 0.30–0.40 vs 0.25) and the shell surface has ribs.

Trocholites kadakaensis sp. nov.

urn:lsid:zoobank.org:act:DF7112C8-6722-44CB-B68C-E09E540C98E6

Fig. 20; Table 11

Diagnosis

Species of the genus *Trocholites* with an adult conch diameter of more than 42 mm. Conch in the last whorl thickly discoidal (CWI ~ 0.48) and evolute (UWI ~ 0.46). Whorl profile moderately depressed (WWI ~ 1.80) with rounded flanks and venter, moderately to weakly embracing (IZR = 0.35–0.15). Whorl width and whorl height slightly decreasing in last half volution; the coiling rate decreases to WER ~ 1.70. Phragmocone chambers at 30 mm diameter moderately long (RCL ~ 0.30). Suture line nearly straight.

Etymology

From Kadaka near Tallinn (Estonia), the locality of the holotype.

Type material

Holotype

ESTONIA • Kadaka (Tallinn); Väo Formation, late Darriwilian Stage; 1920; Deubel Coll.; illustrated in Fig. 20; MB.C.11563.

Paratype

ESTONIA • 1 spec.; Tallinn; late Darriwilian Stage; Prantl and Zázvorka Coll.; NM-S6032.

Description

Holotype MB.C.11563 (Fig. 20) is an incompletely preserved conch, which is almost in the terminal growth stage, measuring 42 mm in diameter. It consists of 3.25 volutions of which the last quarter volution belongs to the body chamber. In the last half volution, both the whorl width and whorl height decrease (from 20.1 mm to 19.8 mm and from 11.5 mm to 10.9 mm, respectively). The conch is discoidal (CWI =

Table 11. Conch measurements, ratios and rates of *Trocholites kadakaensis* sp. nov.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.11563	41.2	19.8	10.9	18.8	9.3	0.48	1.82	0.46	1.67	0.15
minus 90°	36.1	20.1	11.2	–	–	0.56	1.80	–	–	–
minus 180°	30.3	–	11.5	13.0	7.5	–	–	0.43	1.76	0.35
NM-S6032	38.7	–	9.9	18.0	–	–	–	0.47	–	–
minus 180°	28.9	–	10.8	–	–	–	–	–	–	–

0.48) and subevolute to evolute (UWI = 0.46). The whorl profile is moderately depressed (WWI = 1.82) with broadly rounded flanks and venter; it changes from strongly to weakly embracing (IZR decreases from 0.36 to 0.15). The coiling rate (WER) decreases from a value of 1.76 to 1.67 (WER_{wh} changes from about 2.60 to 1.85 in the last half a whorl). Only small remains of the shell are preserved; its ornament consists of indistinct, low lirae. On the venter of the terminal body chamber, there are extremely fine and low longitudinal (spiral) lines. The phragmocone chambers are moderately long (RCL = 0.30 at dm = 30 mm). The suture line is almost straight and forms a very shallow and wide external lobe.

Paratype NM-S6032 is a partially preserved conch in the late ontogenetic stage with a maximum measurable diameter of 39 mm. Two volutions are preserved of which the last ~150 degrees of the outer volution belong to the body chamber. In the last half volution, the whorl height decreases from 10.8 to 9.9 mm. The conch is subevolute to evolute with UWI = 0.47 at the largest conch diameter. The whorl profile has broadly rounded flanks and a broadly rounded venter. The coiling rate based on whorl height (WER_{wh}) decreases from 2.55 to 1.80 in the last half whorl. The suture line is almost straight with a very shallow and wide external lobe. At a diameter of 29 mm, remains of the siphuncle are preserved; the siphuncle is located near the dorsal shell wall but it is not in contact with it.

Remarks

Holotype MB.C.11563 belongs to the representatives of *Trocholites* with a relatively large conch. Aside from the size, it has moderately long phragmocone chambers (RCL ~ 0.30) and the body chamber is contracted in both width and height. Very similar to this specimen is holotype MB.C.9718 of *T. zaryensis* sp. nov., but this is smaller in the adult size (36 mm) and differs in the shape of the terminal body

Fig. 20. *Trocholites kadakaensis* sp. nov.; holotype MB.C.11563 (Deubel Coll., 1920) from Kadaka (Tallinn; Estonia); dorsal, lateral and ventral views. Scale bar units = 1 mm.

chamber. In *T. zaryensis*, the height of the last whorl shows an increase in contrast to a decrease in *T. kadakaensis* sp. nov.; it also shows a slight flattening of the venter.

Similar in conch geometry is also the holotype of *T. baldri* sp. nov. In its last whorl, however, the decrease of the body chamber height is greater than in the holotype of *T. kadakaensis* sp. nov.; the former is also smaller in adult size (~ 30 mm).

The decrease of the body chamber width and height is present also in the neotype of *Trocholites contractus*. In that specimen, however, the proportions of the body chamber change much more rapidly and the adult conch diameter is smaller (~ 33 mm vs 41 mm). In addition, umbilicus in the last whorl of *T. contractus* is wider (UWI ~ 0.53 vs 0.46), the expansion rate is lower (WER ~ 1.60 vs 1.70) and the whorl profile is more depressed (WWI ~ 1.95 vs 1.80); phragmocone chambers are longer (RCL ~ 0.23 vs 0.30).

The two specimens of *T. vodickai* sp. nov. differ because their last whorl is more discoidal (CWI ~ 0.40 vs 0.48) and the whorl profile is much less depressed (WWI ~ 1.25–1.50 vs 1.80) without any distinct decrease in width and height towards the terminal aperture.

The last whorl in the holotype of *Trocholites splendor* sp. nov. differs in having a narrower umbilicus (UWI ~ 0.35 vs 0.46), less depressed (WWI ~ 1.35 vs 1.80) whorl profile with increasing instead of decreasing whorl width and whorl height of the terminal body chamber.

The holotype of *Trocholites ruedemanni* is similar to the holotype of *T. kadakaensis* sp. nov. in expansion rate and imprint zone rate of the adult growth stage but differs from it by the slight uncoiling of the mature body chamber, shell ornament (nodes and costae) and a narrower umbilicus (UWI = 0.32 vs 0.43 at dm ~ 30 mm).

In the apertural part of the body chamber of the specimen MB.C.11563, there are several circular openings with a diameter of ~ 3 mm; these are identified as borings that belong to the ichnospecies *Trypanites sozialis* Eisenack, 1934 (see Knaust *et al.* 2023; Vinn *et al.* 2023).

Trocholites luna sp. nov.
urn:lsid:zoobank.org:act:0E391219-F3BE-44A3-8ECB-42526225CF54
Fig. 21; Table 12

Diagnosis

Species of the genus *Trocholites* with an adult conch diameter of about 50 mm. Conch in the last whorl thinly discoidal (CWI ~ 0.38) and evolute (UWI ~ 0.52) with low coiling rate (WER ~ 1.60). Whorl

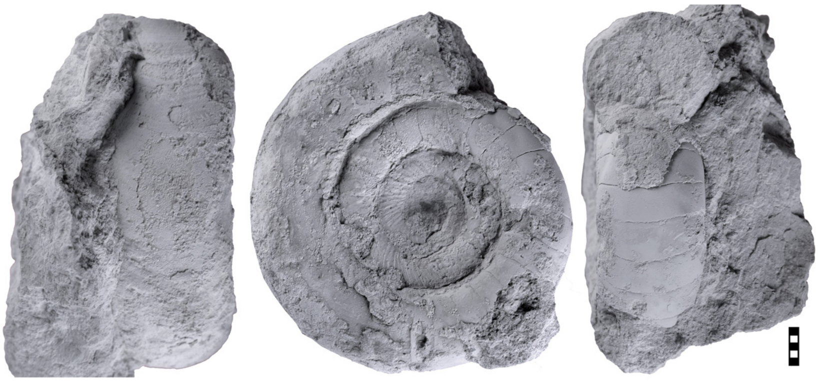

Fig. 21. *Trocholites luna* sp. nov.; holotype MB.C.32174 (Krueger 1970 Coll.) from Oderberg (Brandenburg); ventral and lateral views. Scale bar units = 1 mm.

Table 12. Conch measurements, ratios and rates of *Trocholites luna* sp. nov.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.32174	47.1	18.0	11.6	24.5	9.9	0.38	1.56	0.52	1.60	0.14
minus 90°	42.1	–	11.7	21.3	–	–	–	0.51	–	–
minus 180°	37.5	–	10.8	18.6	–	–	–	0.50	–	–

profile moderately depressed (WWI ~ 1.55) with rounded flanks and slightly flattened venter, weakly embracing (IZR ~ 0.14). Shell ornament with raised lirae or accumulation of lirae in the inner whorls, venter of body chamber with low, regularly spaced annuli and fine lirae. Phragmocone chambers long (RCL ~ 0.38). Suture line straight.

Etymology

From the Latin '*luna*' (nomen) = 'the Moon', referring to the shape of the relatively large conch of the holotype.

Type material

Holotype

GERMANY – **Brandenburg** • Oderberg; Ordovician; 1970; Krueger Coll.; illustrated in Fig. 21; MB.C.32174

Description

Holotype MB.C.32174 (Fig. 21) is a specimen partially embedded in the rock matrix. The conch has a diameter of 48 mm and represents the adult growth stage. It is thinly discoidal (CWI = 0.38) and evolute (UWI = 0.52) with a low coiling rate (WER = 1.60). In the last half volution, the whorl profile has continuously rounded flanks and slightly flattened venter; the whorl profile is moderately depressed (WWI = 1.56) and weakly impressed dorsally (IZR = 0.14). The body chamber is longer than half of a volution; the proximity of aperture is indicated by inconspicuous ventral flare. The ornament of the inner whorls consists of sharp raised lirae or accumulations of lirae; the venter of the terminal body chamber has low and equally spaced annuli and fine lirae. The phragmocone chambers are long (RCL = 0.38). The suture line is nearly straight, but extends with a very low saddle across the venter.

Remarks

Trocholites luna sp. nov. is similar to *T. vortex* sp. nov., but differs in the lower coiling rate (WER = 1.60 vs 1.80), the more slender conch (CWI = 0.38 vs 0.47), the more depressed whorl profile (WWI = 1.56 vs 1.45) and the wider umbilicus (UWI = 0.52 vs 0.45) in the adult growth stage.

The holotype of *Trocholites luna* sp. nov. is rather similar to the neotype of *T. macrostoma* with respect to conch width and umbilical width, but differs in the less depressed last whorl (WWI = 1.56 vs 1.72) and the presence of annuli on the venter of the body chamber.

The two specimens of *T. vodickai* sp. nov. differ from the holotype of *T. luna* sp. nov. in the smaller adult size (40 mm vs 50 mm); the last whorl in the former is less evolute (UWI ~ 0.46 vs 0.52) and the shell ornament in inner whorls has fine, rursiradiate lirae instead of sharply raised lirae or accumulation of lirae.

Table 13. Conch measurements, ratios and rates of *Trocholites splendor* sp. nov.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.32175	48.9	24.6	18.3	17.7	–	0.50	1.34	0.36	–	–
minus 90°	41.2	23.6	15.6	15.0	–	0.57	1.52	0.37	–	–

Trocholites splendor sp. nov.
urn:lsid:zoobank.org:act:F1186D76-F91F-4FA4-B804-E73305EE1E11
Fig. 22; Table 13

Diagnosis

Species of the genus *Trocholites* with an adult conch diameter of 50 mm. Conch in the last whorl thickly discoidal (CWI ~ 0.50) and subevolute (UWI ~ 0.35). Whorl profile weakly depressed (WWI ~ 1.35). Whorl width and whorl height slightly increasing in last quarter volution. Shell ornament with sharp lirae with fine growth lines on outer whorl; inner whorls with thin ribs or thickened lirae.

Etymology

From the Latin '*splendor*' (nomen), referring to the splendid ornament in the juvenile whorls in the holotype.

Type material

Holotype

POLAND – **West Pomerania** • Ustronie Morskie; probably Lasnamägi Regional Stage; Müldner Coll.; illustrated in Fig. 22; MB.C.32175.

Description

Holotype MB.C.32175 (Fig. 22) is a conch with 49 mm diameter and with 3.5 preserved volutions, the last of which is largely preserved as an internal mould. A little more than half of the last whorl belongs to the body chamber; at a short distance from the aperture, the internal mould possesses a conspicuous, thick ridge with a sinus-like ventral extension. The conch is thickly discoidal (CWI decreases from 0.57 to 0.50 in the last quarter of the last whorl) and subevolute (UWI = 0.36); the whorl profile is weakly depressed (WWI decreases from 1.52 to 1.34 in the last quarter whorl). The shell ornament is best preserved in inner whorls, where it consists of thin ribs or thickened lirae. Sharp lirae with fine growth lines are locally preserved in outer whorl; the ornament elements are not visible on the surface of the

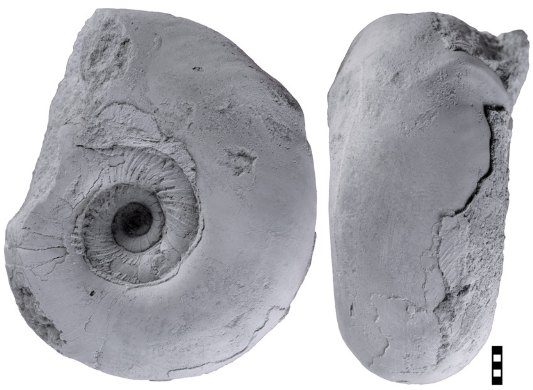

Fig. 22. *Trocholites splendor* sp. nov.; holotype MB.C.32175 (Müldner Coll.) from Ustronie Morskie (West Pomerania); lateral and ventral views. Scale bar units = 1 mm.

internal mould. The length of the phragmocone chambers can be measured in the first 2.5 whorls; the chambers are very long in the earliest half a whorl (RCL = 0.81) and then become significantly shorter to RCL = 0.44. At the end of the phragmocone, the RCL is only about 0.20. The conspicuous thickening or ridge near the aperture of the terminal body chamber is interpreted as a growth anomaly.

Remarks

The holotype of *Trocholites splendor* sp. nov. is closely similar to some specimens of *T. hospes*, but it possesses thin ribs or thickened lirae on the surface of inner whorls, instead of only fine lirae in *T. hospes*. The shell ornament alone may not be a reliable character to form a basis for species distinction; however, the conch of *T. splendor* is more slender (CWI = 0.50 at dm = 49 mm) and less depressed (WWI = 1.34 at dm = 49 mm) than in specimens of *T. hospes* (Fig. 12).

The last whorl in the holotype of *Trocholites kadakaensis* sp. nov. differs in being more evolute (UWI ~ 0.46 vs 0.35), more depressed (WWI ~ 1.80 vs 1.35) and decreasing instead of increasing whorl width and whorl height of the terminal body chamber.

Trocholites triangulus sp. nov.

urn:lsid:zoobank.org:act:DA076484-0576-40B8-8666-5C40700CFCB6

Fig. 23; Table 14

Diagnosis

Species of the genus *Trocholites* with an adult conch diameter of 26 mm. Conch in the last whorl thinly discoidal (CWI ~ 0.33) and evolute (UWI ~ 0.55). Whorl profile depressed (WWI ~ 1.50) with rounded flanks, venter narrowed down, whorl widest dorso-laterally. Whorl width and whorl height increasing in last quarter volution. Phragmocone chambers moderately long (RCL ~ 0.38). Suture line straight.

Etymology

From the Latin '*triangulus*' (nomen) = 'a triangle', referring to the shape of the apertural whorl profile of the holotype given by the narrowed venter.

Material examined

Holotype

GERMANY – **Mecklenburg-Vorpommern** • Göhren (Isle of Rügen); Lasnamägi Regional Stage; 1968; Krueger Coll.; illustrated in Fig. 23; MB.C.32176.

Fig. 23. *Trocholites triangulus* sp. nov.; holotype MB.C.32176 (Krueger Coll., 1968) from Göhren (Isle of Rügen, Mecklenburg-Vorpommern); lateral view and reconstruction of apertural view. Scale bar units = 1 mm.

Table 14. Conch measurements, ratios and rates of *Trocholites triangulus* sp. nov.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.32176	25.1	8.4	5.6	14.2	–	0.33	1.50	0.57	–	–
minus 180°	–	7.7	5.3	10.3	–	–	1.44	–	–	–

Description

Specimen MB.C.32176 (Fig. 23) is a small adult conch with only 25 mm diameter; it is extremely discoidal (CWI = 0.33) and evolute (UWI = 0.57) with a depressed last whorl (WWI = 1.50). The venter of the outer whorl is not rounded but is narrowed down and the whorl appears to be widest dorsolaterally. The relative chamber length (RCL) is 0.38. The body chamber has a length of slightly more than half a volution and its aperture possesses lateral and ventrolateral flares (the ventral part cannot be seen).

Remarks

The holotype of *Trocholites triangulus* sp. nov. is similar to specimens MB.C.32161 and MB.C.32160, which belong to *T. depressus*, and specimen MB.C.32182 (*T.* sp. 4) (Fig. 7). However, the former differs by the ventrally narrowed external volution. The arched, keel-like shape of the outer ventral side of the conch is known in specimens of *Trocholites gracilis* from the late Chazyan Valcour Limestone of New York (Flower 1943); the adult conch size (dm 24 mm) is similar to *Trocholites triangulus* and suture line in both species is essentially straight. The last half a whorl in the latter is, however, depressed, instead of slightly compressed (WWI = 1.50 vs 0.93).

Trocholites tureki sp. nov.
urn:lsid:zoobank.org:act:789D9C9E-67E0-45E5-9F31-3FCE54C8FB0F
Fig. 24; Table 15

Trocholites incongruus – Angelin 1880: 11, pl. 9 figs 15–16, 18.

Diagnosis

Species of the genus *Trocholites* with conch in adult growth stage discoidal (CWI ~ 0.40) and evolute (UWI ~ 0.48). Whorl profile weakly depressed (WWI ~ 1.46) and weakly impressed (IZR ~ 0.17), rounded from lateral and ventral side. Coiling rate is low (WER ~ 1.71). Shell ornament with low annuli and / or widely spaced, and lirae.

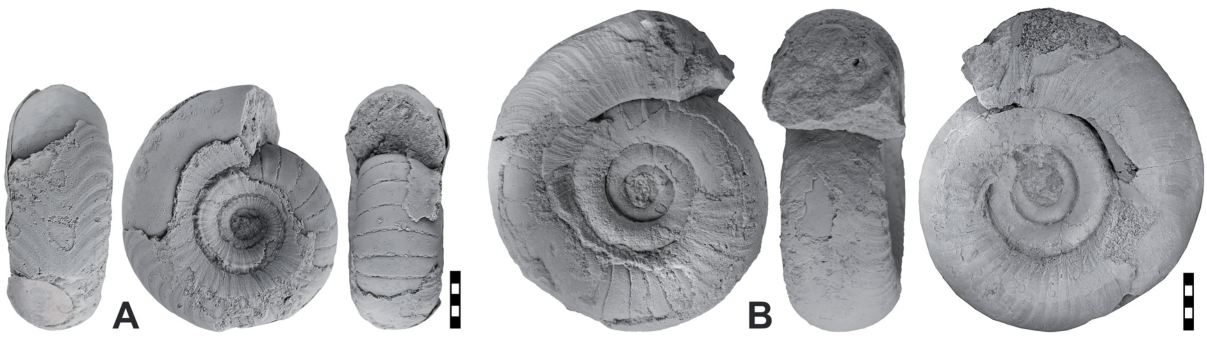

Fig. 24. *Trocholites tureki* sp. nov. **A**. Holotype NRM Mo 152354 (Wegelin Coll.), Altsarbyn (earlier spelling Alsarbyn, Dalarna, Sweden); previously figured by Angelin (1880: pl. 9 figs 15–16, 18); ventral, lateral and dorsal views. **B**. Paratype GIT 362-721-2 (Toom Coll.), Osmussaar 1 (Estonia); lateral and dorsal views. Scale bar units = 1 mm.

Table 15. Conch measurements, ratios and rates of *Trocholites tureki* sp. nov.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
NRM Mo 152354	22.1	9.1	6.3	10.6	5.2	0.41	1.46	0.48	1.71	0.17
minus 90°	19.4	8.1	6.5	8.15	–	0.42	1.25	0.42	–	–
minus 180°	17.1	7.6	5.3	7.0	–	0.44	1.44	0.41	–	–
minus 270°	14.6	7.2	4.8	6.0	–	0.49	1.50	0.41	–	–
GIT 362-721-2	27.8	11.2	8.0	12.7	–	0.40	1.40	0.46	–	–
minus 90°	24.3	9.7	7.5	10.8	–	0.40	1.29	0.44	–	–
minus 180°	–	9.30	7.14	9.28	–	–	1.30	–	–	–
minus 270°	–	9.0	6.0	8.0	–	–	1.50	–	–	–

Etymology

After Vojtěch Turek (Prague, Czech Republic) in the honour of his contribution to the knowledge on Palaeozoic cephalopods.

Type material

Holotype

SWEDEN • Altsarbyn (earlier spelling Alsarbyn), Dalarna; Darriwilian Stage; Wegelin Coll.; illustrated by Angelin (1880: pl. 9 figs 15–16, 18), re-illustrated here in Fig. 24A; NRM Mo 152354.

Paratype

ESTONIA • 1 spec.; Osmussaar 1; Uhaku Regional Stage; Toom Coll.; illustrated in Fig. 24B; GIT 362-721-2.

Description

Holotype NRM Mo 152354 (Fig. 24A) is a subadult or adult conch with 22 mm diameter with nearly three whorls preserved. The last 45 degrees of the conch belong to the body chamber, which is incomplete. In the last 270 degrees, the conch becomes increasingly discoidal (CWI = 0.49–0.41) and increasingly umbilicate (UWI = 0.41–0.48). The whorl profile is rounded from ventral and lateral sides and weakly depressed; the WWI decreases from 1.50 (dm = 14.6 mm) to 1.25 (dm = 19.4 mm) and then again increases to 1.46 at the body chamber (dm = 22 mm). The coiling rate at the maximum diameter is low (WER = 1.71). The shell ornament consists of closely spaced, thin to raised lirae and low ribs, which are not reflected on the internal mould of the conch; the ribs are present from earliest preserved volution up to the external volution, where they form a rather deep ventral sinus. In the internal volutions, node-like elements are present laterally. The phragmocone chamber length (RCL) is 0.29 in the external volution; suture lines are almost straight with a shallow external lobe.

Paratype GIT 362-721-2 (Fig. 24B) is a nearly complete conch with 28 mm diameter and consists of four whorls; the last half a whorl belongs to the incomplete body chamber. At the maximum diameter, the conch is discoidal (CWI = 0.40) and evolute (UWI = 0.46). The whorl profile is ventrally and laterally rounded and weakly depressed; the WWI decreases from 1.50 to 1.29 (dm = 24 mm) and then increases to 1.40 (dm = 28 mm). The shell ornament consists from 1) widely spaced ribs which are in the last half a whorl replaced by 2) narrowly spaced ribs or accumulations of lirae (less prominent ventrally than laterally), and 3) fine lirae. Only the riblets are reflected on the internal mould of the conch. The phragmocone chamber length (RCL) is ~ 0.25 in the external volution and the last chamber is shortened; suture lines are almost straight.

Remarks

Holotype NRM Mo 152354, previously illustrated by Angelin (1880), was used by Schröder (1891) as one of three syntypes of *Trocholites remelei*. All three specimens (NRM Mo 152355, NRM Mo 152354, MB.C.11562) are assigned here to different species on the basis of substantial differences in conch geometry and shell ornament. Holotype NRM Mo 152354 specifically differs from lectotype MB.C.11562 of *Trocholites remelei* by being more discoidal (CWI = 0.41 vs 0.59 at dm ~ 22 mm), more evolute (UWI = 0.71 vs 0.87 at dm ~ 22 mm), less rapidly expanding (WER = 1.71 vs 1.87 at dm ~ 22 mm) and its whorls are less impressed (IZR = 0.17 vs 0.34 at dm ~ 22 mm); the ornament in NRM Mo 152354 is not visible on internal mould. The holotype NRM Mo 152354 also differs from paratype NRM Mo 152355 of *Trocholites freyjae* sp. nov. because it is narrower (CWI = 0.41 at dm 22 mm vs 0.50 at dm 26 mm) with less depressed whorls (WWI = 1.46 at dm 22 mm vs 1.76 at dm 26 mm); in addition, the shell surface is annulated in NRM Mo 152355 (but with sharp lirae in NRM Mo 152354).

The holotype is unique in the collection by the presence of distinct lirae and annuli covering the entire shell surface and is therefore placed in a separate species. Another specimen, GIT 362-721-2, is assigned to the new species because it corresponds to the holotype in shell geometry. The only difference between the two is the presence of widely spaced ribs on the inner whorls of GIT 362-721-2. Most similar to both specimens is the specimen MB.C.32182 of *T.* sp. 4 and some representatives of *T. depressus* (Fig. 7), which also have annuli or ribs on the shell surface. In the latter two species, however, the shell ornament is much finer and / or irregular in spacing and thickness. In addition, the specimens of *Trocholites depressus* generally have lower coiling rate (WER ~ 1.65 vs 1.71) in the adult growth stage.

Trocholites vodickai sp. nov.

urn:lsid:zoobank.org:act:6CA0C13A-9BDC-41B9-8E08-AFE05FB363C5

Fig. 25; Table 16

Diagnosis

Species of the genus *Trocholites* with an adult conch diameter of about 40 mm. Conch in the last whorl thinly discoidal (CWI ~ 0.40) and evolute (UWI ~ 0.46). Whorl profile weakly depressed (WWI = 1.25–1.50) with rounded flanks and slightly flattened venter in the adult stage. Shell ornament with fine, rursiradiate lirae; internal mould of body chamber with faint annular impressions. Phragmocone chambers moderately long (RCL = 0.30–0.40). Suture line straight.

Etymology

After Jakub Vodička (Prague, Czech Republic), for his contribution to the chitinozoan research in Bohemia.

Type material

Holotype

POLAND – **West Pomerania** • Ustronie Morskie; Lasnamägi or Uhaku regional stages; Müldner Coll.; illustrated in Fig. 25A; MB.C.32177

Paratype

GERMANY – **Brandenburg** • 1 spec.; Hindenberg near Calau; Ordovician; Krueger Coll.; illustrated in Fig. 25B; MB.C.32178.

Description

Holotype MB.C.32177 (Fig. 25A) is an adult conch with 41 mm diameter, of which the last ~ 220 degrees of the external volution belongs to the body chamber. In the last quarter volution, the conch becomes

Table 16. Conch measurements, ratios and rates of *Trocholites vodickai* sp. nov.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.32177	40.9	16.3	12.8	18.7	–	0.40	1.27	0.46	–	–
minus 90°	37.8	17.5	12.7	16.6	–	0.46	1.37	0.44	–	–
MB.C.32178	39.3	17.3	11.5	17.9	–	0.44	1.50	0.45	–	–
minus 90°	36.9	17.0	11.9	13.7	–	0.46	1.43	0.37	–	–

more discoidal (CWI decreases from 0.46 to 0.40) and slightly more evolute (UWI changes from 0.44 to 0.46); the whorl profile shows broadly rounded flanks and venter. It is decreasingly depressed; during the last quarter of a volution, the WWI decreases from 1.37 to 1.27. The body chamber shows a terminal aperture with flares and a ventral sinus. The ornament consists of fine, rursiradiate lirae; faint annular impressions are present on the internal mould of the terminal body chamber. The phragmocone chambers are moderately long (RCL = 0.33).

Paratype MB.C.32178 (Fig. 25B) is a conch in the adult growth stage; it is distorted at one side and has a diameter of 39 mm. More than half of the last volution belongs to the body chamber. In the last quarter whorl, the conch is discoidal (CWI changes slightly from 0.46 to 0.44) and increasingly evolute (UWI changes from 0.37 to 0.45). The whorl profile is weakly depressed (WWI increases from 1.43 to 1.50) and shows broadly rounded flanks and a slightly flattened venter. At the maximum conch diameter, the whorl height appears to decrease slightly (from 11.9 mm to 11.5 mm) from about the mid-length of the terminal body chamber. The body chamber begins to produce flares at its terminal aperture. The shell is ornamented by fine, rursiradiate lirae; the internal mould of the body chamber has shallow annular impressions. The phragmocone chambers are rather long (RCL = 0.38).

Remarks

Trocholites vodickai sp. nov. is rather similar to *T. macrostoma* but the latter has a more strongly depressed adult body chamber (WWI ~ 1.70 vs 1.25–1.50 in *T. vodickai*) and a wider umbilicus (UWI ~ 0.55 vs ~ 0.45).

Trocholites vodickai sp. nov. shows some similarity to *T. vortex* sp. nov., but the former are smaller in adult size (40 in contrast to more than 50 mm), the last whorl is more discoidal (CWI ~ 0.40 vs 0.47) with shorter phragmocone chambers in the last volution (RCL = 0.30–40 vs 0.47).

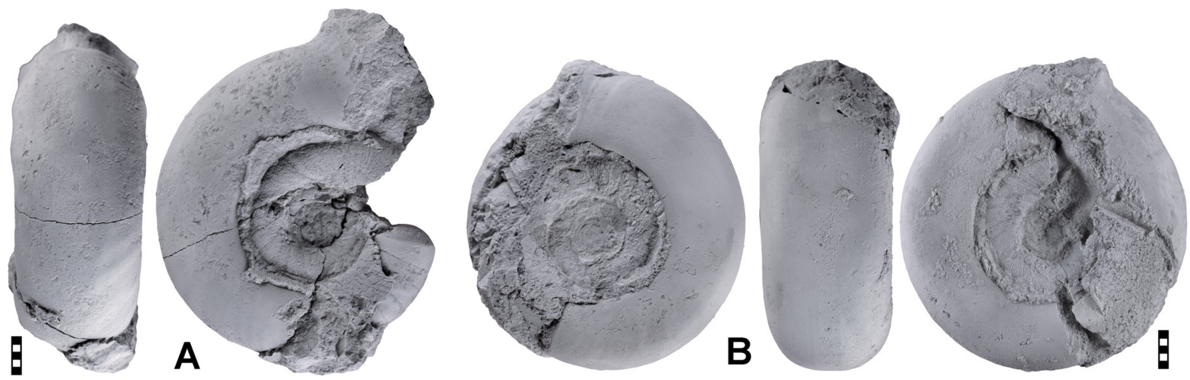

Fig. 25. *Trocholites vodickai* sp. nov. **A**. Holotype MB.C.32177 (Müldner Coll.) from Ustronie Morskie (Poland); ventral and lateral views. **B**. Paratype MB.C.32178 (Krueger Coll.) from Calau (Brandenburg); lateral and ventral views. Scale bar units = 1 mm.

Trocholites luna sp. nov. differs from *T. vodickai* sp. nov. in the greater adult size (50 mm vs 40 mm); the last whorl is more evolute (UWI ~ 0.52 vs 0.46) and the shell ornament in inner whorls has raised lirae or accumulation of lirae instead of fine, rursiradiate lirae.

The two specimens of *T. kadakaensis* sp. nov. differ from those of *T. vodickai* sp. nov. because their last whorl is less discoidal (CWI ~ 0.48 vs 0.40) and the whorl profile is much more depressed (WWI ~ 1.80 vs 1.25–1.50) with a distinct decrease in width and height towards the terminal aperture.

In the holotype of *T. zaryensis* sp. nov., the last whorl is also less discoidal (CWI ~ 0.57 vs 0.40) and slightly more narrowly evolute (UWI ~ 0.42 vs 0.46); the whorl profile is more depressed (WWI ~ 1.82 vs 1.25–1.50).

Trocholites depressus is generally rather similar in conch geometry to *T. vodickai* sp. nov. but the specimens of the former tend to have a more depressed whorl profile (WWI up to 1.60) in the last volution and the ornament on inner whorls has ribs.

Geographic and stratigraphic occurrence

Northern Poland and northern Germany; late Darriwilian, Middle Ordovician.

Trocholites vortex sp. nov.

urn:lsid:zoobank.org:act:115DF999-F5D6-4FE3-8853-72A8F451CC7C

Fig. 26; Table 17

Diagnosis

Species of the genus *Trocholites* with an adult conch diameter of about 50 mm. Conch in the last whorl thickly discoidal (CWI ~ 0.47) and evolute (UWI ~ 0.46) with moderately high coiling rate (WER ~ 1.80). Whorl profile weakly depressed (WWI ~ 1.45), rounded, moderately embracing (IZR ~ 0.20). Shell ornament with growth lines or extremely fine, regularly spaced lirae; venter and outer flanks with thin and irregularly spaced annuli or raised lirae. Phragmocone chambers long in all growth stages (RCL ~ 0.45). Suture line nearly straight.

Etymology

From the Latin '*vortex*' (nomen) = 'a whirl', referring to the perfectly spiral shape of the holotype.

Type material

Holotype

GERMANY – **Mecklenburg-Vorpommern** • Parchim; Lasnamägi or Uhaku regional stages; 1969; Helms Coll.; illustrated in Fig. 26; MB.C.22574.

Description

Holotype MB.C.22574 (Fig. 26) is a nearly complete conch with 49 mm diameter and is composed of five whorls; the initial chamber has probably not been preserved. The body chamber is preserved in length of about 230 degrees, but does not have the terminal aperture preserved. In the last half volution, the conch proportions change only slightly; the conch becomes more thickly discoidal (CWI changes from 0.45 to 0.47), less evolute (UWI decreases from 0.48 to 0.45) and the whorl profile becomes less depressed (WWI decreases from 1.52 to 1.45). The last whorl is moderately impressed (IZR = 0.19) and moderately expanding (WER= 1.80). The venter of the body chamber has two longitudinal grooves separated by a single ridge. The shell ornament consists of growth lines or extremely fine, regularly

Table 17. Conch measurements, ratios and rates of *Trocholites vortex* sp. nov.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.22574	49.2	–	15.5	22.1	12.6	–	–	0.45	1.80	0.19
minus 90°	42.9	20.1	13.9	19.8	–	0.47	1.45	0.46	–	–
minus 180°	37.2	16.8	11.0	17.8	–	0.45	1.52	0.48	–	–

spaced lirae. On the venter and outer flanks, there are thin and irregularly spaced annuli or raised lirae. The phragmocone chambers are long (RCL = 0.47); the suture line is almost straight.

Remarks

Compared to representatives of other species of *Trocholites*, the holotype of *T. vortex* sp. nov. has a large conch diameter of about 50 mm. This may not yet represent the adult stage as there is no evidence of the terminal aperture and the rate of growth of the body chamber height and width does hardly change. In addition, the last phragmocone chambers are not shortened.

Some specimens of *Trocholites hospes* attain comparatively large adult conch diameters, but their conchs with diameters of around 50 mm are much stouter (CWI ~ 0.60 vs ~ 0.45 in *T. vortex* sp. nov. at 50 mm diameter) and more narrowly umbilicate (UWI ~ 0.35 vs ~ 0.45) with whorls more strongly impressed dorsally (IZR ~ 0.30 vs ~ 0.30).

Trocholites vortex sp. nov. differs from *T. luna* sp. nov. in adult size exceeding 50 mm, the higher coiling rate (WER = 1.80 vs 1.60), the wider adult body chamber (CWI = 0.47 vs 0.38), the less depressed whorl profile (WWI = 1.45 vs 1.56) and the narrower umbilicus (UWI = 0.45 vs 0.52).

Trocholites vortex sp. nov. also resembles *T. vodickai* sp. nov. in umbilical and whorl width, but *T. vortex* has a greater adult size (over 50 mm vs 40 mm) and the phragmocone chambers are longer (RCL = 0.30–0.40 in last whorl of *T. vodickai*).

Compared to *T. vortex* sp. nov., the two specimens of *T. kadakaensis* sp. nov. are smaller in adult size, have a lower coiling rate (WER ~ 1.70 vs 1.80) and the whorl profile is more depressed at dm ~ 40 mm (WWI ~ 1.80 vs ~ 1.50).The specimens of *T. depressus* reach up to max. 40 mm diameter in adult size;

Fig. 26. *Trocholites vortex* sp. nov.; holotype MB.C.22574 (Helms Coll., 1969) from Parchim (Mecklenburg-Vorpommern); ventral and lateral views; reconstruction of apertural view. Scale bar units = 1 mm.

Table 18. Conch measurements, ratios and rates of *Trocholites zaryensis* sp. nov.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.9718	36.4	20.6	11.3	15.4	–	0.57	1.82	0.42	–	–
minus 90°	31.5	21.5	11.0	13.0	–	0.68	1.96	0.41	–	–

they are generally more discoidal (CWI = 0.35–0.40 vs 0.47) with a much lower coiling rate (WER ~ 1.65 vs 1.80) and the ornament on inner whorls has ribs.

Trocholites zaryensis sp. nov.
urn:lsid:zoobank.org:act:DB8D668B-9A0C-4F0F-B279-31D4CDED0A17
Fig. 27; Table 18

Diagnosis

Species of the genus *Trocholites* with an adult conch diameter of about 36 mm. Conch in the last whorl thickly discoidal (CWI ~ 0.57) and subevolute (UWI ~ 0.42). Whorl profile moderately depressed (WWI ~ 1.82) with rounded flanks and slightly flattened venter. Whorl width slightly decreasing, whorl height slightly increasing in last quarter volution. Phragmocone chambers at 30 mm diameter moderately long (RCL ~ 0.30). Suture line nearly straight.

Etymology

From Żary (Poland), the locality of the holotype.

Type material

Holotype

POLAND • Żary; probably Darriwilian Stage; 1860; Kirchner Coll.; illustrated in Fig. 27; MB.C.9718.

Description

Holotype MB.C.9718 (Fig. 27) is a conch of an individual in the terminal growth stage with 36 mm diameter. The last nearly three quarters of the conch belong to the body chamber, which is preserved as an internal mould. In the last quarter of a whorl, the conch shape changes from pachyconic to thickly

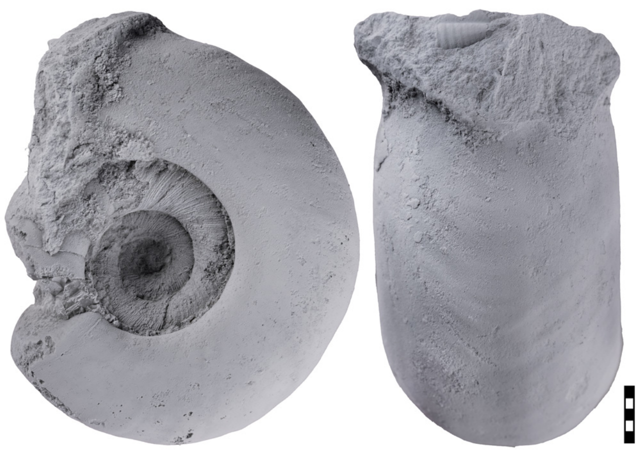

Fig. 27. *Trocholites zaryensis* sp. nov.; holotype MB.C.9718 (Kirchner Coll., 1860) from Żary (Poland); lateral and ventral views. Scale bar units = 1 mm.

discoidal (CWI decreases from 0.68 to 0.57) and stays subevolute (UWI ~ 0.42); the whorl profile is moderately depressed (WWI decreases from 1.96 to 1.82) with broadly rounded flanks and venter. The whorl width decreases slightly (from 21.5 mm to 20.6 mm), but the whorl height increases slightly (from 11.0 mm to 11.3 mm) near the aperture. The venter of the terminal body chamber becomes slightly flattened; the aperture possesses ventral and lateral flares. The shell is visible in the inner whorls; it is ornamented with rursiradiate lirae. The internal mould of the body chamber has indistinct annular ridges. The phragmocone chambers are moderately long (RCL = 0.30 at dm = 30 mm).

Remarks

Holotype MB.C.9718 of *Trocholites zaryensis* sp. nov. is very similar to holotype MB.C.11563 of *T. kadakaensis* sp. nov., which has a larger adult size (42 mm) and in which the terminal body chamber decreases in width as well as in height. Also, the last whorl in the holotype of *T. kadakaensis* is more discoidal (CWI ~ 0.48 vs 0.57).

Trocholites zaryensis sp. nov. differs from *T. hospes* in the shape of the body chamber and the much smaller conch with a fully adult diameter about 42 mm, in contrast to *T. hospes* with 50–60 mm. In addition, the whorl width in the last whorl slightly decreased in *T. zaryensis*.

Compared to the holotype of *T. zaryensis* sp. nov., the two specimens of *T. vodickai* sp. nov. are more discoidal (CWI ~ 0.40 vs 0.57) and slightly more widely evolute (UWI ~ 0.46 vs 0.42); the whorl profile is less depressed (WWI ~ 1.25–1.50 vs 1.82).

The holotype of *Trocholites ruedemanni* differs from the holotype of *T. zaryensis* sp. nov. by the slightly uncoiled terminal body chamber, presence of nodes and fine costae on the shell of last two whorls, much less depressed whorl profile in the last volution (WWI = 1.54 vs 1.96 at dm ~ 31 mm) and a narrower umbilicus (UWI = 0.32 vs 0.41 at dm ~ 31 mm).

Trocholites sp. 1

Fig. 28; Table 19

Material examined

GERMANY • 1 spec.; probably Brandenburg; Ordovician; Neben and Krueger Coll.; illustrated in Fig. 28; MB.C.32179.

Description

Specimen MB.C.32179 (Fig. 28) is a conch with a maximum diameter of 36 mm; it was sectioned in transverse plane. The conch consists of about 4.5 volutions. During ontogeny between 3.6 and 35.4 mm conch diameter, the relative conch width and coiling rate decrease markedly (CWI from 0.89 to 0.49; WER from 2.60 to 1.74) and the umbilical width increases (UWI changes from 0.21 to 0.41). The whorl profile has convex flanks and a flattened venter, which becomes rounded adaperturally; the dorsal impression (IZR) first increases from 0.17 to 0.37 up to 15 mm conch diameter and thereafter decreases from 0.37 to 0.23 in the subadult and adult stage. The whorl profile generally becomes less depressed during ontogeny (WWI decreases from 2.44 to 1.57), but the decrease is not gradual. The siphuncle appears to be located near the dorsal shell wall in inner whorls and moves to the subdorsal position in later whorls; the RSH is between 0.20–0.16.

Remarks

In several of the specimens of *Trocholites*, the shell wall is noticeably thickened at the ventral and lateral sides of the conch and particularly the umbilical wall. This is best seen in specimen MB.C.32179, where

Table 19. Conch measurements, ratios and rates of *Trocholites* sp. 1.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.32179	35.41	17.46	11.09	14.53	8.58	0.49	1.57	0.41	1.74	0.23
minus 180°	26.83	15.98	9.78	9.56	6.87	0.60	1.63	0.36	1.81	0.30
minus 360°	19.96	13.23	7.49	6.40	5.07	0.66	1.77	0.32	1.80	0.32
minus 540°	14.89	10.16	6.08	4.33	3.86	0.68	1.67	0.29	1.82	0.37
minus 720°	11.03	7.85	4.48	3.24	3.06	0.71	1.75	0.29	1.91	0.32
minus 900°	7.98	5.32	3.31	2.26	2.45	0.67	1.61	0.28	2.09	0.26
minus 1080°	5.52	4.15	2.41	1.46	1.93	0.75	1.72	0.26	2.36	0.20
minus 1260°	3.60	3.19	1.65	0.75	1.37	0.89	1.93	0.21	2.60	0.17
minus 1440°	2.23	2.92	1.20	–	1.14	1.31	2.44	–	4.15	0.05

the shell wall is about 0.5 mm thick at a conch diameter of 35 mm and even up to 0.7 mm thick at the umbilical wall.

The specimen MB.C.32179 is kept in open nomenclature due to insufficient preservation of external morphology and the siphuncle; also, it cannot be reliably inferred, whether the specimen represents an adult or subadult growth stage. However, some comparisons to other specimens of *Trocholites* are still possible. Both the whorl width and whorl height of the terminal body chamber gradually increase in the specimen of *Trocholites* sp. 1, as it does in *T. glacialis* sp. nov. and *T.* sp. 3. However, in *T.* sp. 1 the whorl profile shows a flattened venter. The whorl profile is, at dm ~ 35 mm conch diameter, less depressed in the specimen MB.C.32179 of *T.* sp. 1 when compared to *T. glacialis* (WWI = 1.57 vs 1.80), but more depressed than in the specimen of *T.* sp. 3 (WWI = 1.80 vs 1.30).

The specimen MB.C.32179 of *Trocholites* sp. 1 differs from the specimen MB.C.32168 of *T. macrostoma* in ontogenetic trajectories between conch diameters of 5 to 25 mm (Fig. 11). In the former specimen, UWI is lower (decrease followed by increase) and CWI higher (increase followed by decrease).

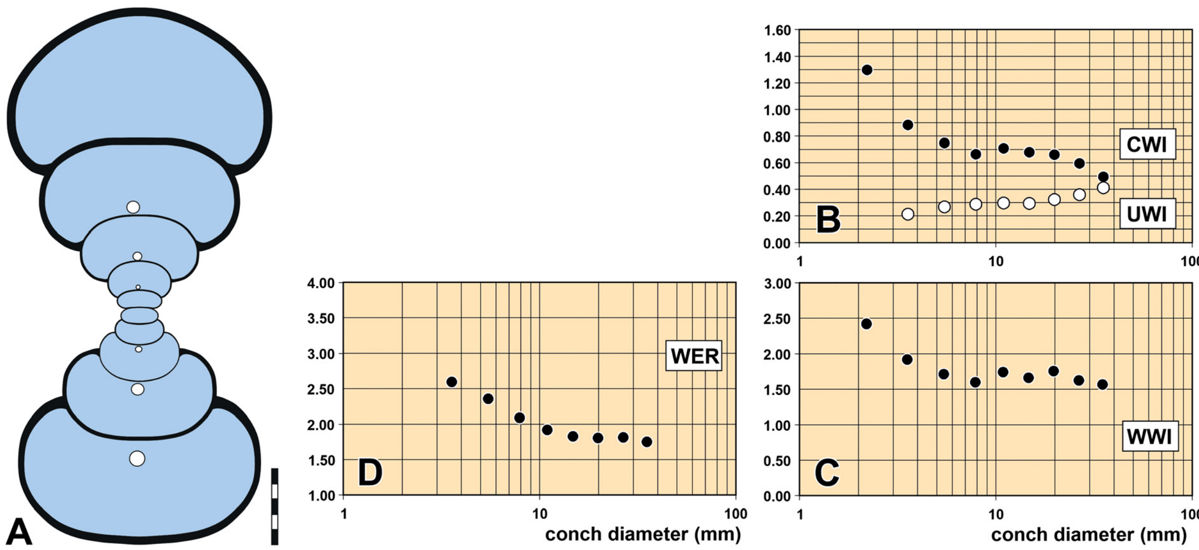

Fig. 28. *Trocholites* sp. 1; MB.C.32179 (Neben and Krueger Coll.), probably from Brandenburg. **A**. Cross section. **B–D**. Ontogenetic development of the conch width index (CWI), umbilical width index (UWI), whorl width index (WWI) and whorl expansion rate (WER). Scale bar units = 1 mm.

Similar to *Trocholites* sp. 1 is *T. zaryensis* sp. nov. but the outer volution of the latter is more discoidal (CWI = 0.57 vs 0.49) and much more depressed (WWI ~ 1.82 vs 1.57); the venter is flattened (vs rounded) all the way up to the aperture. In *T. kadakaensis* sp. nov., the whorl profile is also much more depressed (WWI ~ 1.82 vs 1.57) than in *Trocholites* sp. 1.

The holotype of *Trocholites ruedemanni* is a very similar in conch geometry to the specimen MB.C.32179 (and also the specimen MB.C.32180 of *T.* sp. 2) but *T. ruedemanni* has nodes and costae on the umbilical wall of the outer two volutions; also the flattening of the ventral side seen in MB.C.32179 is not present (Flower 1943).

Trocholites **sp. 2**
Fig. 29; Table 20

Material examined

POLAND • 1 spec.; Międzyzdroje; Darriwilian; illustrated in Fig. 29; MB.C.32180.

Description

A transverse section was made from specimen MB.C.32180 (Fig. 29), which is a conch with about 29 mm diameter. Three outer whorls are preserved; a part of the conch belongs to the body chamber. During ontogeny between 4.3 and 28.5 mm diameter, the conch decreases in width ratio and coiling rate (CWI from 0.74 to 0.55; WER from 2.52 to 1.66) and increases in umbilical width (UWI changes from 0.18 to 0.47). The whorl profile is rounded from all sides, moderately impressed and increasingly depressed (WWI change from 1.66 to 1.97). The whorl height and width gradually increase with conch growth. The siphuncle is not visible clearly in the section but appears to be marginodorsal or nearly so, and medium in diameter (estimated RSH between 0.15 and 0.20).

Remarks

Specimen MB.C.32180 is left in open nomenclature here because of poor preservation of external characters, as well as the siphuncle. The specimen appears most similar to MB.C.32179 of *T.* sp. 1 in

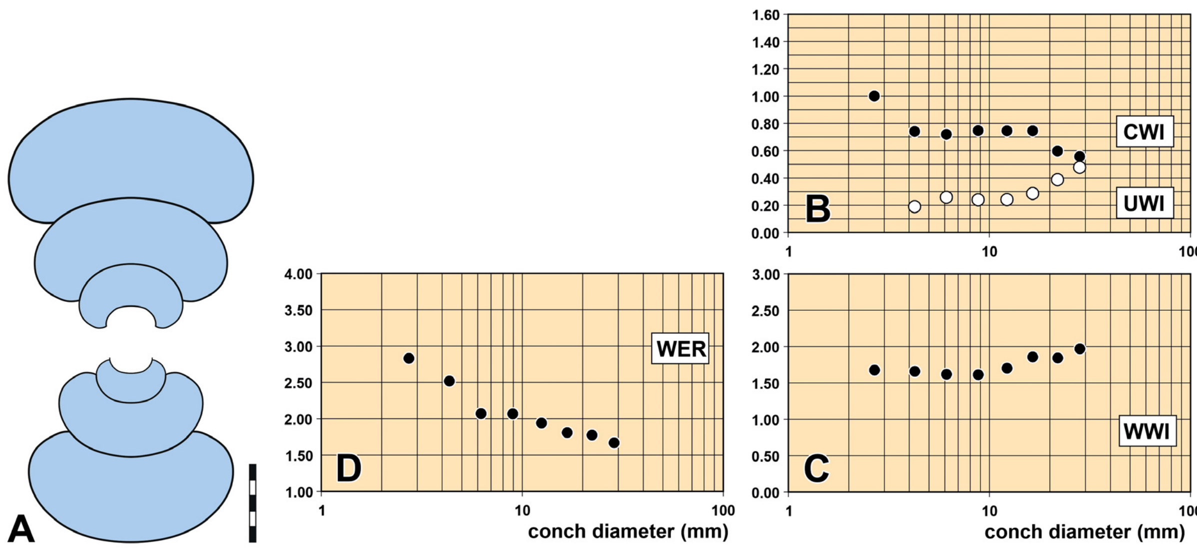

Fig. 29. *Trocholites* sp. 2; MB.C.32180 from Międzyzdroje (Poland). **A**. Cross section. **B–D**. Ontogenetic development of the conch width index (CWI), umbilical width index (UWI), whorl width index (WWI) and whorl expansion rate (WER). Scale bar units = 1 mm.

Table 20. Conch measurements, ratios and rates of *Trocholites* sp. 2.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.32180	28.51	15.71	7.98	13.42	6.37	0.55	1.97	0.47	1.66	0.20
minus 180°	22.14	13.10	7.11	8.38	5.48	0.59	1.84	0.38	1.77	0.23
minus 360°	16.66	12.35	6.65	4.60	4.24	0.74	1.86	0.28	1.80	0.36
minus 540°	12.42	9.21	5.42	2.87	3.49	0.74	1.70	0.23	1.93	0.36
minus 720°	8.93	6.64	4.13	2.05	2.71	0.74	1.61	0.23	2.06	0.34
minus 900°	6.22	4.45	2.75	1.54	1.89	0.71	1.62	0.25	2.06	0.31
minus 1080°	4.33	3.19	1.93	0.77	1.60	0.74	1.66	0.18	2.52	0.17
minus 1260°	2.73	2.73	1.63	1.10	1.11	1.00	1.67	–	2.84	0.32

the ontogenetic trajectories of conch dimensions and ratios (Fig. 11). However, the whorl profile in MB.C.32180 becomes more depressed (instead of less depressed) in growth (WWI generally increases from ~ 1.7 up to ~ 2). Also, the ventral side of the whorls is not flattened in MB.C.32180.

The conch geometry in the specimen MB.C.32180 is also similar in several aspects (mainly WER) to the geometry of the specimen MB.C.32168 (*T. macrostoma*). However, the ontogenetic trajectories differ between conch diameters of 5 to 25 mm. In that interval in MB.C.32180, the UWI is lower (decreases and then increases) and CWI is higher (increases and then decreases); WWI is similar in late growth stages but lower in earlier growth stages.

Trocholites **sp. 3**
Fig. 30; Table 21

Material examined

GERMANY • 1 spec.; probably Brandenburg; Ordovician; Neben and Krueger Coll.; illustrated in Fig. 30; MB.C.32181.

Description

A transverse section was produced from specimen MB.C.32181 (Fig. 30). This is a specimen with 31 mm conch diameter and shows 1.5 volutions preserved. During the last volution, the conch decreases in the whorl width ratio (CWI changes from 0.56 to 0.42) and increases in the umbilical width ratio (UWI changes from 0.34 to 0.42), while the coiling rate remains nearly constant (WER ~1.80). The last volution of the conch shows a decelerated increases in height, while the whorl width increases gradually. The whorl profile shows rounded flanks and venter; the whorl profile is widest in its dorsal half (i.e., not in the middle of the flank). The WWI is between 1.65 and 1.47 but changes in a fluctuating manner; at the greatest conch diameter, the whorl profile is weakly depressed (WWI = 1.30). The depth of the imprint zone is also irregular and decreases from a value of IZR = 0.33 to 0.23. The diameter of the siphuncle is about 0.20 of the apertural height; it has a position close to the dorsal shell wall or is even in contact.

Remarks

The insufficient preservation of the specimen MB.C.32181 prevents its unequivocal taxonomic assignment; the specimen is thus left in open nomenclature.

In *Trocholites* sp. 3, both whorl width and whorl height of the terminal body chamber gradually increase, which is similar to *T. glacialis* sp. nov. and *T.* sp. 1. However, the whorl profile of *T.* sp. 3 is, at 30 mm conch diameter, much less depressed (WWI ~1.30 in *T.* sp. 3, but ~1.80 in both *T.* sp. 1 and *T. glacialis*).

Table 21. Conch measurements, ratios and rates of *Trocholites* sp. 3.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.32181	30.37	13.82	9.84	12.51	7.58	0.43	1.30	0.41	1.78	0.23
minus 180°	22.80	12.40	7.73	8.52	5.56	0.54	1.60	0.37	1.75	0.28
minus 360°	17.24	9.62	6.55	5.78	4.37	0.56	1.47	0.34	1.80	0.33
minus 540°	12.86	8.08	4.91	7.96	3.55	0.63	1.65	–	1.91	0.28

Trocholites **sp. 4**
Fig. 31; Table 22

Material examined

GERMANY – **Brandenburg** • 1 spec.; Liepe; Lasnamägi or Uhaku Regional Stage, late Darriwilian; Müldner Coll.; illustrated in Fig. 31A; MB.C.32182.

Description

A transverse section was prepared from specimen MB.C.32182 (Fig. 31), but the conch is re-crystallised internally and therefore, some dimensions had to be estimated. The specimen has a conch diameter of 24 mm; it is thinly discoidal (CWI = 0.40), subevolute (UWI = 0.43) and moderately expanding (WER = 1.82). The whorl profile is weakly depressed (WWI = 1.26) and moderately impressed dorsally (IZR = 0.18). Flanks and venter are broadly convex. The maximum width of the whorl profile is reached in the midflank area. The ornament is poorly preserved and consists of irregularly spaced narrow ribs and lirae, which are straight on the flank and form a ventral sinus. The suture line is straight. The phragmocone chambers are moderately long (RCL = 0.26 at wh = 6.7 mm). Siphuncle can be measured at the largest whorl height, where it has a rather narrow diameter (RSH) of 0.21; it is close to the dorsal side throughout ontogeny.

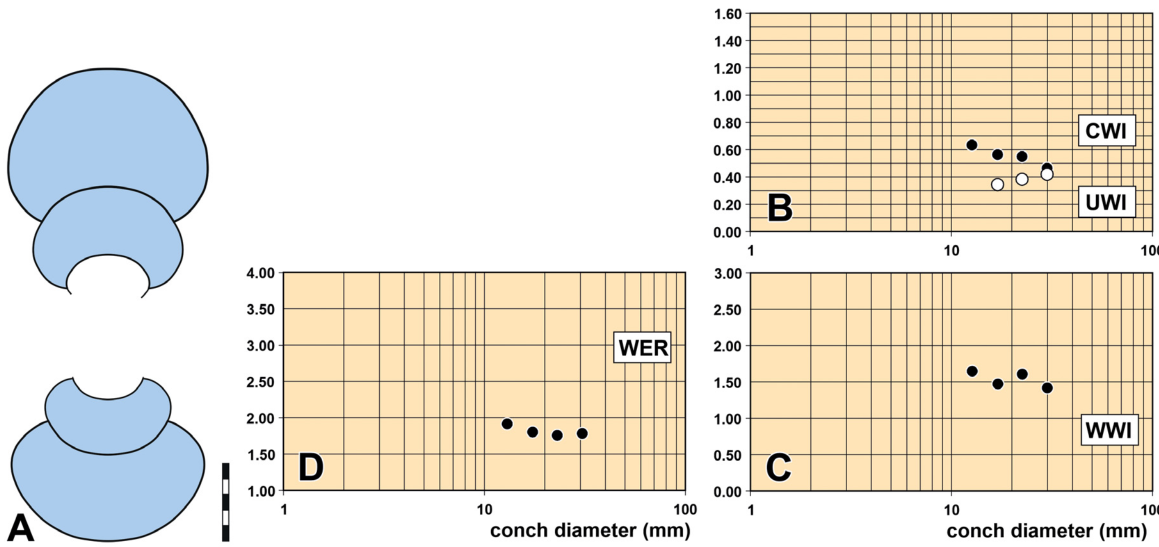

Fig. 30. *Trocholites* sp. 3; MB.C.32181 (Neben and Krueger Coll.), probably from Brandenburg. **A**. Cross section. **B–D**. Ontogenetic development of the conch width index (CWI), umbilical width index (UWI), whorl width index (WWI) and whorl expansion rate (WER). Scale bar units = 1 mm.

Table 22. Conch measurements, ratios and rates of *Trocholites* sp. 4.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.32182	23.5	9.3	7.4	10.2	6.1	0.40	1.26	0.43	1.82	0.18
minus 180°	17.4	7.5	5.9	7.2	–	0.43	1.27	0.41	–	–

Remarks

The specimen MB.C.32182 is left in open nomenclature because re-crystallisation prevented accurate measurements of internal conch characters.

In conch geometry, *Trocholites* sp. 4 is most similar to *T. depressus*, particularly to specimen MB.C.32161 (Fig. 7). However, the siphuncle does not seem to be in contact with the dorsal shell wall in *T.* sp. 4 and is much narrower (RSH = 0.21 vs 0.30 in *T. depressus*).

The specimen of *Trocholites* sp. 4 is also nearly identical in conch geometry to the two specimens of *T. tureki* sp. nov. (Fig. 7), but the ornament in the former specimen is much finer and less regularly developed.

Genus ***Curtoceras*** Ulrich, Foerste, Miller & Furnish, 1942

Type species

Lituites Eatoni Whitfield, 1886; by original designation.

Diagnosis

Genus of the family Trocholitidae with slowly expanding (WER decreasing up to ~ 1.80), subevolute to evolute conch (UWI increasing up to ~0.55), discoidal to extremely discoidal in shape (CWI decreasing up to ~ 0.30), with some part of the last half a whorl widely uncoiled. Whorl profile weakly compressed, equidimensional or weakly depressed (WWI ~ 0.90–1.10); whorls weakly embracing or not embracing, rounded or slightly flattened across venter and / or flanks. Siphuncle ventral in initial chamber, subdorsal or subcentral after one volution, septal necks short (<0.20 of chamber height), orthochoanitic. Shell surface smooth or with raised lirae, low ribs or annuli that form ventral sinus. Suture line nearly straight

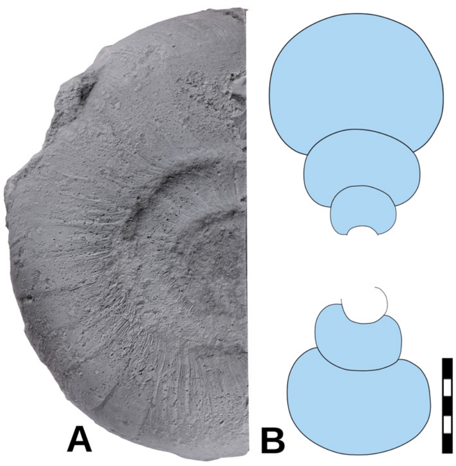

Fig. 31. *Trocholites* sp. 4; MB.C.32182 (Müldner Coll.) from Liepe (Brandenburg). **A**. Lateral view. **B**. Cross section. Scale bar units = 1 mm.

or with shallow lateral and / or ventral lobe (Ulrich *et al.* 1942; Furnish & Glenister 1964; Kröger & Aubrechtová 2018).

Species included

North America (Billings 1862; Whitfield 1886; Foerste 1938): *Lituites Eatoni* Whitfield, 1886; *Lituites internastriatus* Whitfield, 1886; ? *Schroederoceras minganense* Foerste in Twenhofel, 1938; ? *Lituites palinurus* Billings, 1862.

Great Britain (Blake 1882): *Nautilus (Trocholites) scoticus* Blake, 1882.

Northern Europe and Russia (Eichwald 1840; Lossen 1860; Schröder 1891; Hyatt 1894; Balashov 1953; Kröger & Aubrechtová 2018): *Curtoceras abditus* Kröger & Aubrechtová, 2018; *Curtoceras kerstovense* Balashov, 1953; *Nautilus teres* Eichwald, 1840; *Curtoceras meyeri* sp. nov.; *Trocholites macromphalus* Schröder, 1891.

Argentina (Aceñolaza *et al.* 1977): *Curtoceras kayseri* Aceñolaza, Durand & Taddei, 1977.

Remarks

The morphology of *Curtoceras* is similar to that of *Trocholites*. The species of *Trocholites* are less discoidal or even pachyconic in conch shape with more depressed and more impressed whorl profile; the body chamber is not uncoiled in *Trocholites* and very often, the terminal aperture bears conspicuous flares. However, a clear separation of the two genera is difficult and possibly subjective; species with a transitional morphology or for which the fully adult growth stage is unknown are difficult to assign unequivocally to one of the two genera.

Discoceras differs from *Curtoceras* in the much larger adult size (over 100 mm) and the presence of frilled, imbricated ornament elements. The whorl profile in *Discoceras* is often more strongly compressed than in *Curtoceras*, and subrectangular, subquadratic or trapezoidal in shape. However, separation of *Curtoceras* and *Discoceras* may be difficult in incomplete specimens or specimens representing juvenile or immature growth stages.

Geographic and stratigraphic occurrence

North America, Argentina, Great Britain, Estonia, Sweden (Island of Öland), St Petersburg and Kaliningrad region of Russia, northern Germany, northern Poland, ?Tibet; Ordovician.

Curtoceras teres (Eichwald, 1840)
Figs 32–35; Table 23

Nautilus teres Eichwald, 1840: 105.
Curtoceras estonicum Balashov, 1953: 207, pl. 6 figs 1–2.

Lituites teres – Eichwald 1860: 1299. — Dewitz 1879: 177, pl. 4 fig. 4. — Schröder 1882: 57–58, pl. 2 fig. 2.
Discoceras teres – Schröder 1891: 161. — Schindewolf 1942: 351, text-fig. 5e; 1944: 218, text-fig.7.
Schroederoceras teres – Hyatt 1894: 467. — Schindewolf 1932: 171, text-fig. 3.
Discoceras (*Schröderoceras*) *teres* – Schindewolf 1939: 60, text-fig. 15, pl. 4 fig. 8.
Curtoceras teres – Balashov 1953: 246, pl. 5 fig. 2, pl. 7 fig. 4. — Dzik 1984: 42, 44.
Lituites Odini – Verneuil in Murchison *et al*. 1845: 360, pl. 25 fig. 8. — Lossen 1860: 23.
Curtoceras estonicum – Stumbur 1962: 136. — Balashov 1962: pl. 9 fig. 7; 1974: pl. 9, fig. 7.
? *„Lituites“ teres* – Holm 1885: 10, pl. 5 figs 5–8.

non *Clymenia Odini* Eichwald, 1840: 107.
non *Clymenia Odini* – Eichwald 1860: 1304, pl. 51 fig. 27.

Diagnosis

Species of the genus *Curtoceras* with an adult conch diameter of 40–50 mm. The adult conch consists of up to 4 volutions; in the last whorl, coiling rate and conch width decrease (WER_{ah} ~ 2.00 and CWI ~ 0.30), umbilical width increases (UWI ~ 0.50). Whorl profile rounded or weakly laterally and ventrally flattened, and very weakly embracing or not embracing (IZR varies between 0.00–0.06). Whorl profile changes from depressed in inner volutions (WWI ~ 1.65), in outer whorl typically equidimensional but may be weakly depressed or weakly compressed in some specimens (WWI as low as 0.82). Body chamber about 180 degrees in length, uncoiled after ~ 120 degrees; terminal aperture with ventral sinus and dorso-lateral and dorsal extension and slight flaring. Shell surface with distinct, regularly spaced lirae with acute and more or less symmetric crests on inner whorls, flattening out towards the outer whorl, where the lirae are slightly imbricated; ventral sinus of ornament present. Siphuncle about 0.16 of corresponding apertural height throughout ontogeny; siphuncle position ventral in initial chamber, central after first 180 degrees, shifted towards the dorsal shell wall in later growth stages (RSP varies between 0.60 and 0.75 of apertural height).

Material examined

ESTONIA • 1 spec.; Tallinn; Ordovician; Kirchner Coll.; illustrated in Fig. 33A; MB.C.9715• 1 spec.; Aari quarry; Lasnamägi Regional Stage (Väo Formation); GIT 426-499 • 1 spec.; Aa; Lasnamägi Regional Stage; Stumbur Coll.; illustrated in Fig. 34C; GIT 426-530 • 1 spec.; Osmussaar cliff; Lasnamägi Regional Stage; Männil Coll.; GIT 697-567-1 • 1 spec.; Osmussaar; Lasnamägi Regional Stage; Schmidt Coll.; illustrated in Fig. 34A; GIT 225-1092 • 1 spec.; Aari quarry; Lasnamägi Regional Stage; Schmidt Coll.; illustrated in Fig. 34B; GIT 225-1062 • 1 spec.; Osmussaar 1; Lasnamägi Regional Stage; TUG 860-1309 • 1 spec.; same data as for preceding; GIT 697-130 • 1 spec.; Sõjamäe; Lasnamägi Regional Stage (Väo Formation); GIT 426-498 • 1 spec.; Kadaka road (Tallinn); Darriwilian Stage; illustrated in Fig. 34D–E; FMNH HS.P31459.

GERMANY – **Mecklenburg-Vorpommern** • 1 spec.; Basedow-Stöckersoll; Ordovician; 2006; Meyer Coll.; illustrated in Fig. 32; MB.C.32183. – **Brandenburg •** 1 spec.; Strausberg; Lasnamägi Regional Stage; Neben and Krueger Coll.; MB.C.32188 • 1 spec.; Leegebruch near Velten; Lasnamägi or Uhaku regional stages; 1951; Gräber Coll.; MB.C.11548a-d • 1 spec.; Oderberg; Ordovician; Neben and Krueger Coll.; MB.C.32187 • 1 spec.; Oderberg; Aseri Regional Stage; 1964; Neben and Krueger Coll.; illustrated in Fig. 35B; MB.C.32186 • 1 spec.; Potsdam; Lasnamägi Regional Stage; illustrated in Fig. 33B; MB.C.11544. – **Locality unknown** • 1 spec.; probably Brandenburg; Ordovician; Neben and Krueger Coll.; illustrated in Fig. 33C; MB.C.32184 • 1 spec.; probably Brandenburg; Ordovician; Neben and Krueger Coll.; illustrated in Fig. 35A; MB.C.32185.

POLAND – **West Pomerania** • 1 spec.; Bydgoszcz; Darriwilian Stage; previously figured by (Schindewolf 1933: text-fig. 8), re-illustrated here in Fig. 33D; MB.C.646 • 1 spec.; Rybokarty near Gryfice; Darriwilian Stage; Wietersheim Coll.; MB.C.11545.

Description

Specimen MB.C.32183 (Fig. 32) is the most complete of the available specimens. It has a total conch diameter of 48 mm and is composed of two and three-quarter volutions. The conch is spirally coiled up to a diameter of 43 mm, the last short segment of the body chamber is detached from the preceding whorl and has an almost straight direction. At 43 mm conch diameter, the conch is subevolute (UWI = 0.40) with a very high coiling rate (WER = 2.39). The umbilical foramen is very small, measuring approximately 1 × 2 mm. The entire specimen is covered with shell material. The ornament consists of coarse, lamellar growth lines with rursiradiate direction; they extend with a low lateral projection and form a very deep and wide ventral sinus.

Specimen MB.C.11544 (Fig. 33B) is an incomplete, but rather well-preserved conch of a nearly adult individual with 44 mm diameter. It consists of 3.25 whorls with the initial chamber preserved. In the last 0.75 volutions, in which the conch diameter grows from 25 mm to 43.5 mm, the conch becomes more discoidal (CWI decreases from 0.39 to 0.30) and the whorl profile changes from weakly depressed to equidimensional (WWI changes slightly from 1.11 to 1.00). Flanks and venter remain broadly convex and the whorls are only very weakly impressed dorsally or not impressed. In the course of the entire ontogeny (from 5.7 mm to 43.6 mm conch diameter), the coiling rate decreases significantly (WER decreases from 5.18 to 2.00) and the umbilicus widens (UWI increases from 0.16 to 0.47). The last quarter of the outer volution belongs to the body chamber, which begins to detach from the preceding whorl. The shell is ornamented with distinct, regularly spaced lirae with symmetric or only slightly imbricated crests; the lirae are sharp especially in the inner whorls, while in the outer whorl, they appear to flatten out. The ornament element extend with a ventral sinus. The phragmocone chambers are moderately long (RCL = 0.25 at dm = 30 mm). The suture line is straight.

Specimen GIT 225-1092 (Fig. 34A) is a nearly complete conch with a diameter of 52 mm and consists of 3.5 whorls; the body chamber occupies one third of the last whorl and is detached from the preceding volution. During ontogeny, the conch width and expansion become smaller (CWI decreases from 0.50 to 0.30, WER decreases from 2.64 to 2.04), while the umbilical width ratio increases (UWI changes from 0.39 to 0.47). The whorl profile is weakly depressed to equidimensional (WWI decreases from 1.30 to 0.99); it shows broadly convex flanks and venter in the inner whorls and becomes weakly flattened laterally and ventrally late in ontogeny. At the maximum conch diameter of 52 mm, the siphuncle is narrow (RSH = 0.13) and has a position between the centre and dorsal shell wall (RSP = 0.64). The shell wall is locally preserved; it is ornamented with sharp, evenly spaced lirae. The adult suture line shows a shallow lateral and a shallow ventral lobe.

Fig. 32. *Curtoceras teres* (Eichwald, 1840), specimen MB.C.32183 (Meyer Coll., 2006) from Basedow-Stöckersoll (Mecklenburg-Vorpommern); lateral view (classic photography and Reflectance Transformation Imaging). Scale bar units = 1 mm.

Specimen GIT 426-530 (Fig. 34C) is a natural transverse section at one side. It is a conch with 50 mm diameter and consists of 3.25 volutions; the last quarter volution belongs to the body chamber. In the last two volutions, the conch becomes more widely umbilicate (UWI increases from 0.20 to 0.44) and less expanded (WER decreases from 3.88 to 2.07). At the maximum diameter of 50 mm, the conch is discoidal (CWI = 0.32) and the whorl profile is nearly circular (WWI = 1.05) with convex flanks and a weakly flattened venter. The initial part of the phragmocone is preserved but the first chamber cannot be measured accurately; the umbilical window is 0.5 × 0.2 mm in diameter. The shell surface is ornamented with sharp, equally spaced lirae, which extend with a steep ventral sinus; some indistinct spiral lines are visible on the body chamber. The phragmocone chambers are rather short (RCL = 0.20 in the last half a whorl). The suture line is almost straight, but extends with a very shallow lateral lobe and a shallow external lobe.

The four specimens MB.C.32187, MB.C.32184 (Fig. 33C), MB.C.9715 (Fig. 33A) and MB.C.11544 (Fig. 33B) are nearly identical in their conch proportions and the shell ornament to specimen GIT 426-530. All of the specimens are adult or nearly adult conchs with about three whorls (dm = 37–47 mm). All show that the body chamber starts to uncoil after about 2.75 whorls (MB.C.9715 and MB.C.11545). In specimen MB.C.9715 (along with GIT 697-567-1 and GIT 225-1062), the aperture is preserved; it has

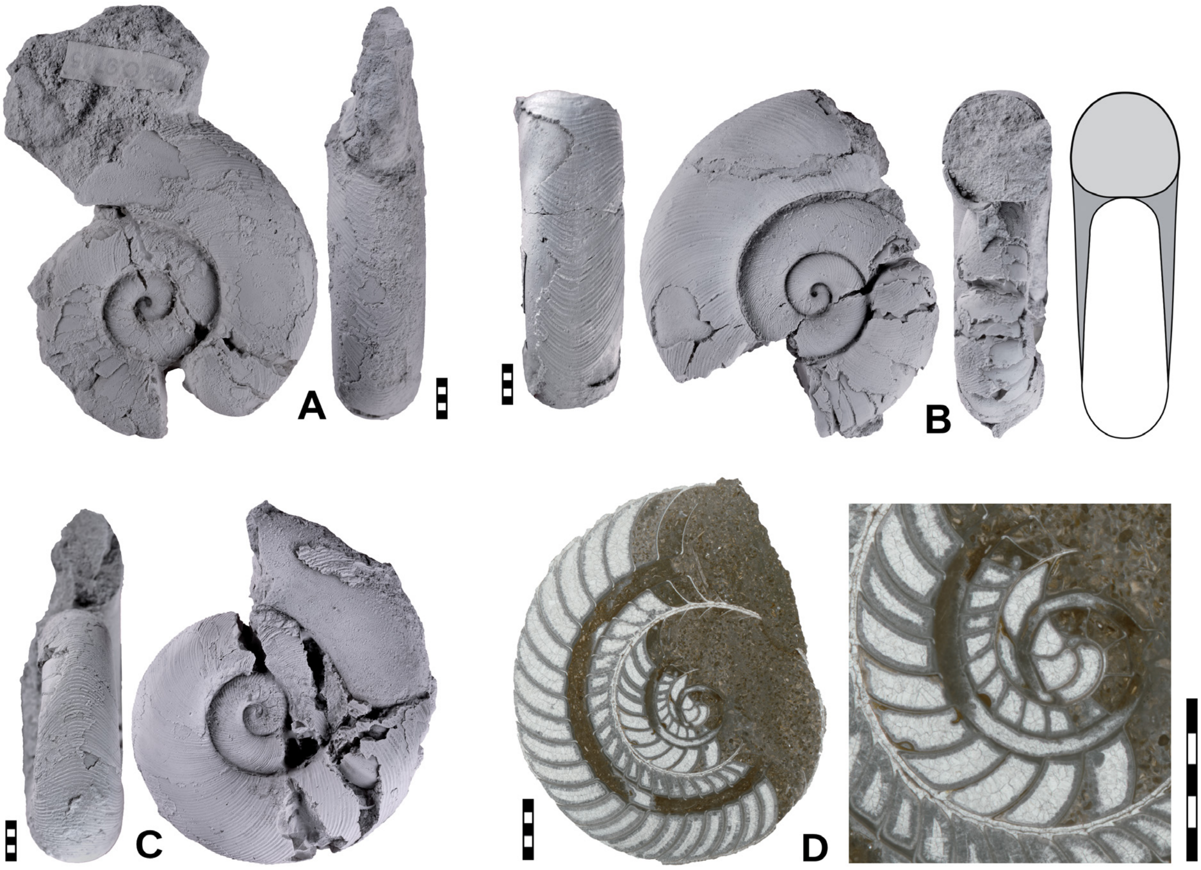

Fig. 33. *Curtoceras teres* (Eichwald, 1840). **A**. Specimen MB.C.9715 (Kirchner Coll.) from Tallinn; lateral and ventral views. **B**. Specimen MB.C.11544 from Potsdam (Brandenburg); lateral and dorsal views, reconstruction of apertural view. **C**. Specimen MB.C.32184 (Neben and Krueger Coll.), probably from Brandenburg; dorsal and lateral views. **D**. Specimen MB.C.646 from Bydgoszcz (West Pomerania); longitudinal section. Scale bar units = 1 mm.

a ventral sinus and a dorsolateral extension. The whorl profile at the maximum conch diameter ranges between weakly compressed and weakly depressed (WWI = 0.82–1.07) with broadly rounded flanks and venter; the dorsal impression is small. The umbilical width ratio (UWI) is between 0.42 and 0.50 and the conch width (CWI) between 0.29 and 0.35. The shell is ornamented with sharp, evenly distributed lirae with acute and more or less symmetric crests. The lirae are particularly distinct on the body chamber, where they form a deep ventral sinus. At the very end of the body chamber in MB.C.9715, the lirae are slightly frilled ventrally.

Specimen MB.C.646 (Fig. 33D) is a sagittal section through a subadult conch with 32 mm diameter and with the first 2.5 whorls preserved. The umbilical window is small (0.50 × 0.25 mm). Throughout ontogeny, the coiling rate of the conch decreases markedly (WER is reduced from 5.56 to 2.18). The siphuncular diameter (RSH) increases during ontogeny from 0.12 up to 0.18. The siphuncle has a ventral position in the initial chamber but during the first three quarters of the length of the first volution migrates towards the dorsal shell wall (RSP = 0.69 at dm = 4.9 mm); up to the largest conch diameter, the relative position of the siphuncle remains approximately the same (RSP = 0.67 at dm = 31 mm). The septal necks are orthochoanitic or loxochoanitic and short (< 0.2 of the segment length). They are thicker than the free part of the septum. The connecting rings are essentially tubular in the first whorl but then

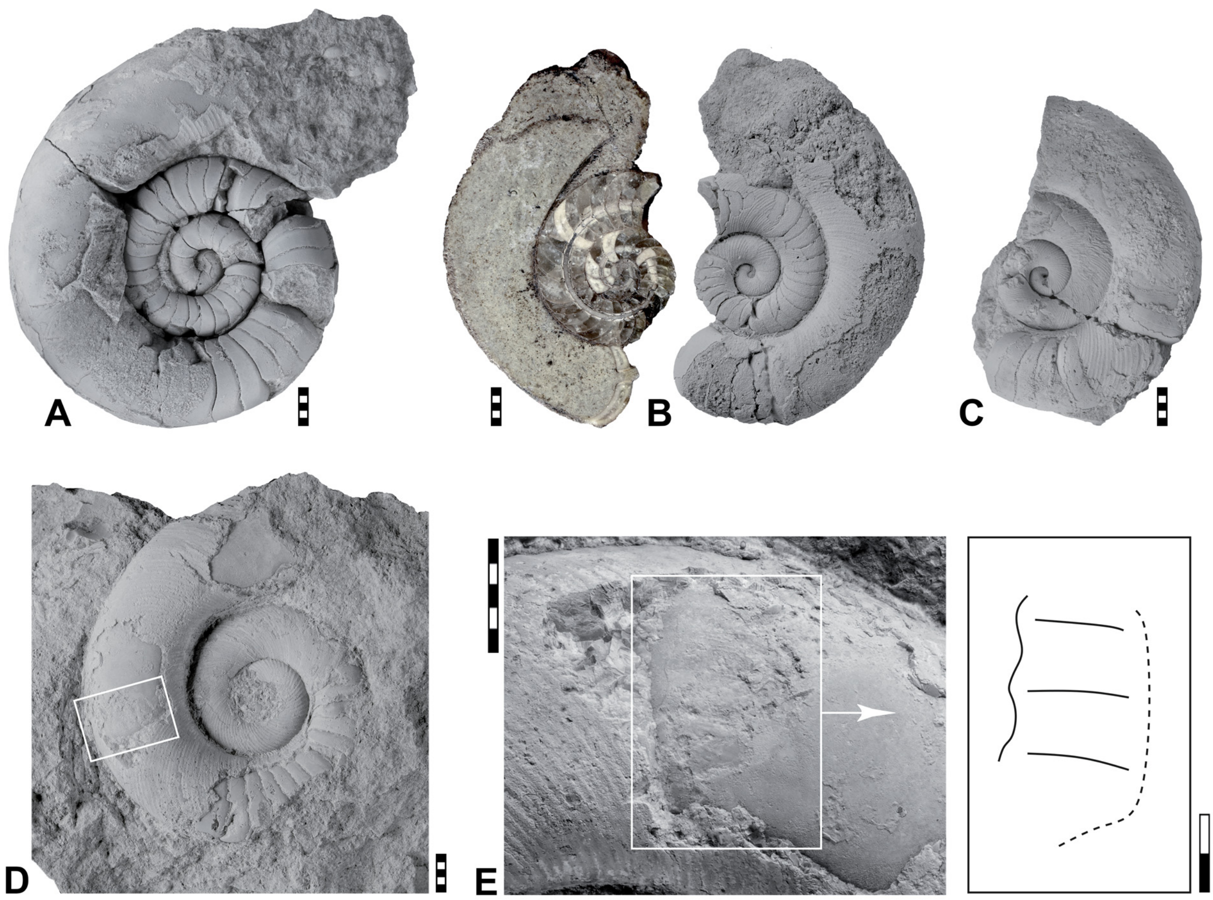

Fig. 34. *Curtoceras teres* (Eichwald, 1840). **A**. Specimen GIT 225-1092 (Schmidt Coll.) from Osmussaar (Estonia); lateral view. **B**. Specimen GIT 225-1062 from Aari (Estonia); longitudinal section and lateral view. **C**. Specimen GIT 426-530 (Stumbur Coll.) from Aa (Estonia); lateral view. **D**. Specimen FMNH HS.P31459 from Tallinn (Estonia); lateral view. **E**. The same specimen, details of muscle attachments. Scale bar units = 1 mm.

become slightly concavo-convex or concave in shape, especially on the ventral side of the siphuncle. The brownish inner layer of the connecting ring wall is homogenous and about as thin as the septa. The outer, dark-grey layer of the ring is much thicker and the thickness is unevenly distributed. The initial chamber of the phragmocone is curved and cup-shaped, 1.82 mm in height and about 2.3 mm in width; the caecum is ~ 0.5 mm long. In the first whorl, the chambers shorten from RCL ~ 0.60 to RCL ~ 0.30. Further chambers change between 0.22 and 0.15. The section through the shell wall in the specimen indicates that the shell was ornamented with rather regularly spaced, slightly imbricated lirae; in the most apical part of the first whorl, the shell surface appears to be smooth. Inside of the conch, the septa are thickened at the point where they are attached to the inner surface of the shell wall.

Two additional specimens, GIT 225-1062 (Fig. 34B) and GIT 426-499, were studied from sagittal sections. The conch morphology is generally the same as in specimen MB.C.646. A difference is that, in GIT 225-1062 (Fig. 34B), the siphuncle is thinner (RSH as low as 0.12) and its diameter does not increase during ontogeny; however, the section through the specimen is not perfectly in the median plane and the values might thus be artificially lower. Both specimens are adult individuals. More complete of the two is the specimen GIT 225-1062, which shows the initial chamber (0.85 × 1.80 mm). The last 185 degrees of the conch is occupied by the body chamber, which detaches from the preceding volution and shows the aperture. At the dorsal surface of the uncoiled part of the body chamber, the shell ornament of sharp, regularly spaced and imbricated lirae is preserved.

Two specimens were sectioned transversely. The larger of the two is specimen MB.C.32185 (Fig. 35A), which is a conch 45 mm in diameter with three whorls preserved. During ontogeny (between 8 mm and 45 mm conch diameter), the conch changes from thinly pachyconic to extremely discoidal (CWI decreases from 0.61 to 0.29) and from subinvolute to subevolute (UWI increases from 0.18 to 0.44); the whorl expansion rate is lowered (WER decreases from 3.57 to 2.00). The whorl profile shows broadly rounded flanks and venter, it changes from weakly depressed to weakly compressed (WWI decreases from 1.24 to 0.96). The siphuncle varies in diameter between 0.17 and 0.14 of the apertural height; it has a subcentral position in the earliest whorl (RSP = 0.55) and then moves further towards the dorsal

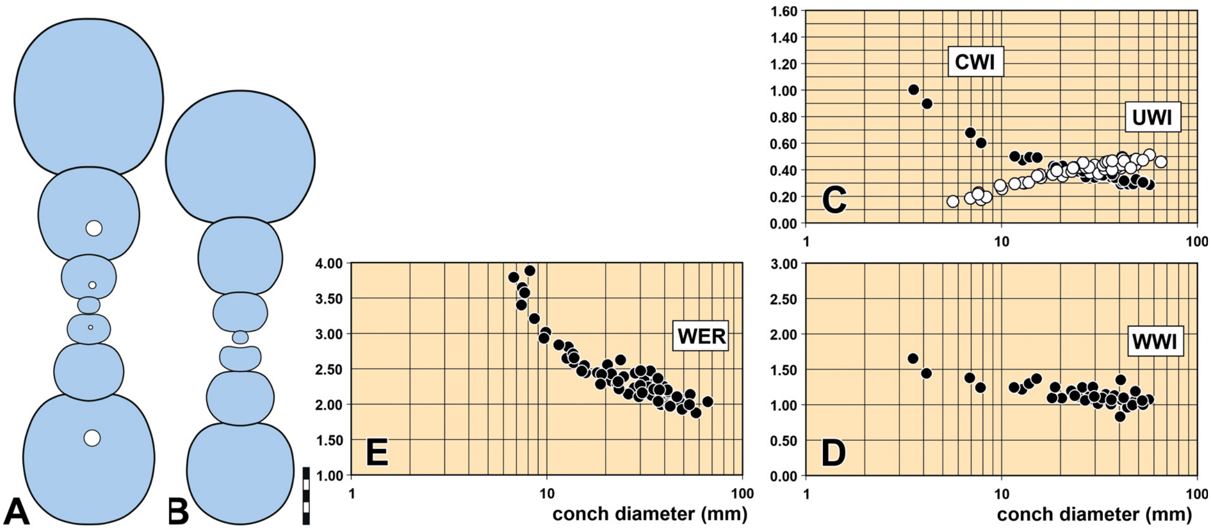

Fig. 35. *Curtoceras teres* (Eichwald, 1840). **A**. Specimen MB.C.32185 (Neben and Krueger Coll.), probably from Brandenburg; cross section. **B**. Specimen MB.C.32186 (Neben and Krueger Coll.) from Oderberg (Brandenburg); cross section. **C–E**. Ontogenetic development of the conch width index (CWI), umbilical width index (UWI), whorl width index (WWI) and whorl expansion rate (WER) of selected specimens. Scale bar units = 1 mm.

Table 23 (continued on next page). Conch measurements, ratios and rates of *Curtoceras teres* (Eichwald, 1840).

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.11544	43.6	13.2	13.0	20.5	13.0	0.30	1.01	0.47	2.03	0.00
minus 90°	37.5	12.7	12.3	16.5	12.3	0.34	1.03	0.44	2.21	0.00
minus 180°	30.0	10.4	9.7	13.2	9.7	0.35	1.06	0.44	2.19	0.00
minus 270°	24.9	9.7	8.8	10.5	8.8	0.39	1.11	0.42	2.39	0.00
minus 360°	20.1	–	7.0	7.8	7.0	–	–	0.39	2.35	0.00
minus 450°	16.0	–	5.8	5.5	5.8	–	–	0.34	2.44	0.00
minus 540°	13.1	–	5.3	4.0	5.3	–	–	0.30	2.81	0.00
minus 630°	10.1	–	4.3	2.6	4.3	–	–	0.26	3.01	0.00
minus 720°	7.7	–	3.7	1.8	3.7	–	–	0.23	3.64	0.00
minus 810°	5.7	–	3.2	0.9	3.2	–	–	0.16	5.18	0.00
MB.C.9715	40.9	12.0	14.5	17.0	–	0.29	0.82	0.42	–	–
MB.C.32187	36.7	12.7	12.7	17.0	12.3	0.35	1.00	0.46	2.26	0.03
MB.C.32184	40.5	–	12.1	18.2	12.1	–	–	0.45	2.03	0.00
minus 90°	34.5	13.3	11.6	14.2	11.6	0.39	1.14	0.41	2.28	0.00
minus 180°	28.4	11.3	10.2	10.8	10.2	0.40	1.11	0.38	2.43	0.00
MB.C.11545	41.5	13.0	12.2	20.6	12.2	0.31	1.07	0.50	2.01	0.00
MB.C.32183	42.8	–	15.1	17.0	15.1	–	–	0.40	2.39	0.00
MB.C.32185	44.5	13.1	13.7	19.4	13.0	0.29	0.96	0.44	2.00	0.05
minus 180°	31.5	11.6	11.5	11.8	10.9	0.37	1.01	0.38	2.34	0.05
minus 360°	20.6	8.9	8.2	7.3	7.7	0.43	1.09	0.36	2.55	0.06
minus 540°	12.9	6.1	5.1	3.9	5.0	0.48	1.21	0.30	2.64	0.02
minus 720°	7.9	4.8	3.9	1.4	3.7	0.61	1.24	0.18	3.57	0.04
minus 900°	4.2	3.8	2.6	–	2.7	0.91	1.44	–	8.21	–
MB.C.32186	38.2	13.1	11.6	17.6	11.1	0.34	1.13	0.46	1.99	0.04
minus 180°	27.1	9.4	8.9	11.3	8.7	0.35	1.05	0.42	2.17	0.03
minus 360°	18.4	7.4	6.8	6.8	6.6	0.40	1.09	0.37	2.44	0.03
minus 540°	11.7	5.9	4.8	3.5	4.8	0.51	1.24	0.30	2.83	0.00
minus 720°	7.0	4.8	3.5	1.3	3.4	0.69	1.38	0.19	3.79	0.02
minus 900°	3.6	3.6	2.2	–	2.4	1.02	1.66	–	9.89	–
FMNH HS.P31459	44.0	–	14.5	19.6	–	–	–	0.45	2.22	–
GIT 426-530	48.6	15.5	14.8	21.5	14.8	0.32	1.05	0.44	2.07	0.00
GIT 225-1092	47.3	14.0	14.2	22.4	14.2	0.30	0.99	0.47	2.04	0.00
minus 90°	39.3	–	13.1	16.8	13.1	–	–	0.43	2.25	0.00
minus 180°	33.1	12.0	11.0	14.5	11.0	0.36	1.09	0.44	2.24	0.00
minus 270°	26.2	10.3	8.3	12.0	8.3	0.39	1.24	0.46	2.14	0.00
minus 360°	23.0	9.3	7.8	9.0	7.8	0.40	1.19	0.39	2.29	0.00
GIT 426-498	57.2	16.5	15.5	29.6	15.5	0.29	1.07	0.52	1.88	0.00
minus 90°	48.8	16.2	13.6	23.7	13.6	0.33	1.19	0.48	1.93	0.00

Table 23 (continued). Conch measurements, ratios and rates of *Curtoceras teres* (Eichwald, 1840).

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
GIT 697-130	42.5	13.6	12.5	20.0	12.2	0.32	1.09	0.47	1.97	0.02
minus 90°	36.9	13.7	12.9	14.8	12.9	0.37	1.06	0.40	2.36	0.00
GIT 697-567-1	41.6	–	12.6	19.1	–	–	–	0.46	–	–
minus 90°	34.9	–	11.3	15.1	–	–	–	0.43	–	–
minus 180°	29.0	–	9.9	12.9	–	–	–	0.44	–	–
minus 270°	23.5	–	8.5	9.8	–	–	–	0.42	–	–
MB.C.646	31.79	–	–	–	10.26	–	–	–	2.18	–
minus 90°	26.29	–	–	–	8.43	–	–	–	2.17	–
minus 180°	21.53	–	–	–	7.41	–	–	–	2.32	–
minus 360°	13.92	–	–	–	5.26	–	–	–	2.58	–
minus 540°	8.86	–	–	–	3.91	–	–	–	3.20	–
minus 720°	4.95	–	–	–	2.85	–	–	–	5.56	–
GIT 426-499		–	16.13	21.51	16.13	–	–	–	–	–
minus 90°	41.50	–	13.36	18.79	13.36	–	–	0.45	2.17	0.00
minus 270°	28.14	–	9.30	11.91	9.30	–	–	0.42	2.23	0.00
GIT 225-1062	34.27	–	–	15.79	10.77	–	–	0.46	2.13	–
minus 180°	23.50	–	–	9.90	7.71	–	–	0.42	2.22	–
minus 270°	19.26	–	–	7.62	6.88	–	–	0.40	2.42	–
minus 360°	15.79	–	–	5.78	5.89	–	–	0.37	2.54	–
minus 540°	9.90	–	–	2.81	4.11	–	–	0.28	2.93	–
minus 630°	7.62	–	–	1.66	3.49	–	–	0.22	3.40	–
minus 720°	5.81	–	–	–	2.97	–	–	–	4.18	–
TUG 860-1309	23.29	–	7.99	9.75	7.99	–	–	0.42	2.32	0.00
minus 90°	19.03	8.00	6.43	–	6.43	0.42	1.24	–	2.28	0.00
minus 180°	15.3	7.6	5.56	5.46	5.56	0.50	1.37	0.36	2.46	0.00

shell wall and maintains the relative distance of RSP = 0.73. The other transversely sectioned specimen MB.C.32186 (Fig. 35B) is nearly identical to specimen MB.C.32185 in conch dimensions and ratios; the only difference is the more depressed whorl profile (WWI = 1.13 at dm = 38 mm).

Specimen FMNH HS.P31459 (Fig. 34D) is a nearly complete conch (only the innermost whorls are covered by sediment) of an adult individual with the total diameter of about 47 mm. One lateral side of the specimen is hidden in the surrounding rock and the first half of the outer volution is slightly distorted; this hindered some measurements. The body chamber occupies the last half of a whorl. The aperture is partly preserved and shows the presence of a rounded and deep hyponomic sinus and very slight lateral flaring. At the base of the body chamber, structures resembling muscle attachment impressions are preserved (Fig. 34E). At the diameter of 44 mm, the conch is subevolute or evolute (UWI ~ 0.45) with a high coiling rate (WER ~ 2.20). The suture lines are straight and relatively closely spaced (RCL ~ 0.25). The ornament consists of rursiradiate lirae that form a deep and wide ventral sinus; the lirae are sharp especially in the inner whorl and flatten out towards later whorls.

Remarks

The holotype of "*Nautilus Teres*" was not available for our study; it was described by Eichwald (1840) but not illustrated in that publication. It came from the Orthoceratite Limestone (C1 horizon, late Darriwilian, Middle Ordovician) of the Estonian island of Osmussaar (formerly Odensholm in Swedish and Odinsholm in German).

Balashov (1953: 246, pl. 5 fig. 2) reproduced and assigned, as "holotype", a specimen of "*Lituites Odini*" figured by Verneuil (1845: 360, pl. 25 fig. 8). Eichwald (1860) had assigned this specimen to "*Nautilus teres*" but he did not state whether it was part of the type collection or not. Furthermore, the present repository of the specimen or the type collection of Eichwald could not be traced. The herein studied material agrees closely with the latter specimen, but designation of a neotype from the presently studied collection is avoided because it cannot be confirmed that the type collection of Eichwald (1840) was lost.

Here we assign 19 specimens to *Curtoceras teres*, which makes it the most abundant species in the studied material and allows some insight into the intraspecific variation. This concerns mainly the shape of the whorl profile. Generally, the WWI decreases as the conch grows (Fig. 11). In the early growth stages, the whorl profile is moderately depressed (WWI = 1.66 in specimen MB.C.32186), but in the adult stage it is between weakly depressed (WWI = 1.13 in specimen MB.C.32186), equidimensional (MB.C.11544, MB.C.32187, MB.C.32185) and weakly compressed (WWI = 0.82 in specimen MB.C.9715); the whorl profile is usually broadly rounded or sometimes weakly flattened ventrally and laterally. The differences in adult whorl profile are not accompanied by differences in any other characters or parameters. The lowest variation is recognised in WER and CWI; both decrease during ontogeny (Fig. 11), particularly in early growth stages (up to dm ~ 5 mm), after that the rate of decrease is getting smaller.

Besides the material described above, the Estonian geoscience data portal eMaapõu (https://geoloogia.info) lists several juvenile specimens of *Curtoceras* (TUG 1745-331 to TUG 1745-337, University of Tartu, Natural History Museum) from the Aseri Regional Stage, which appear to fall within the variation observed in *C. teres*. These specimens support the extension of the stratigraphic range of the species to the Aseri Regional Stage (Darriwilian Stage).

Curtoceras teres is similar to the stratigraphically coeval *C. estonicum* (Island of Osmussaar and Tallinn Region of Estonia). According to the original description of Balashov (1953), the latter differs by having a square-shaped whorl profile in later growth stages and more sinuous suture lines; also, the siphuncle is closer to the dorsal side in *C. estonicum* than in *C. teres*. In the herein studied collection, there are four specimens (GIT 225-1092, GIT 697-130, GIT 426-498, TUG 860-1309) which have weakly rectangular whorl profile producing a ventral lobe and dorso-lateral saddle in the suture lines. However, there is no difference in conch geometry between these specimens, the holotype of *C. estonicum* described by Balashov (1953) and the representatives of *C. teres* with rounded whorl profile studied herein. For this reason and considering the variability of whorl profile shape in late growth stages of the latter, *Curtoceras estonicum* is synonymised with *C. teres* here.

In contrast to *Curtoceras teres*, the early Sandbian *C. kerstovense* from the St Petersburg Region (Russia) attains much larger adult size (up to 80 mm) with only the very end of the body chamber uncoiled from the preceding volution. *Curtoceras abditus* from the Keila Regional Stage (Late Ordovician) of Estonia differs from *C. teres* mainly in the reticulate shell ornament with strong transverse ornament elements, and in having a generally more robust conch in the early growth stage.

Among the species of *Trocholites*, *Curtoceras teres* is most similar to *T. depressus*, especially in umbilical width (UWI) and conch width (CWI). However, *T. depressus* has a much lower and much less rapidly

Table 24. Conch measurements, ratios and rates of *Curtoceras meyeri* sp. nov.

specimen	dm	ww	wh	uw	ah	CWI	WWI	UWI	WER	IZR
MB.C.11550	41.1	18.9	14.0	18.1	13.4	0.46	1.35	0.44	2.20	0.04

decreasing coiling rate (particularly in early and mid-ontogeny; WER = 2.7–1.6 vs 9.9–1.9), the whorl profile tends to be more depressed (WWI = 1.67–1.2 vs 1.66–0.82 in ontogeny) and the siphuncle is much wider (RSH ~ 0.30 vs 0.16) with a marginodorsal position; the ornament in *T. depressus* has ribs on inner whorls instead of just sharp lirae.

Geographic and stratigraphic occurrence

Sweden (Island of Öland), Estonia, St Petersburg and Kaliningrad regions of Russia, northern Germany and northern Poland; Aseri–Uhaku regional stages, Darriwilian, Middle Ordovician.

Curtoceras meyeri sp. nov.
urn:lsid:zoobank.org:act:69962EDA-B814-4DA9-84FA-8592B6E57609
Fig. 36; Table 24

Diagnosis

Species of the genus *Curtoceras* with an adult conch exceeding 40 mm in diameter. At 40 mm diameter, the conch is discoidal (CWI ~ 0.45) and subevolute (UWI ~ 0.45) with high coiling rate (WER ~ 2.20); whorl profile with rounded flanks and venter, weakly depressed (WWI ~ 1.35) and weakly embracing (IZR = 0.05). Shell surface with lirae. Phragmocone chambers short (RCL ~ 0.10). Suture line almost straight or with a very shallow lateral lobe and a ventral saddle. Siphuncle subdorsal (RSP ~ 0.85) and narrow (RSH ~ 0.15).

Etymology

Named after Günter Meyer (Bernau), who donated a well-preserved *Curtoceras* specimen to be studied herein.

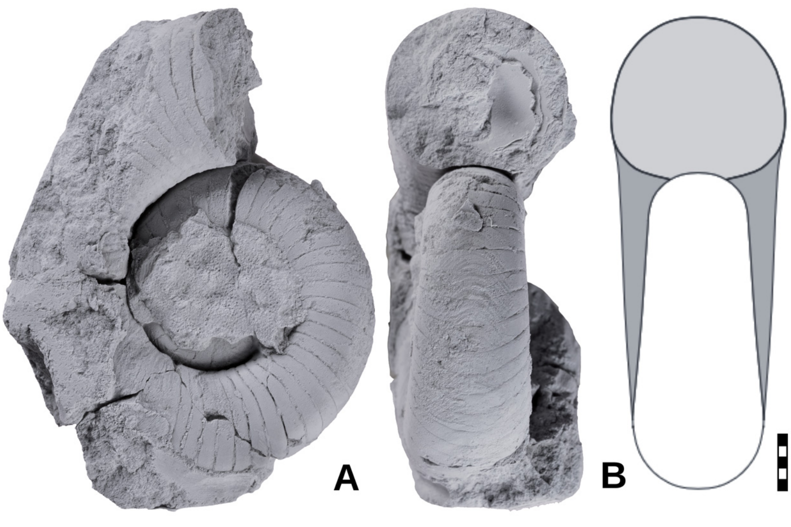

Fig. 36. *Curtoceras meyeri* sp. nov.; holotype MB.C.11550, probably from Brandenburg. **A**. Lateral and dorsal views. **B**. Reconstruction of apertural view. Scale bar units = 1 mm.

Type material

Holotype

GERMANY • unspecified locality in northern Germany; ?Lasnamägi Regional Stage; illustrated in Fig. 36A; MB.C.11550.

Description

Holotype MB.C.11550 (Fig. 36A) is a subadult conch with 41 mm diameter and has almost three whorls preserved; the body chamber is missing. In the last half whorl, the conch is discoidal (CWI = 0.46) and subevolute (UWI = 0.44); the coiling rate is high (WER = 2.20). The whorl profile has broadly rounded flanks and venter; it is weakly depressed (WWI = 1.35) and weakly embracing (IZR = 0.04) (Fig. 36B). The shell ornament is preserved only in a small area on the venter, where it consists of lirae that extend into a ventral sinus. The phragmocone chambers are short (RCL = 0.11). The suture line is almost straight or possesses a very shallow lateral lobe; however, on the venter of at least the last whorl, the suture line extends into a progressively pronounced saddle. The siphuncle is subdorsal in position (RSP = 0.85) and about 0.16 in relative diameter (RSH).

Remarks

Curtoceras meyeri sp. nov. differs from other species of *Curtoceras* in the increasingly pronounced external saddle of the suture line starting with the third whorl, combined with the comparably high WWI and comparatively short phragmocone chambers.

Discussion

Coiled cephalopods are among the most characteristic fossils in the Middle and Late Ordovician rocks of Baltoscandia and their erratics, and were already studied in the 18th and 19th centuries (e.g., Bertrand 1763; Eichwald 1840, 1860; Angelin 1880; Remelé 1890; Holm 1891; Schröder 1891). The majority of these cephalopods belong to two independently evolved orders (Pohle *et al.* 2022), the Lituitida of the subclass Orthoceratoidea and the Tarphyceratida of the subclass Multiceratoidea. Coiled conchs are additionally present in representatives of two multiceratoid families of uncertain phylogenetic position at the order level (Pohle *et al.* 2022), the Uranoceratidae Hyatt in Zittel, 1900 and Apsidoceratidae Hyatt, 1884. The occurrence of coiled conchs in different groups illustrates the multiple origin of coiling in the evolution of the Cephalopoda (Kröger 2005; Pohle *et al.* 2022).

Knowledge of the Baltoscandian coiled cephalopods is unevenly distributed. While the Baltoscandian lituitids have recently been extensively revised (Aubrechtová & Meidla 2020; Aubrechtová & Korn 2022) and phylogenetically analysed (Fang *et al.* 2021), a comprehensive systematic treatment of the two “barrandeoceratid” families mentioned above is lacking, and only a few taxonomic studies have been published (Strand 1933; Balashov 1953; Frye 1982; Dzik 1984; Kröger 2013). Some Baltoscandian tarphyceratids have been studied rather intensively in the past, in particular the Early-Middle Darriwilian members of the family Estonioceratidae, see Balashov (1953) and King (2014) for a summary and further references, and the Late Ordovician representatives of the genus *Discoceras* of the family Trocholitidae (e.g., Strand 1933; Balashov 1953; Sweet 1958; Stumbur 1962; Dzik 1984; Kröger 2013; Kröger & Aubrechtová 2018, 2019), but a review for other members of the order is missing. In the present project, we start to fill this gap by reviewing *Trocholites* and *Curtoceras* (both family Trocholitidae).

We have studied over eighty specimens coming from in-situ limestones of northern Estonia and Sweden, as well as from erratic boulders in northern Germany and Poland (Fig. 1). Stratigraphically, most of the specimens are from the middle-late Darriwilian limestone strata; only a few specimens assigned to *Curtoceras* come from younger, early Sandbian limestones. The studied collection includes the type and published specimens of Angelin (1880), Remelé (1880, 1890), Schröder (1891), Foerste (1930), Schindewolf (1933) and Neben & Krueger (1971, 1973). Included in the study are also specimens illustrated by Eichwald (1860) and re-illustrated and re-described by Balashov (1953) but these could only be studied on the basis of high-resolution photographs provided by St Petersburg State University.

In the course of the study, the Baltoscandian species of both genera were redefined, taking into account ontogenetic changes, trajectories and variation of morphological characters. Implementing the ontogenetic trajectories (Figs 7, 11–12) helped to distinguish taxa, which would otherwise be difficult to tell apart using only external characters or measurements taken only from outer volutions and terminal body chambers. This shows the importance of studying as much of the ontogeny as possible. Unfortunately, sectioning was not possible for many specimens studied herein and preservation sometimes hindered investigation of those that could be sectioned.

The morphological variation (Figs 7, 11–12) could be evaluated especially in *Trocholites hospes*, *T. depressus* and *Curtoceras teres*, where sufficient material was available. In *T. hospes*, the variation mainly concerned the size of the adult conch, which resulted in apparent differences in the degree of depression of the whorl profile. Similarly, in *T. depressus*, the variation in adult conch size contributed to differences in ww/wh ratio and dorsal impression between specimens; in addition, ribs are of variable thickness or may be absent on the shell surface of some specimens. The shape of the whorl profile is also variable in late growth stages of *Curtoceras teres*, where the profile might be anywhere between weakly depressed and weakly compressed and between broadly rounded and weakly flattened ventrally and laterally.

The above indicates that analyses of ontogenetic changes and morphological variation (including adult size variation leading to comparison of non-corresponding growth stages) are essential to the proper definition of the trocholitid taxa. Future studies based on a greater number of (sectioned) specimens are needed to show whether some of the species described herein are in fact synonymous or, on the contrary, need to be further split.

In total, 16 species of *Trocholites* and two species of *Curtoceras* are recognised in this work, of which 11 and one, respectively are new. Neotypes are proposed for some species defined by Schröder (1891), since the type material was probably lost during World War II; for the same reason, some species could not be considered herein, although they are valid. Three species of Eichwald (1840), *Trocholites depressus*, *T. odini* and *T. incongruus*, are synonymised and a neotype is selected.

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