The tarphyceratid cephalopod Trocholites in the Middle–Upper Ordovician of the Prague Basin—the Baltican element in peri-Gondwana

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The tarphyceratid cephalopod *Trocholites* in the Middle–Upper Ordovician of the Prague Basin —the Baltican element in peri-Gondwana

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The vast majority of cephalopods of the order Tarphyceratida are known from regions that were located at mid- or low palaeolatitudes during the Ordovician (mainly Baltica, Laurentia, and Chinese palaeoblocks). Only a handful of tarphyceratid specimens are known from high palaeolatitude regions of peri-Gondwana and Gondwana. Here, we describe the two best-preserved trocholitid cephalopods known to date from the Ordovician of the Prague Basin. The first is from the late Darriwilian/early Sandbian Dobrotivá Formation and is assigned to *Trocholites fugax*, a species previously recorded from roughly coeval strata of Iberia, France, and Bohemia. The specimen thus strengthens previous hypotheses regarding the interchange of non-benthic faunas between Baltica and different regions of peri-Gondwana during the Middle/Late Ordovician boundary interval. The second specimen, assigned to a new species of *Trocholites chaloupkai* sp. nov., is from the late Sandbian–early Katian Zahořany Formation and thus represents one of the stratigraphically youngest *Trocholites* in the Ordovician of peri-Gondwana. Internal structures of the shell of the holotype of the new species were studied using micro-CT tomography. This revealed that *T. chaloupkai* sp. nov. closely resembles the stratigraphically older (Darriwilian) species *Trocholites depressus* from Estonia.

Key words: Tarphyceratida, *Trocholites*, micro CT, Darriwilian, Sandbian/Katian, Prague Basin, Baltica, peri-Gondwana.

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Introduction

Coiled cephalopods of the order Tarphyceratida Flower in Flower and Kummel, 1950, are represented in the Ordovician of the Prague Basin only by the genus *Trocholites* Conrad, 1838. This genus is globally distributed in Ordovician rocks, particularly those in Northern Europe, Northern America, and China. During the Ordovician, these regions were located at mid- or low palaeolatitudes (Cocks and Torsvik 2021). By contrast, trocholitids were remarkably scarce at high palaeolatitudes, limited only to time intervals associated with faunal migrations induced by climatic and oceanographic changes (Vandenbroucke et al. 2013; Cocks and Torsvik 2021). Only a single trocholitid species, *Trocholites fugax* Babin and Gutiérrez-Marco, 1992 (= ?*Lituites primulus* Barrande, 1865), has been reported from the Ordovician strata of Bohemia (Manda 2008). Besides Bohemia, the species is known from Iberia and Armorica (France) suggesting faunal connections along the shelf of peri-Gondwana during the late Darriwilian (Dobrotivian; Babin and Gutiérrez-Marco 1992; Babin et al. 1996; Sá and Gutierréz-Marco 2009; Evans 2000). In this report, we extend the previous study by Manda (2008) and describe two relatively well-preserved trocholitid specimens from the Ordovician of the Prague Basin.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank: lsid:zoobank.org:pub:8DCA09D5-DDA7-42DC-921C-B5B-5D80CE6CD

Institutional abbreviations.—NM, National Museum, Prague, Czech Republic.

Other abbreviations.—ah, apertural height; cl, cameral length; CWI, conch width index; dm, shell diameter across centre of umbilicus; fh, foramen height; iz, imprint zone; uw, umbilical width; IZR, imprint zone rate; RCL, relative cameral length; RSH, relative septal foramen height; UWI, umbilical width index; WER, whorl expansion rate calculated based on either whorl height (WERwh) or aperture height (WERah); wh, whorl height; ww, whorl width; WWI, whorl width index.

Material and methods

Two specimens were available for study, NM L 63625 and NM L 63626.

The internal mould and its counterpart (NM L 63625-a, b) were collected by Vincenc Marek (Beroun, Bohemia) during or before 1910 at Březová Hůrka near Starý Plzenec (Fig. 1: Locality 1), where strata of the middle–upper Dobrotivá Formation (upper Darriwilian–lower Sandbian; Middle–Upper Ordovician; Fig. 2) are exposed. The fossil is preserved in a black silty shale. The phragmocone is not significantly deformed. The body chamber is crushed and compacted while its adapertural half is missing.

The second specimen (NM L 63626) is an isolated, undeformed internal mould of a phragmocone comprised of a brown-red pelosiderite. It was collected by the private collector Miloš Chaloupka (Prague, Czech Republic) around the year 1994 in Praha-Štěrboholy (Fig. 1: Locality 2). The specimen originated from silty shales excavated for the construction of a shopping centre (northeast of the intersection of the Prague ring motorway with the Průmyslová Street). The shale beds were assigned to the upper Zahořany Formation (lower Katian; Upper Ordovician; Fig. 2) based on the characteristic lithology, as well as the common occurrence of the cystoid *Aristocystites bohemicus* Barrande, 1887, represented mainly by the massive basal portions.

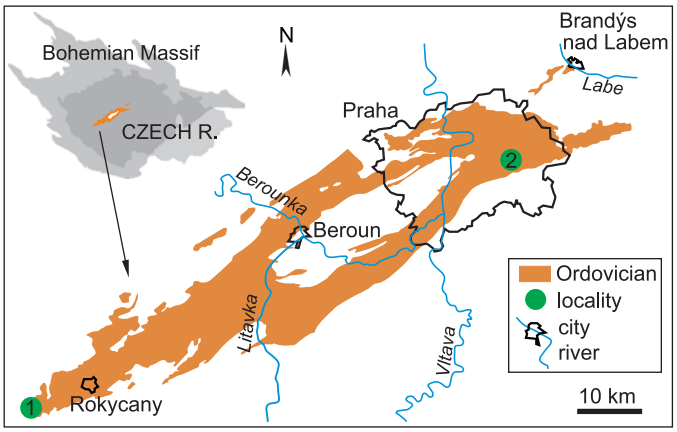

Fig. 1. Map of Ordovician rocks of the Prague Basin and position of the localities, from which the two studied specimens originate: Locality 1, Březová Hůrka near Starý Plzenec; Locality 2, Praha-Štěrboholy. Modified from Manda (2008).

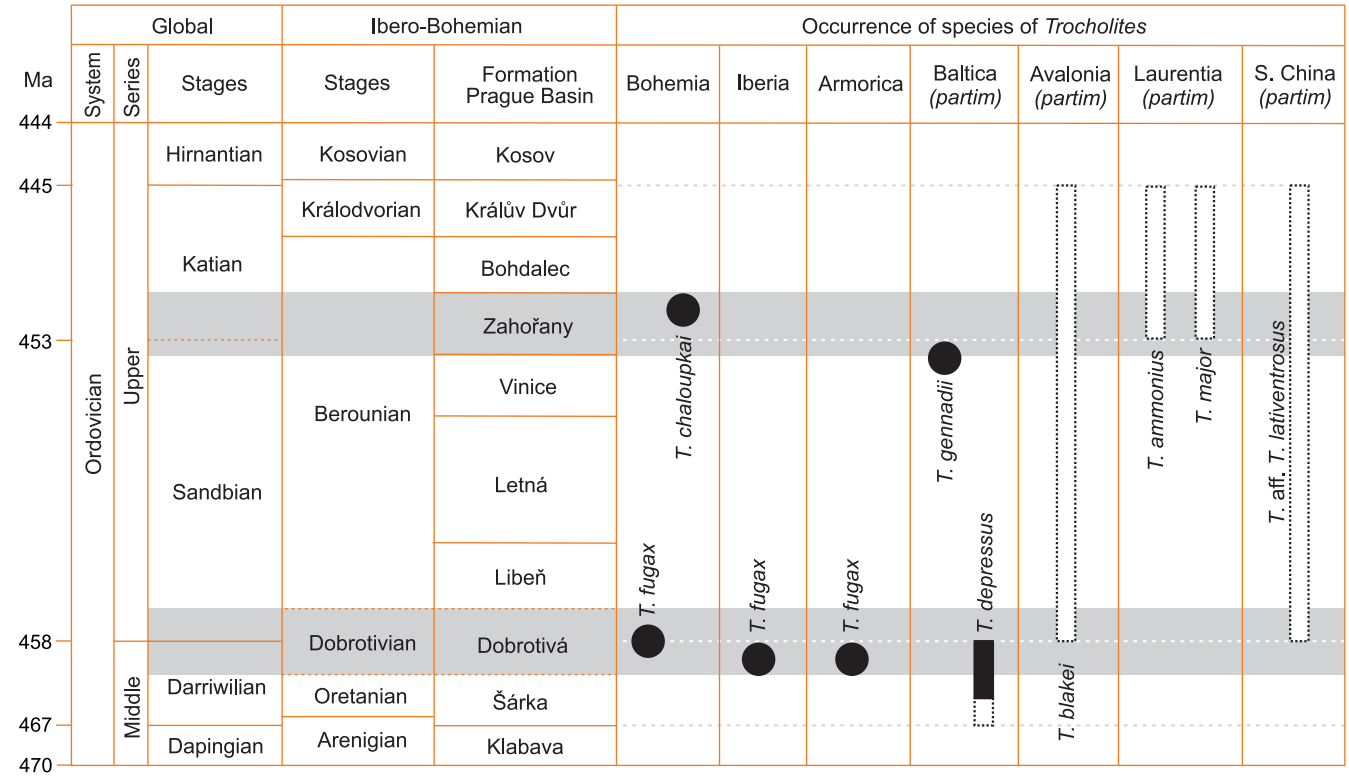

Fig. 2. Correlation of the Dobrotivá and Zahořany formations (greyed-out levels) with global and Ibero-Bohemian chronostratigraphic units, and the herein discussed occurrence of *Trocholites*. Modified from Kraft et al. (2015), Fatka and Budil (2022), and Kraft et al. (2023).

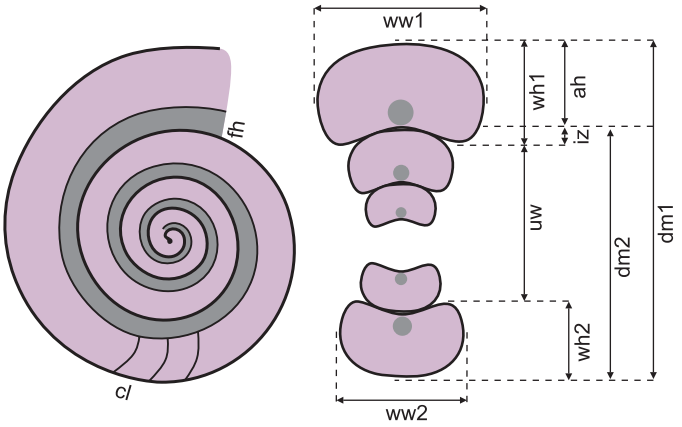

Fig. 3. Parameters used to measure and describe the specimens studied herein (after Korn 2010). Abbreviations: ah, apertural height; cl, cameral length; dm, shell diameter across centre of umbilicus; fh, foramen height; iz, imprint zone; uw, umbilical width; wh, whorl height; ww, whorl width. Line drawings are based on NM L 63626 (holotype of *Trocholites chaloupkai* sp. nov.).

The specimens were studied under a binocular microscope and measured to obtain standard shell parameters of Korn (2010) (Fig. 3, Table 1). The distance of septa is expressed as the relative cameral length (Pohle et al. 2022) and calculated as cameral length vs. whorl height (RCL = cl/wh). The size of the siphuncle is expressed as the relative septal foramen height (Pohle et al. 2022) and calculated as the height of the septal foramen *vs.* whorl height (RSH = fh/wh).

Both specimens were coated in ammonium chloride prior to photography. Photographing was performed using a SONY ILCE-7RM3 camera. NM L 63626 was scanned using the micro-tomograph SkyScan 1172 and the shell reconstructed with N-Recon software; final photographs were then prepared in the Avizo 9.1.1. software. Detailed images of shell ornament in NM L 63626 were made with a Hitachi S-3700N scanning electron microscope.

Geological settings

The majority of Ordovician sediments in the Czech Republic occur in the Barrandian area of the Teplá-Barrandian Unit (central Bohemia). There, a denudation relict of a narrow, linear, tectonically predisposed, rift-type basin is preserved, which is termed the Prague Basin. The sedimentation in this basin started with opening of the Rheic ocean in the Tremadocian (Early Ordovician) and terminated with the onset of the Variscan orogeny in the Givetian (Middle Devonian). The lithology of the Prague Basin infilling gradually changes from prevailingly clastic (Ordovician) to carbonate rocks (upper Silurian–lower Middle Devonian), reflecting drift of peri-Gondwanan terrains from high palaeolatitudes towards the palaeoequator; the sedimentation was accompanied with volcanic activity in multiple intervals. The generally continuous, unmetamorphosed and richly fossiliferous marine rock succession of the Prague Basin is among the most classical and best studied globally with several global stratotypes established in the upper Silurian and Devonian part of the succession. For summary and references on the development of the Prague Basin see Havlíček in Chlupáč et al. (1998), Vacek and Žák (2019) and Kraft et al. (2023).

Ordovician strata of the Prague Basin are divided in twelve formations. Their lithology and fossil content reflect the opening and deepening of the sedimentary basin associated with the interplay between global changes including eustasy, and local volcanic and synsedimentary tectonic activity and changing palaeogeographic position of the region. The rocks of the Dobrotivá Formation were formed during the Middle/Late Ordovician boundary interval (late Darriwilian and earliest Sandbian; Fig. 2). The succession consists of the relatively deeper-water black shale and the shallow-water sandy deposits. Body fossils are best preserved in carbonatic nodules within the shelly facies. Meanwhile, they are usually rare in the sandy facies, which, however, contain common ichnofossils. For summary and further discussion on the lithology, depositional conditions, stratigraphy and faunal assemblages of the Dobrotivá Formation, see Havlíček and Vaněk (1996), Mikuláš (1998), Havlíček in Chlupáč et al. (1998), Fatka and Mergl (2009) and Fatka and Vodička (2022).

Cephalopod assemblages of the Dobrotivá Formation consist mainly from straight-shelled orthoceratoids attributable to species of the orders Orthoceratida and Pseudo-

Table 1. Measurements (in mm) of the two trocholitid specimens studied herein. Ratios from Korn (2010). In bold are the main coiling parametres of Korn (2010). Abbreviations: ah, apertural height; cl, chamber length; dm, shell diameter across centre of umbilicus; fh, foramen height; iz, imprint zone; uw, umbilical width; ww, whorl width. CWI, conch width index; dm, shell diameter across centre of umbilicus; fh, foramen height; iz, imprint zone; IZR, imprint zone rate; uw, umbilical width; RCL, relative cameral length; RSH, relative septal foramen height; UWI, umbilical width index; WER, whorl expansion rate calculated based on either whorl height (WERwh) or aperture height (WERah); wh, whorl height; ww, whorl width; WWI, whorl width index.

Taxonomy	Coll. no.	dm1	dm2	ww1	ww2	wh1	wh2	WWI	uw	ah	iz	WERwh	WERah	IZR	UWI	CWI	fh	RSH	fh/ah	cl	RCL
Trocholites chaloupkai	NM L 63626	23.3	17.6	11.5	8.9	6.9	5.2	**1.67**	11.2	5.7	1.2	**2.01**	**1.75**	**0.17**	**0.48**	**0.49**	1.6	**0.23**	**0.28**	2.2	**0.33**
		17.6	13.3	8.9	6.8	5.2	4.2	**1.70**	8.2	4.3	0.9	**2.03**	**1.76**	**0.17**	**0.47**	**0.51**	1.1	**0.21**	**0.25**		
		13.3	9.9	6.8		4.2		**1.63**		3.4	0.8	**2.13**	**1.80**	**0.19**		**0.51**					
Trocholites fugax	NM L 63625	30.5	21.8			11.9	8.7		9.9	8.7	3.2	**2.70**	**1.96**	**0.27**	**0.32**					2.7	**0.28**
		21.8				8.7	5.8		7.2			**2.78**			**0.33**						

rthoceratida (Marek 1999; Manda 2008; Aubrechtová 2015; Aubrechtová et al. 2020); rare are the representatives of the Lituitida (Aubrechtová and Turek 2018) and Tarphyceratida (Manda 2008).

The stratigraphically younger, late Sandbian–early Katian (Fig. 2), Zahořany Formation is preserved mainly in the central part of the Prague Basin. The succession is formed mostly by rather monotonous siltstone beds, which only rarely contain intercalations of silty sandstone and silty shale. The siltstone beds often have carbonate cement, locally developed are nodules and lenses of fossiliferous, clayish limestone. Dark grey or black shale beds of the Zahořany Formation are restricted to the central, deepest part of the basin. For further details on the lithology, depositional conditions, stratigraphy and faunal assemblages of the Zahořany Formation, see Mikuláš (1998), Havlíček in Chlupáč et al. (1998), Fatka and Mergl (2009), Ernst et al. (2014), and Fatka and Budil (2022).

The cephalopods of the Zahořany Formation belong to the orders Orthoceratida and Pseudorthoceratida (Marek 1999); the below studied specimen of *Trocholites* is the only coiled cephalopod known to date from the Zahořany Formation.

Systematic palaeontology

Class Cephalopoda Cuvier, 1797

Subclass: Multiceratoidea Mutvei, 2013

Order Tarphyceratida Flower in Flower and Kummel, 1950

Family Trocholitidae Chapman, 1857

Genus *Trocholites* Conrad, 1838

Type species: *Trocholites ammonius* Conrad, 1838, by original designation; Upper Ordovician, Trenton Limestone, New York, USA.

Trocholites fugax Babin and Gutiérrez-Marco, 1992

Fig. 4.

?1865 *Lituites primulus* Barr.; Barrande 1865: pl. 99: 12.
1992 *Trocholites fugax* n. sp.; Babin and Gutiérrez-Marco 1992: 530–534, figs. 3a–h, 4a–f.
?1992 *Lituites primulus*; Babin and Gutiérrez-Marco 1992: 534.
1996 *Trocholites fugax*; Babin et al. 1996: 107, pl. 1: 1–3.
1996 "cyrtokonní nautiloid"; Mergl 1996: 23.
1999 "*Lituites*" *primulus* Barrande; Vaněk 1999: 8.
?1999 *Curtoceras primulus*; Marek 1999: 415, 416.
2008 *Trocholites fugax* Babin and Gutiérrez-Marco, 1992; Manda 2008: 330–332, fig. 3.
2009 *Trocholites fugax* Babin and Gutiérrez-Marco; Sá and Gutiérrez-Marco 2009: 9–12, fig. 2A, B.
2010 *Trocholites fugax* Babin and Gutiérrez-Marco, 1992; Rábano et al. 2010: 420.
2013 *Trocholites fugax* Babin and Gutiérrez-Marco, 1992; Evans et al. 2013: 28.
2015 *Trocholites fugax* Babin and Gutiérrez-Marco, 1992; Aubrechtová 2015: 208.
2018 *Trocholites fugax* Babin and Gutiérrez-Marco, 1992 (= ?*Lituites primulus* Barrande, 1865); Aubrechtová and Turek 2018: 402.

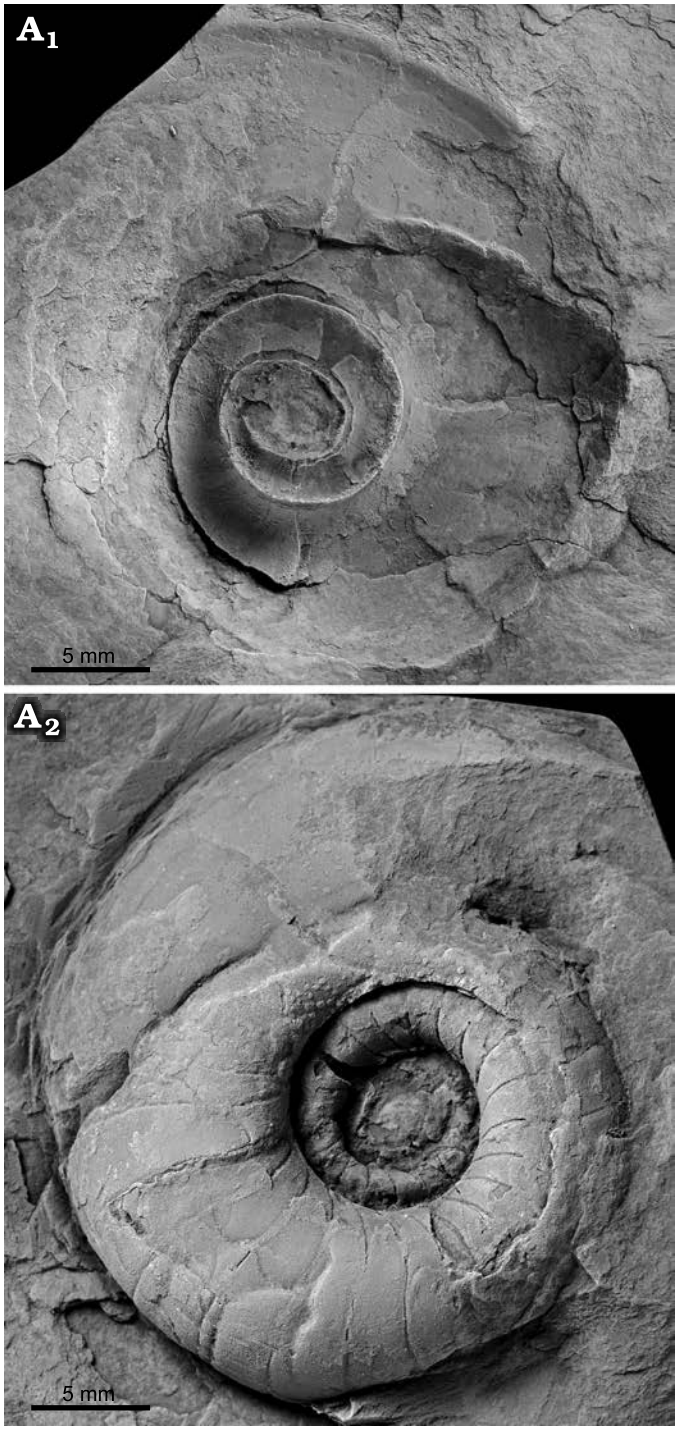

Fig. 4. Tarphyceratid cephalopod *Trocholites fugax* Babin and Gutiérrez-Marco, 1992, from Březová Hůrka near Starý Plzenec, central Bohemia, Dobrotivá Formation (upper Middle–lower Upper Ordovician). **A**. NM L 63625a, b, counterpart (A_1) and part (A_2).

Material.—Single specimen NM L 63625a, b from the locality Březová Hůrka near Starý Plzenec (Fig. 1: Locality 1), middle to uppermost Dobrotivá Formation (upper Darriwilian–lower Sandbian, Middle–Upper Ordovician).

Description.—NM L 63625 is 31 mm in diameter with two outer whorls preserved; the inner whorls and at least the adapertural 90° of the body chamber are missing (as indi-

cated by remains of umbilical seams on the surface of the last preserved whorl). At the maximum diameter, the shell is subevolute (UWI = 0.32), with the last whorl moderately impressed (IZR ~0.27 at dm = 31 mm) and moderately expanded (WER based on apertural height ~1.96 at dm = 31 mm). The relative cameral length (RCL) is about 0.30 in the outer whorl (chambers moderately long). The sutures form a low lobe ventrally and are slightly sinuous on the flanks. There are no traces of the shell ornament apparent on either the internal or external moulds of the specimen.

Remarks.—The internal mould of the body chamber, especially the umbilical wall, shows numerous circular or semicircular structures (0.2–0.3 mm in diameter). The structures are herein interpreted as abiotic.

Trocholites fugax was earlier described by Babin and Gutiérrez-Marco (1992), Babin et al. (1996) and Sá and Gutiérrez-Marco (2009) from the Dobrotivian (upper Darriwilian) of southern Europe. Later, Manda (2008) reported the species from the Prague Basin. Based on new information (Michal Mergl, personal communication 2023), the specimens described by Manda (2008) originate from the upper or uppermost part of the Dobrotivá Formation (uppermost Darriwilian or lowermost Sandbian). Minor differences in shell morphology between the specimens studied by Manda (2008) and other representatives of *T. fugax* including NM L 63625 (submarginal siphuncle, lower expansion rate, apparently uncoiled body chamber) are herein interpreted as resulting from the deformation and breakage of the former specimens, or alternatively minor intraspecific variation.

The representatives of *T. fugax* differ from NM L 63626 (here assigned to *T. chaloupkai* sp. nov.) in the greater expansion rate (WER based on whorl height = 2.78 vs. 2.00; dm ~22 mm), narrower umbilicus (UWI = 0.33 vs. 0.48; dm ~22 mm) and less sinuous (vs. sinuous) suture lines.

Stratigraphic and geographic range.—Upper Middle–lower Upper Ordovician, Iberian Peninsula (Portugal and Spain), Armorican Massif (France), central Bohemia (Czech Republic); Dobrotivian Regional Stage.

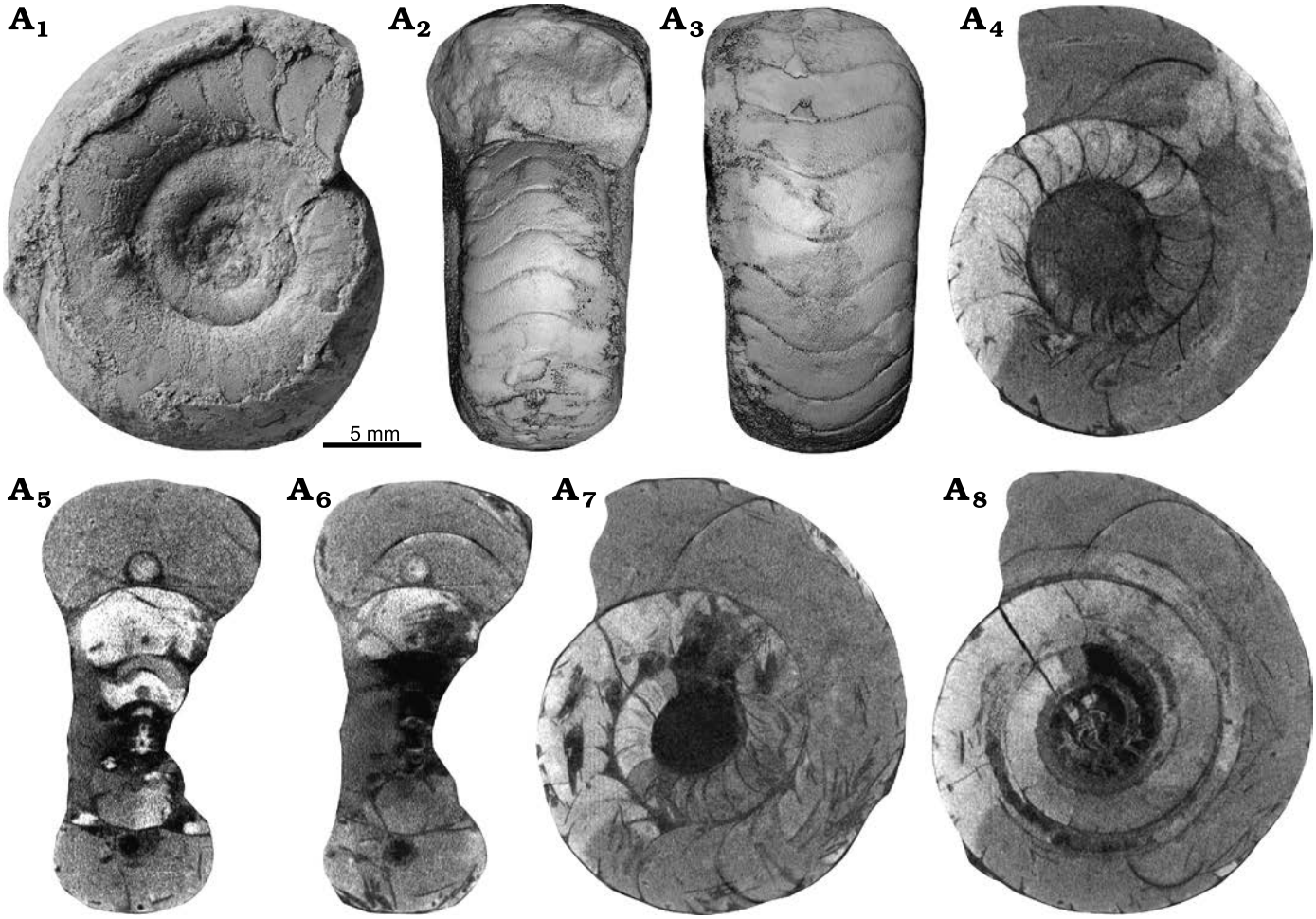

Fig. 5. Tarphyceratid cephalopod *Trocholites chaloupkai* sp. nov. from Praha-Štěrboholy, central Bohemia, upper part of the Zahořany Formation (lower Katian, Upper Ordovician). Holotype NM L 63626, optical microscope photograph of whitened specimen in lateral view (A_1); micro-CT images showing frontal (A_2) and ventral (A_3) views, note ventral lobe of suture line; virtual longitudinal sections in sagittal plane showing partly preserved septa in last (A_4) and penultimate (A_7) whorls; virtual longitudinal section in median plane (A_8) showing the siphuncle and the earliest whorl of the phragmocone; virtual transverse sections in slightly eccentric (A_5) and central (A_6) planes documenting whorl profile shape and siphuncle.

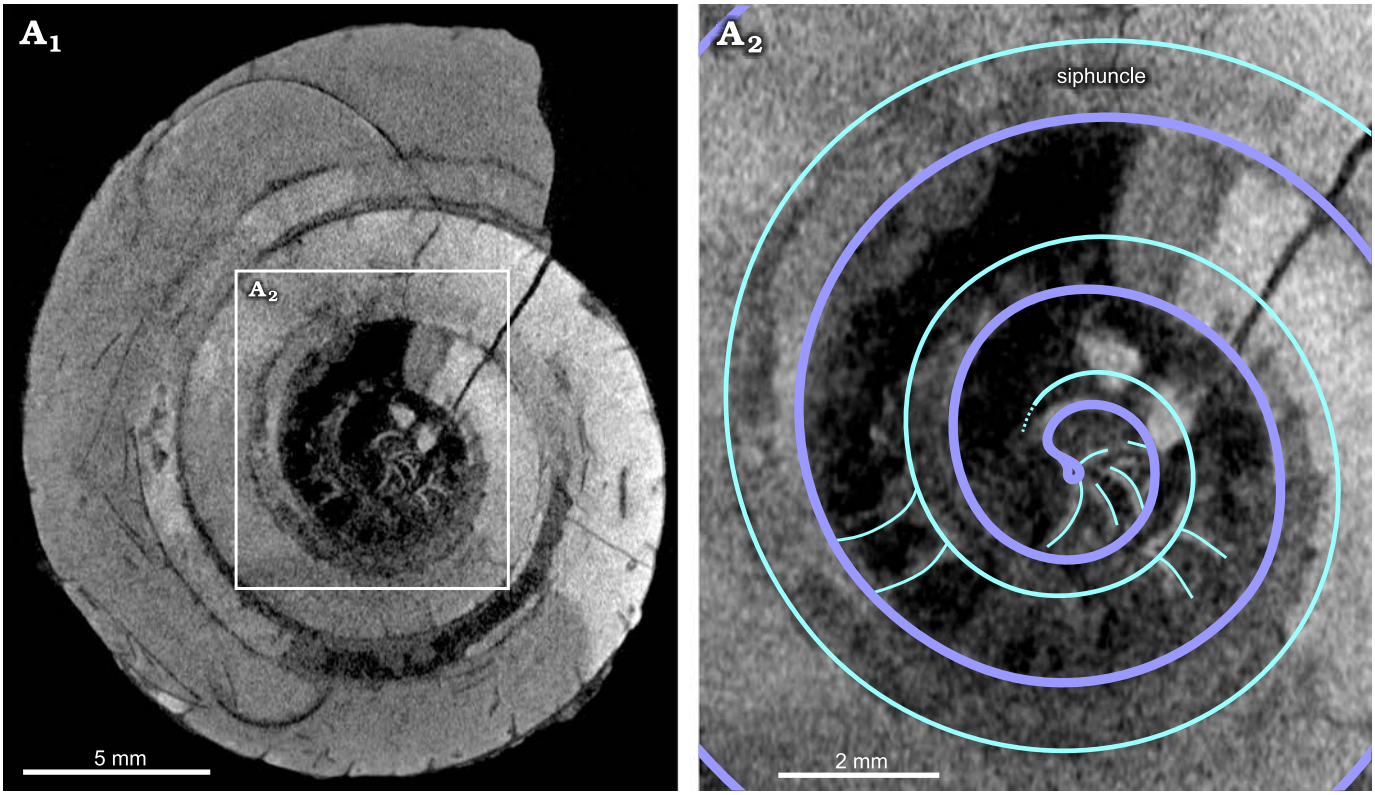

Fig. 6. Tarphyceratid cephalopod *Trocholites chaloupkai* sp. nov. from Praha-Štěrboholy, central Bohemia, upper part of the Zahořany Formation (lower Katian, Upper Ordovician). **A**. Holotype NM L 63626, detail of apicalmost part of the phragmocone (A_1) and drawing (A_2) indicating line of contact of whorls, position of siphuncle, position of (partly fragmented) septa and shape of initial chamber and umbilical window.

Trocholites chaloupkai sp. nov.

Figs. 5–7.

Zoobank LSID: urn:lsid:zoobank.org:act:0F372BB0-E1D8-4895-9ECA-1A6FCD830A10

Etymology: Named after Miloš Chaloupka, who collected the holotype.

Holotype: NM L 63626, moderately preserved phragmocone with shell remains, undeformed but incomplete adaperturally.

Type locality: Praha-Štěrboholy, Central Bohemia, Czech Republic.

Type horizon: Upper Zahořany Formation, lower Katian, Upper Ordovician.

Material.—Holotype only.

Diagnosis.—*Trocholites* with evolute, thickly discoidal shell (UWI = 0.50, CWI = 0.50), moderately expanding (WER = 1.80) in later whorls; whorl profile depressed (WWI = 1.70), moderately impressed (IZR = 0.17); at the beginning of the last whorl ventrally slightly flattened and laterally rounded. Siphuncle marginodorsal in inner whorls and very slightly removed from the dorsal shell wall in the last 0.50 whorl; septal foramen height ~0.23 of corresponding whorl height at shell diameter ~23 mm. Sutures with rounded ventral lobe, rounded ventro-lateral saddle and shallow lateral lobe. Shell ornament consisting of fine transverse elements forming a net-like (fenestrate) pattern.

Description.—The holotype NM L 63626 is a phragmocone 26 mm in diameter. It consists of four whorls but scars representing remains of the umbilical seams indicate the former presence of at least one more whorl (Fig. $5A_1$). The micro-CT images show the embryonic shell and the small, drop-shaped umbilical window (~0.5 mm in diameter) (Figs. $5A_8$, 6, SOM 1, 2, Supplementary Online Material available at http://app.pan.pl/SOM/app68-Aubrechtova_etal_SOM.pdf). In the last preserved whorl (dm = 13–23 mm), the shell is thickly discoidal (CWI = 0.51–0.49) and evolute (UWI = 0.47–0.48), while the whorl expansion rate slowly decreases (WER = 1.80–1.75). The whorl profile is moderately impressed (IZR = 0.19–0.17) and moderately depressed (WWI changes from 1.63 to 1.70 and to 1.67, respectively) with slightly flattened ventral side and rounded flanks (Fig. $5A_5$, A_6; SOM 1, 2). The siphuncle is in contact with the dorsal shell wall in inner whorls and slightly removed from it in the last half a whorl (Figs. 5, 6; SOM 1, 2); it is of medium size (RSH = 0.23 at wh = 6.9 mm; fh/ah = 0.30 at the same wh). The phragmocone chambers are moderately long (RCL = 0.33 at wh = 7 mm) (Fig. $5A_4$, A_7; SOM 1, 2). The sutures extend into a rounded ventral lobe, a pronounced, rounded ventro-lateral saddle and a shallow lateral lobe (Fig. $5A_2$, A_3). The shell ornament is comprised of transverse elements that are organised in a fine, net-like (fenestrate) pattern (Fig. 7). The transverse elements of the ornament are slightly inclined (steeper side oriented adaperturally) and sinuous; neighbouring elements merge at more or less regular intervals so that apparent longitudinal organisation is formed.

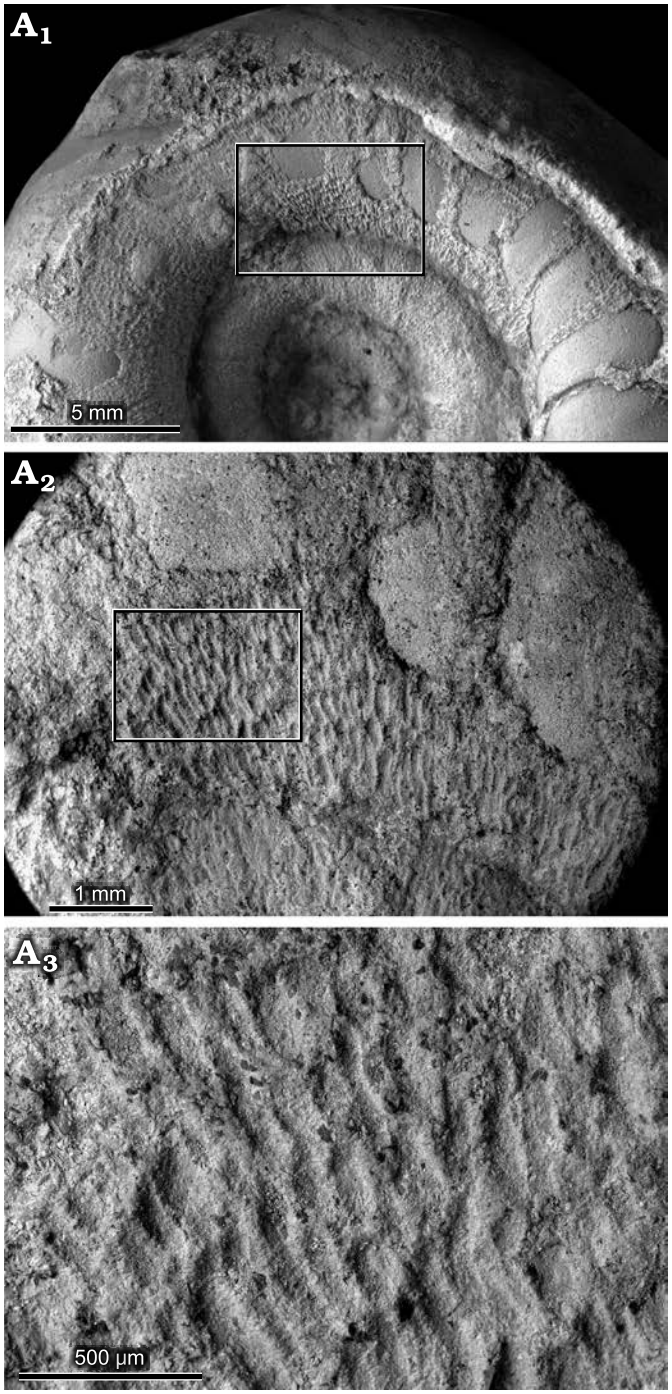

Fig. 7. Tarphyceratid cephalopod *Trocholites chaloupkai* sp. nov. from Praha-Štěrboholy, central Bohemia, upper part of the Zahořany Formation (lower Katian, Upper Ordovician). **A**. Holotype NM L 63626, general view on shell ornament (A_1); SEM image of shell ornament (A_2) on umbilical wall of the outer whorl, coalescent ornament elements form a net-like (fenestrate) pattern; SEM image with detail of shell ornament (A_3), transverse elements have a lamellar character and are imbricated adaperturally, the elements form undulating ridges that are locally coalescent with each other.

Remarks.—The holotype NM L 63626 has a unique, finely fenestrate shell ornament. The ornament might represent remains of crenulate elements similar to those known in the species of *Dawsonoceras* (Kröger and Isakar 2006), *Discoceras* (Manda and Turek 2018; Kröger and Aubrechtová 2018) or *Glyptodendron* (Evans et al. 2015). However, in the holotype of *Trocholites chaloupkai* sp. nov., the widest points of the cell-like structures are offset from each other by half of a wavelength and in contact at these points (David H. Evans, personal communication 2023). Most similar to that is the shell ornament previously figured and discussed in specimens of *T. ammonius* Conrad, 1838, and *T. major* Ruedemann, 1926, from the Upper Ordovician of North America (see also Hall 1847 and Hyatt 1894). However, these specimens differ from the holotype of *T. chaloupkai* sp. nov. in having nearly straight suture line and siphuncle located in the middle between the centre of the shell and its dorsal wall.

Ventral lobe of suture line appears to be present in the holotype of *Trocholites blakei* Hyatt, 1894, from the Upper Ordovician Bala Series of Great Britain. Original figure of Blake (1882) shows that the specimen might also have similar WER as the holotype of *T. chaloupkai* sp. nov. However, too little is known about the holotype and single described specimen of *T. blakei* to make a reliable comparison with *T. chaloupkai* sp. nov. .

The specimen from the Upper Ordovician of Yunnan (SW China), classified by Zhang and Chen (2002) as *Trocholites* aff. *Trocholites lativentrosus* Lai and Wang in Wang, 1981, appears to have a nearly identical conch geometry and whorl profile to the holotype of *T. chaloupkai* sp. nov. However, the former specimen differs in shell ornament—it has simple lirae on the shell surface.

Among the *Trocholites* species from Baltica, the holotype of *T. chaloupkai* sp. nov. is nearly identical in shell geometry to the representatives of *T. depressus* (Eichwald, 1840) from the Darriwilian (Middle Ordovician) of Estonia (Balashov 1953; Kröger and Keupp 2004; Martina Aubrechtová and Dieter Korn, MS unpublished material). However, the ventral surface of the shell of the new species is slightly flattened and associated with the development of ventrolateral saddles and a ventral lobe; by contrast, suture lines are nearly straight or with a very low ventral saddle in *Trocholites depressus*.

The holotype of *Trocholites chaloupkai* sp. nov. differs from the holotype of the stratigraphically slightly older (late Sandbian) *T. gennadii* Kröger and Aubrechtová, 2018, from Estonia in the shape of whorl profile (ventrally flattened vs. rounded) and shape of suture lines (sinuous vs. straight).

The holotype of *Trocholites chaloupkai* sp. nov. is distinguished from the representatives of the other species reported from Ordovician rocks of peri-Gondwana, *T. fugax* by its lower expansion rate (WER based on wh = 2.01 vs. 2.22–2.82 at dm ~23 mm) which decreases adaperturally, its wider umbilicus (UWI = 0.48 vs. 0.36 at dm ~23 mm) and its smaller imprint zone (IZR = 0.17 vs. 0.34 at dm ~23 mm). Also, the suture line of the new species is more sinuous (vs. nearly straight in *T. fugax*) with a pronounced ventral lobe.

Stratigraphic and geographic range.—Type horizon and locality only.

Discussion

Cephalopod assemblages in the Ordovician of the Prague Basin are mostly composed of indeterminable orthoconic cephalopods, the majority of which probably belong to the orders Orthoceratida Kuhn, 1940, and Pseudorthoceratida Flower and Caster, 1935. More diverse assemblages are known only from some restricted intervals, such as the Klabava, Šárka, and Dobrotivá formations (Dapingian–Darriwilian, Middle Ordovician) and the Králův Dvůr Formation (upper Katian–lowermost Hirnantian, Upper Ordovician). Some extremely rare elements occur in these intervals, which are otherwise known from distant palaeocontinents, especially Baltica (e.g., Marek 1999; Manda 2008; Aubrechtová 2015; Aubrechtová and Turek 2018; Aubrechtová and Turek 2023). These include particularly lituitid, actinoceratid, endoceratid, and oncoceratid cephalopods and the herein discussed tarphyceratid cephalopods of of the genus *Trocholites*.

Only about a dozen specimens attributable to *Trocholites* have been collected in the Prague Basin since the time of Barrande (1865) and most of them were described and evaluated by Manda (2008). In the present study, we extend the knowledge on these palaeobiogeographically important cephalopods by describing two well-preserved specimens, which we assign to the species *Trocholites fugax* and *T. chaloupkai* sp. nov.

Trocholites fugax was originally described by Babin and Gutiérrez-Marco (1992) (see also Babin et al. 1996 and Sá and Gutiérrez-Marco 2009) from the upper Middle Ordovician strata of Armorica and Iberia, and from coeval or slightly younger rocks of Bohemia (Manda 2008). The specimen NM L 63625 (Fig. 4) further confirms the presence of the species in the Ordovician of the Prague Basin and strengthens the hypotheses on faunal interchange between Baltica and peri-Gondwana during the late Darriwilian–early Sandbian times. Other cephalopods in the Dobrotivá Formation indicating these relationships are the lituitids *Lituites lituus* Montfort, 1808, *Trilacinoceras* cf. *discors* (Holm, 1891) (see Aubrechtová and Turek 2018), and the orthoceratoid *Bactroceras* sp. (Aubrechtová et al. 2020). It is noteworthy that these migrations were not unidirectional. Warm-water elements such as tarphyceratids spread from low to high palaeolatitudes during occasional dispersion events. But for other cephalopods, such as orthoceratoids, the story was different; these originated in the high palaeolatitudes already during the Early Ordovician and gradually expanded towards the palaeoequator, becoming common components of warm-water assemblages during the Middle and Late Ordovician (Kröger et al. 2009; Kröger and Evans 2011; Kröger 2013; Aubrechtová 2015).

The holotype of *T. chaloupkai* sp. nov. (NM L 63626, Figs. 5, 6) from the lower Katian part of the Zahořany Formation represents the first record of tarphyceratids in the Upper Ordovician of the Prague Basin. The non-destructive micro-CT scanning has not been previously applied on Ordovician cephalopods (SOM 1, 2), with the exception of a specimen mentioned by Kouraiss et al. (2019) and preliminary results of a study presented by Aubrechtová and Turek (2023). It was shown by the latter works, as well as by the present investigation, that the micro-CT has potential to reveal internal shell structures in certain Ordovician body fossils, where the shell and internal structures would be destroyed using standard sectioning and polishing. Besides that replacing two-dimensional sections with three-dimensional virtual models brings substantial new data on the geometry, organisation and growth of septa, siphuncle and cameral and endosiphuncular deposits (Aubrechtová and Turek 2023).

The investigation showed that the holotype of *T. chaloupkai* sp. nov. is nearly identical in shell geometry to representatives of *Trocholites depressus* from the upper Darriwilian (Middle Ordovician) of Estonia (Kröger and Keupp 2004; Martina Aubrechtová and Dieter Korn, MS unpublished material) but differs in the shape of the whorl profile, course of suture lines and shell ornament. Very similar to the holotype of *T. chaloupkai* sp. nov. is also a specimen classified as *Trocholites* aff. *Trocholites lativentrosus* from the Upper Ordovician of southwest China (Zhang and Chen 2002), which differs only in the type of shell ornament (simple lirae).

Havlíček et al. (1994), Havlíček (1998) and Fatka and Mergl (2009) concluded that there must have been an effective barrier against faunal interchange between high and low palaeolatitudes during the Berounian (i.e., Sandbian–Katian; Late Ordovician). Indeed, the composition of the benthic fauna of the Zahořany Formation shows similarities to assemblages from other areas of peri-Gondwana and Gondwana, such as Morocco, Spain (Dastanpour et al. 2006; Nardin 2007; Ebbestad et al. 2019; Nohejlová and Lefebvre 2022) and Bolivia (Benedetto 2013). The cephalopods of the Zahořany Formation consist of taxonomically unrevised, straight shelled cephalopods with central-subcentral siphuncle, which have been suggested to be similar to the assemblages from Iran (Dastanpour et al. 2006; Ghavidel-Syooki et al. 2015). The newly described single specimen of *T. chaloupkai* sp. nov. is thus the only nektonic element (Westermann 1998) indicating some connections between the Prague Basin and lower palaeolatitudes during the Sandbian–Katian boundary interval. It also belongs among the stratigraphically youngest Ordovician *Trocholites* from peri-Gondwana and Gondwana.

Conclusions

Two well-preserved tarphyceratid specimens assigned to the species *Trocholites fugax* and *T. chaloupkai* sp. nov. are described from the Middle and Upper Ordovician of the Prague Basin. Their occurrence implies faunal interchange between the high palaeolatitude peri-Gondwana and the low palaeolatitude regions, especially Baltica, during the late Darriwilian–early Sandbian and late Sandbian–early Katian times.

Trocholites chaloupkai sp. nov. is the first tarphyceratid species described from the Upper Ordovician of Bohemia. The single specimen was studied using the non-destructive micro-CT scanning, which has not been extensively applied to Ordovician cephalopods before. The method enabled a 3D study of shell geometry, septa and siphuncle, and morphological changes during ontogeny.

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