Micro-CT reveals 3D endosiphuncular structure in Late Ordovician actinoceratid cephalopod from the Prague Basin (Czech Republic)

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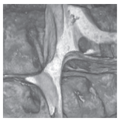

The first unequivocal actinoceratid cephalopod from the late Katian (Late Ordovician) shales of the Prague Basin (Central Bohemia), *Adamsoceras*? *hanusi* sp. nov., is described. The only specimen contains several fragmented but undeformed siphuncular segments. The shell wall, septa, ectosiphuncle and annulosiphonate deposits are dissolved but their original shape is reflected by cavities left after them inside the specimen. The endosiphuncular canal system inside the siphuncle is preserved, including the central canal, radial canals and perispatium. The shape of the empty spaces and structures inside the siphuncle indicate that the growth of the annulosiphonate deposits was irregular and uneven; the deposits pushed back the original soft tissue inside the siphuncle and the present irregular structure of the endosiphuncular system was thus formed. The preservation of the central and radial canals additionally shows that the walls of the individual blood vessels running through the canals must have been soft, elastic, and probably had a higher preservation potential than the rest of the soft tissue. Consequently, the shape of the endosiphuncular system is different in each median section and each segment, and assignment to a particular system type is thus not possible. We conclude that definition of taxa based on previously established types of endosiphuncular systems might be artificial in at least some actinoceratids. • Key words: Actinoceratida, micro-CT, siphuncle, endosiphuncular deposits, Katian, Late Ordovician, Králův Dvůr Formation.

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Members of the Ordovician–Carboniferous? (see Kröger & Mapes 2007 and Pohle *et al*. 2022) order Actinoceratida (Teichert, 1933) are unique among other cephalopods by the structure of their siphuncles, which contain heavy calcareous deposits enclosing a complex system of canals. The organisation of this system was depicted already 170 years ago by Saemann (1852) (see also Troedsson 1926), and discussed later by Barrande (1855a, b; 1877). In the 20th century, the most detailed reconstructions and discussions on the origin and terminology of endosiphuncular structures were given by Teichert (1933, 1934, 1935); these were then elaborated on by Flower (1955a, 1957, 1964), Teichert (1964), Mutvei (1964) and Wade (1977a, b). Later, Mutvei (1996, 2002) described pores in the ultrastructure of the connecting rings and objected to some ideas of Teichert and Flower (see also Mutvei 1964), especially with regard to primary nature of the endosiphuncular canal system and the symmetric growth of endosiphuncular deposits.

Typically, the internal structure of actinoceratid shells is described using oriented sections. Teichert (1933, 1935), however, based his conclusions on specimens, in which all hard parts were diagenetically dissolved, and where only internal moulds of phragmocone chambers and spaces originally occupied by soft tissues are preserved. This preservation allowed him to study the internal shell structures in three dimensions. A similar type of preservation has recently been identified in a specimen of an actinoceratid cephalopod from the late Katian part of the Králův Dvůr Formation (Prague Basin, Central Bohemia; Figs 1, 2). The undeformed siphuncle in this specimen contains remains of the endosiphuncular system. All hard parts were dissolved leaving behind cavities that mirror the shape of the original calcareous structures. The originally non-calcified spaces inside the shell were preserved by intruding sediment (phragmocone chambers) or pyritization (endosiphuncle). In other words, the specimen is an internal mould of the axial canal, radial canals and perispatium, with some remains of the phragmocone chambers. This preservation enabled the study of the specimen using micro-tomography. Below, we describe the results of this investigation and

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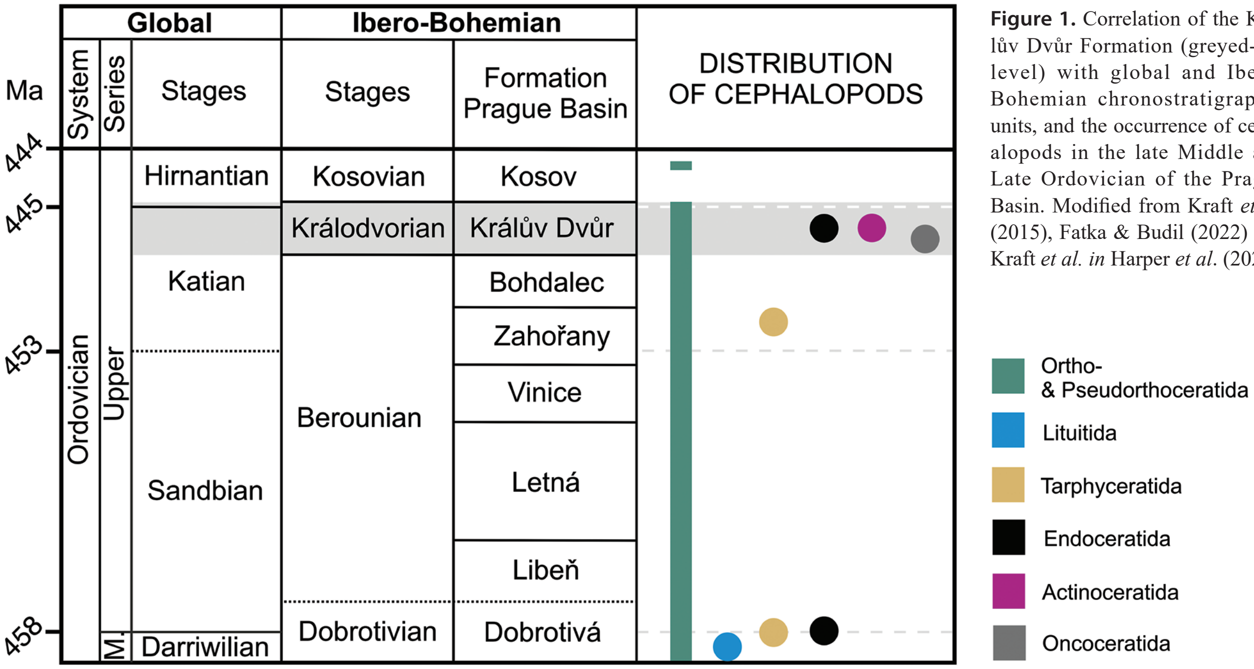


Figure 1. Correlation of the Králův Dvůr Formation (greyed-out level) with global and Ibero-Bohemian chronostratigraphic units, and the occurrence of cephalopods in the late Middle and Late Ordovician of the Prague Basin. Modified from Kraft *et al.* (2015), Fatka & Budil (2022) and Kraft *et al. in* Harper *et al.* (2023).

discuss their implications for the knowledge on the structure and functioning of the siphuncle in actinoceratid cephalopods. Additionally, we discuss the taxonomic position and palaeobiogeographic significance of the specimen**.**

Material and geological setting

Material. – The single specimen NM-L46568(a-e) comes from the collection of F. Hanuš purchased in 1922 by the National Museum, Prague. It is an internal mould of nine undeformed siphuncular segments and strongly flattened and damaged remains of four phragmocone chambers (Fig. 3).

The specimen is fragmented in five pieces: (i) the largest fragment, NM-L46568a, contains four siphuncular segments herein denoted by the numbers 9, 8, 7 and 6; the segments 9 and 6 are incomplete (cut off transversely in the middle). Remains of phragmocone chambers are preserved on one side of the fragment, while the other side is represented by a small isolated fragment NM-L46568b. (ii) The fragment NM-L46568c contains two siphuncular segments herein denoted by the numbers 5 and 4. (iii) The fragment NM-L46568d contains two siphuncular segments herein denoted by the numbers 3 and 2; however, in segment 2, internal structures are poorly preserved. (iv) The fragment NM-L46568e contains a single siphuncular segment herein denoted by the number 1; the segment was not studied under micro-CT because the internal structures are not preserved.

Locality. – The studied specimen comes from grey-green clay shales of the Late Ordovician Králův Dvůr Formation (Fig. 1). The locality is Praha-Michle (Fig. 2). The specimen was in the collection associated with a fragment of an endoceratid siphuncle, and an undetermined bivalve. Additionally, two orthoceratoid cephalopods from the same locality were later found in the collection.

The precise location of the site Praha-Michle remains uncertain. The only specification given by F. Hanuš (1923) is that it was a construction site, from which specimens representing twenty species of various fossil groups were obtained, including the stratigraphically significant trilobite *Remopleurides* (= *Amphytrion*) *radians* (Barrande, 1846). In the Praha-Michle district (5.5 km^2), the extension of the built-up area during the second half of the 20th century allowed the study of facies development and stratigraphy in two nearby sites – Jezerka and Reitknechtka (Havlíček & Mergl 1982, Štorch & Mergl 1989). Both sites record the highest levels of the Králův Dvůr Formation and the lower levels of the overlying Kosov Formation. The facies development is very similar at both sites (clay or silty shales, locally with muddy limestone nodules; Štorch & Mergl 1989). However, the faunal list of these localities of the latter authors does not contain the trilobite *Amphytrion radians* mentioned by Hanuš (1923). This species is abundant especially in the middle (Šnajdr 1990) and higher levels of the Králův Dvůr Formation (*Raphanoglossa* community; Havlíček *in* Chlupáč 1998). It is thus likely that the excavation from which the material of F. Hanuš from Praha-Michle originated, was located at another site,

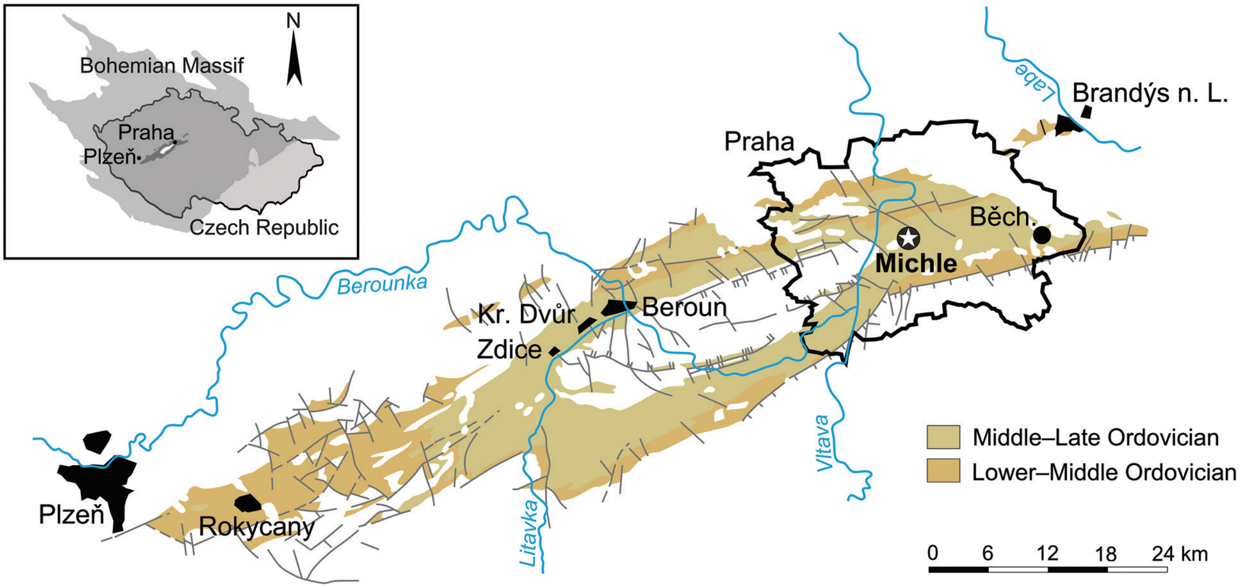


Figure 2. Occurrence of Ordovician rocks of the Prague Basin (Central Bohemia) and position of the Praha-Michle district, from which the studied specimen originates. Redrawn from geological map 1 : 500 000 available online at the map portal of the Czech Geological Survey (*https://mapy.geology.cz/geocr500/*). Abbreviations: Běch. – Běchovice; Brandýs n. L. – Brandýs nad Labem; Kr. Dvůr – Králův Dvůr.

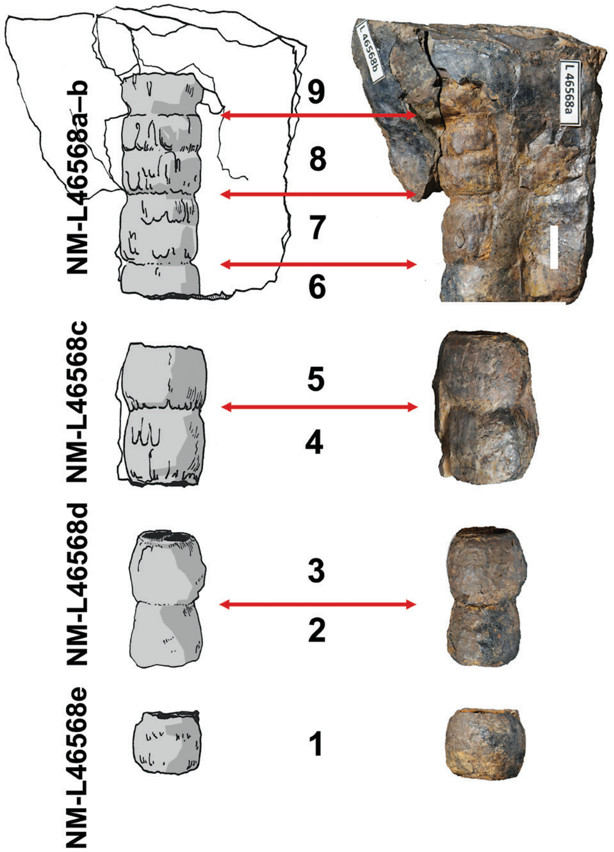


Figure 3. Illustration of the fragments of the specimen NM-L46568a-e studied herein with indication of numbering (1–9) of the individual segments as used in the text. Drawing by J. Sklenář (National Museum, Prague).

capturing slightly lower positions of the Králův Dvůr Formation.

Geological setting. – The Králův Dvůr Formation is preserved only in the central part of the Prague Basin between Zdice and Praha-Běchovice (Fig. 2). The thickness of the Králův Dvůr Formation is between 25 and 200 m (Havlíček 1981), with lowest values to the north of the Prague Fault and highest values in the type area of Králův Dvůr (Havlíček *in* Chlupáč *et al*. 1998). The dominant lithofacies of the Formation, from which the specimen studied herein originates, are grey and green claystones with silt admixture (Havlíček 1982). Locally high content of pyrite implies oxygen-deficiency of the sea floor. This is shown *e.g.* by the newly collected material from the subway line construction site in Praha-Pankrác (street Na Strži), which is located about 1.5 km from the locality of the herein studied specimen.

Lithologically and palaeontologically distinct is the upper part of the Formation, where clayey carbonates appear suddenly (Havlíček & Vaněk 1966, Štorch & Mergl 1989, Brenchley & Štorch 1989). The onset of the sedimentation of carbonates across the exclusively siliciclastic environments of the whole Mediterranean Province and occurrence of faunal elements otherwise known from low palaeolatitudes (especially Baltica) was suggested to reflect a period of global warming (Boda Event; Fortey & Cocks 2005, Fatka & Mergl 2009; see also summary and references in Melchin *et al*. 2013). The carbonates are overlaid by greenish silty shales and followed by the first diamictite layer of the Kosov

Formation (Štorch & Mergl 1989, Brenchley & Štorch 1989, Štorch 1990).

The abundance of fossils in the Králův Dvůr Formation declines from the SW (near Králův Dvůr and Zdice) towards the NE (Prague region). The benthic assemblages are interpreted as relatively deep-water (Havlíček 1982, Štorch & Mergl 1989). The diversity of the individual assemblages is mostly low but the total diversity of the Králův Dvůr Formation is very high (Kraft *et al. in* Harper *et al*. 2023). The most common are vagile elements (trilobites, ostracods), while sessile elements are represented by minute, thin-shelled brachiopods (Havlíček *in* Chlupáč *et al.* 1998). Cephalopods are only locally abundant. The prevailing preservation of diagenetically compressed internal moulds usually hinders more precise taxonomic determination. The majority of cephalopod specimens are orthoceratoids (e.g. *Bactroceras*, *Isorthoceras*, *Kionoceras*; see Marek 1999, Aubrechtová 2015). Other cephalopod groups have been recognised in only three cases: a single oncoceratid specimen of *Diestoceras primum* (Barrande, 1865), an indeterminable endoceratid fragment mentioned above and the actinoceratid *Adamsoceras*? *hanusi* sp. nov. studied herein (Fig. 1).

Due to the problematic correlation of the Late Ordovician strata of the Prague Basin and other regions of peri-Gondwana with the British standard scale (see Gutiérrez-Marco *et al.* 2017 for summary and references), regional chronostratigraphic units were introduced by Havlíček & Marek (1973); for the Králův Dvůr Formation, the Králodvor Regional Series was defined (used as Kralodvorian Stage since Fatka *et al. in* Cooper *et al*. 1995; Fig. 1). Based on a recent detailed revision of graptolites, the Formation was established to be mid Katian to earliest Hirnantian in age (Kraft *et al.* 2015).

Methods and terminology

Individual fragments were studied using the X-ray microtomograph SkyScan 1172. For reconstruction of different sections and the structure of the siphuncle, the N-Recon software was used; photographs were prepared in the software Avizo 9.1.1.

Orientation. – The adapertural-adapical direction in the longest fragment (NM-L 46568a) is clear from the traces of two septa revealed by the micro-CT scan. Based on the comparison with NM-L 46568a, the adapertural orientation of the other fragments was determined. In addition, since endosiphuncular deposits generally extend more forwards (adaperturally) than backwards (adapically) (see, *e.g.* Teichert 1964), the larger size of the void spaces left after the dissolution of the endosiphuncular deposits indicates an adapertural direction.

Determining the dorsoventral (and lateral) orientation in the fragments is rather difficult. Bilateral symmetry is indicated only by the flattened central canal, which is widened and strongly asymmetric in one, supposedly dorso-ventral, direction. Thus, the sections showing thin, more or less straight central canal are interpreted as lateral sections.

Reconstruction of hard parts. – Since no original hard structures are preserved, they had to be reconstructed. The septal necks were placed at the narrowest points of the siphuncle remains. Based on the overall shape of the fragments, it was assumed that the septal necks were suborthochoanitic or cyrtochoanitic with free brims (connecting rings not adnate to the septum). The course of the connecting rings was reconstructed based on the presumed curvature at the septal necks and the areas where the segments are isolated from the matrix. The outer surface of each segment possibly represents an imprint of the inner side of the connecting ring, thus more or less reflecting the shape of the siphuncle wall. It was also assumed that the connecting ring had more or less the same curvature dorso-ventrally and laterally, since the transverse section through the siphuncle is circular in shape in all fragments examined.

Terminology and measurements. – As the siphuncle is undeformed, some measurements were possible based on the reconstruction described above. The siphuncle compression ratio (SCR) and the relative siphuncular shape (RSS) (Tab. 1) were calculated. The apical angle, shell diameter, relative chamber length and relative siphuncular diameter had to be estimated due to the flattening and fragmentation of the remains of the chamber filling.

The general terminology of cephalopod shells and their internal structures has been adopted from Teichert (1964), Flower (1964) and Pohle *et al*. (2022). For the description of the actinoceratid endosiphuncle, Wade (1977a, b) and Mutvei (1964, 1996) introduced a slightly different terminology, which is compared in Tab. 2.

Individual structures are referenced in the text and figure captions as summarised in Tab. 3.

Systematic palaeontology

Class Cephalopoda Cuvier, 1797
Subclass Orthoceratoidea Teichert, 1967 *in* Teichert & Yochelson (1967)

Remarks. – The authorship of the taxon name remains unclear as there are several possible authors (*e.g*. McCoy 1844, Kuhn 1940, Teichert *in* Teichert & Yochelson 1967)

Table 1. Ratios used to describe siphuncular segments of actinoceratid specimen studied herein. Abbreviations: sh – segment height (mid-segment height of the siphuncle); sl – siphuncular segment length; fh – septal foramen height; SCR – siphuncle compression ratio; RSS – relative siphuncular shape.

Ratio	Reference	Calculated as	Explanation
SCR	Pohle *et al.* 2022	sh/sl	SCR < 0.80 = segments elongated SCR ≥ 0.80 < 1.20 = segments quadratic SCR ≥ 1.20 < 3 = segments slightly broadened SCR ≥ 3 = segments strongly broadened
RSS	Pohle *et al.* 2022	sh/fh	RSS < 0.95 = concave RSS ≥ 0.95 < 1.05 = tubular RSS ≥ 1.05 < 1.50 = slightly expanded RSS > 1.50 = strongly expanded

but resolving this complicated issue is beyond the scope of the present study. Therefore, to avoid further confusion, we follow King & Evans (2019), Pohle *et al.* (2022) and Pohle (personal communication, 2023) and consider Teichert *in* Teichert & Yochelson (1967) as the author of the subclass name Orthoceratoidea (despite Teichert *in* Teichert & Yochelson 1967 stated Kuhn 1940 as the author of the subclass).

Order Actinoceratida Teichert, 1933
Family Ormoceratidae Saemann, 1852

Remarks. – The genus *Adamsoceras* has been placed in the family Ormoceratidae by *e.g.* Aronoff (1979), Dzik (1984), Frey (1995) or Mutvei (1996), and the same classification is tentatively followed herein. Note, however, that other authors (*e.g.* Flower 1964, 1968, 1976; Stait 1984; Stait & Burrett 1984; King *in* Olóriz & Rodríguez-Tovar 1999) classified the genus in the family Wutinoceratidae Shimizu & Obata, 1935.

Genus *Adamsoceras* Flower, 1957

Type species. – *Adamsoceras isabelae* Flower, 1957 (original designation); from Pogonip Limestone, Middle Ordovician; Ikes Canyon, Toquima Range, Nevada, USA.

Diagnosis. – Ormoceratids with a longiconic, slowly expanding shell (apical angle 4–5°), cross-section typically slightly depressed, sutures with low ventral lobes, length of phragmocone chambers increasing with ontogeny; siphuncle fairly close to venter, siphuncular segments 20–25% of shell diameter, not adaperturally adnate, slightly wider than long (SCR < 1.50), thick, layered and strongly expanded connecting rings (RSS > 1.50), endosiphuncular canal system of reticular type (compiled from Flower 1957 and Frey 1995 and modified).

Occurrence. – Estonia, Sweden (Island of Öland), Norway, Poland (erratic boulders), ?Czech Republic, USA (Nevada, Utah), Canada (Newfoundland), China (?Xinjiang and Manchuria), Australia (Tasmania); Middle–Late Ordovician.

Adamsoceras? *hanusi* sp. nov.
Figures 3–12

Types. – NM-L46568 (holotype), figured herein at Figs 3–12.

Table 2. Summary of terminology of actinoceratid siphuncle as used by different authors and the present study.

Teichert 1964	Mutvei 1964	Mutvei 1996	Wade 1977a, b	Pohle *et al.* 2022	This study
endosiphuncular canal system				canal system	endosiphuncular canal system
central canal	dorso-ventral canal	axial canal	axial space axial canals	central canal	central canal
radial canals		interannular space	radial canals	radial canals	interannular spaces containing radial canals
perispatium		perispatium	perispatium	perispatium	perispatium
endosiphuncular deposits	endoperibolic deposits (subdivided into conical, annular, lamellar)	endosiphuncular annular deposits	annular siphuncle deposits, annular siphonal deposits, siphuncular deposits	endosiphuncular deposits, annular deposits	endosiphuncular deposits, annular deposits

Table 3. Explanation of abbreviations used herein in Figures.

Abbreviation	Explanation/comments	Figures
d-v	Position of dorso-ventral section	all
lat	Position of lateral section	all
pc	Phragmocone chambers infilling	4A, B; 5A, B; 6B; 7B; 8B, E; 9C, E; 10A, D; 12B
cr	Connecting rings (reconstructed)	4B, 8E, 11B
sn	Septal necks (reconstructed)	4B, 8E
s	Septa (reconstructed)	4B
sf	Position of septal foramen (*i.e.* septal neck)	5A, B; 8A, B; 11A
sf_1	Imprint of outer surface of annulosiphonate deposits at the septal foramen.	4A; 8B, E
p	Infilling of perispatium	4B; 5A; 6A; 7C, F, 8C, D, E; 9C, E, 10D; 11B; 12B, C
cc	Central canal	all
cc_1	From the dorso-ventral section, the central canal is wide, irregular in thickness and locally shifted from the central axis of the siphuncle.	4B; 8E; 11D, E, F
cc_2	Central canal consists from multiple, fused canals, sometimes arranged in a flattened form.	5A, B; 7A; 11C; 12A
cc_3	Near and at the septal foramen, the central canal is the thickest and irregular in shape in cross-section.	6A, 7A, 9A, 12A
cc_4	Towards mid-segment length, the central canal becomes thinner and its cross-section remains irregular; radial canals (rc_1) start to branch off.	7C, E; 9C, E; 10D
cc_5	From the longitudinal lateral section, the central canal is thin and more or less straight.	11B, F
rc	Radial canals	all
rc_1	Thin radial canals branching off perpendicularly from the central canal at about the segment mid-length.	4B; 5A, B; 7B, E; 8C, D, E; 9F; 10D; 11B
rc_2	Horizontal "grooves" *or* differently coloured areas on the outer surface of the specimen correspond to gaps between annulosiphonate deposits where radial canals (rc_1) open into the perispatium.	4A
rc_3	Some radial canals are comparatively thick and may even exceed the diameter of the central canal; these join the perispatium in the first half of the segments.	4B; 5A, B; 7C; 8D, E; 9C; 11E, F
rc_4	Longitudinally extended light-coloured areas on the outer surface of specimen *and* ridge-like structures on the inner surface correspond to gaps between annulosiphonate deposits where radial canals (rc_3) open into the perispatium (p).	4A, B; 5A; 7D; 8B; 9F; 10A–C
rc_5	Radial canals commonly bifurcate as they get closer to the perispatium.	7E; 9A, E; 12C
rc_6	Spike-like remains of radial canals, which were supposedly interrupted during the late growth stage of annulosiphonate deposits. Note lobate spaces between the spikes.	11B, 12B
rc_7	In earlier phases of development of individual deposits, radial canals have a shape of longitudinally flattened lamella which widens towards the perispatium in a shovel-like form; the latter may be manifested on the surface of the specimen as longitudinally extended light-coloured areas (rc_4).	8C–E; 9C, D; 10A, B; 11C, D

Type horizon and locality. – Králův Dvůr Formation, upper Katian Stage, Králodvor Regional Stage, Upper Ordovician; locality Praha-Michle, Czech Republic.

Material. – Only the holotype.

Etymology. – After F. Hanuš, who collected the holotype.

Diagnosis. – Low expansion rate (> 5°), siphuncle subcentral or central, siphuncular segments quadratic or slightly broadened and slightly or strongly expanded, not adnate. Endosiphuncular canal system asymmetrically developed. Central canal irregular in form and dimensions, flattened, commonly displaced from the median plane of the siphuncle. Radial canals branch off from the central canal at about the mid-length of each segment. Radial canals are either thin and oriented at right angles to the central canal, or thick and curved backwards, terminating in the perispatium at about 0.75 of the length of the preceding segment. Additional narrower radial canals may branch off from the wider radial canals in the proximity of the central canal.

Table 4. Dimensions and ratios of siphuncular segments in the specimen NM-L46568. Abbreviations: sl – siphuncular segment length; sh – segment height (mid-segment height of the siphuncle); fh – septal foramen height; SCR – siphuncle compression ratio; RSS – relative siphuncular shape.

Segment no.	sl	sh	fh	SCR	RSS
9	–	–	–	–	–
8	18	20	14	1.2	1.4
7	16	20	13	1.3	1.5
6	–	–	–	–	–
5	16	22	14	1.4	1.6
4	19	21	15	1.1	1.4
3	16	18	12	1.1	1.5
2	17	19	13	1.1	1.4
1	–	–	–	–	–
median				1.2	1.5

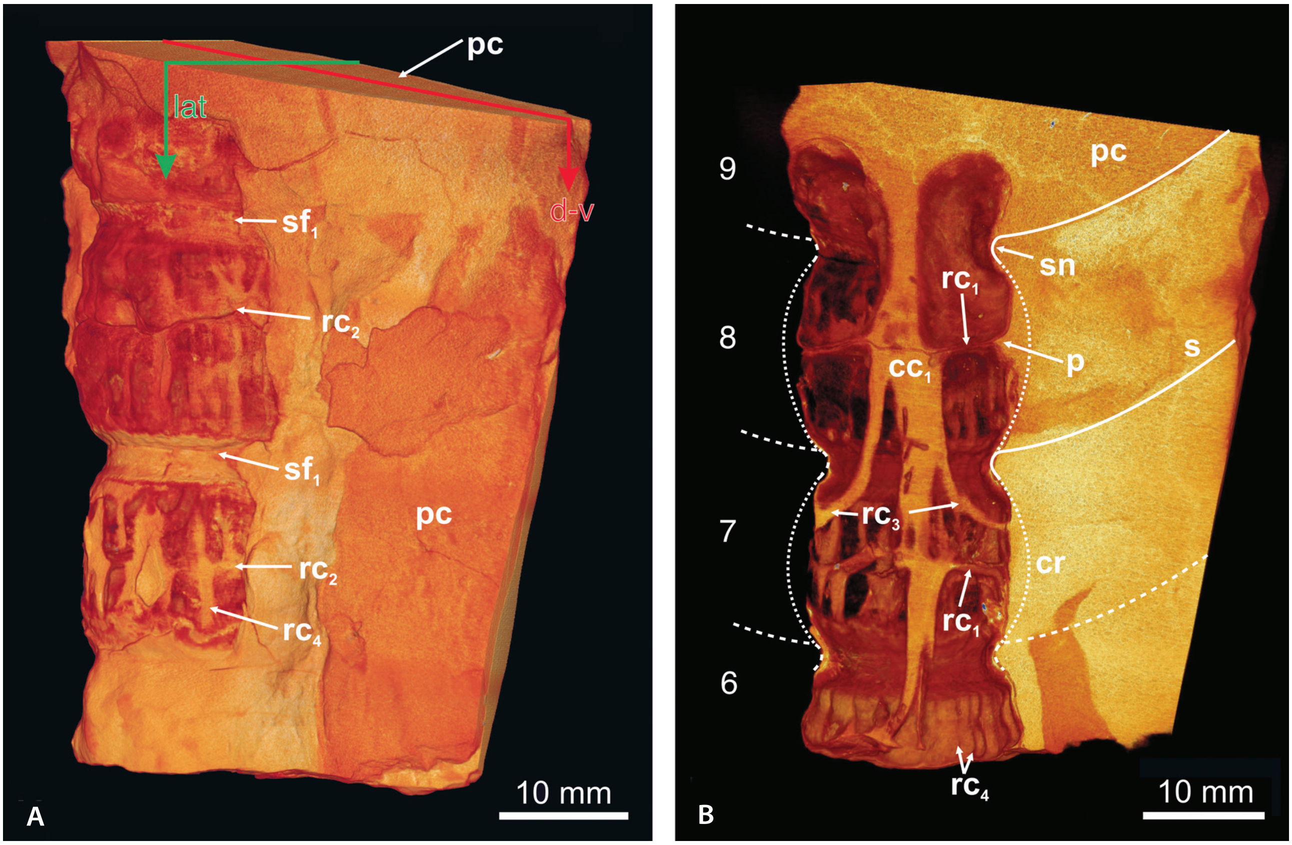


Figure 4. Micro-CT images of segments 9–6 of the holotype of *Adamsoceras*? *hanusi* sp. nov., NM-L46568, upper Katian Králův Dvůr Formation, Praha-Michle, Czech Republic. A – outer view with arrows indicating the positions of dorso-ventral (red arrow) and lateral (green arrow) sections used in subsequent images; note the compacted infilling of phragmocone chambers (pc). B – longitudinal dorso-ventral section with reconstruction of septal necks (sn), connecting rings (cr) and septa (s). For abbreviations see Tab. 3.

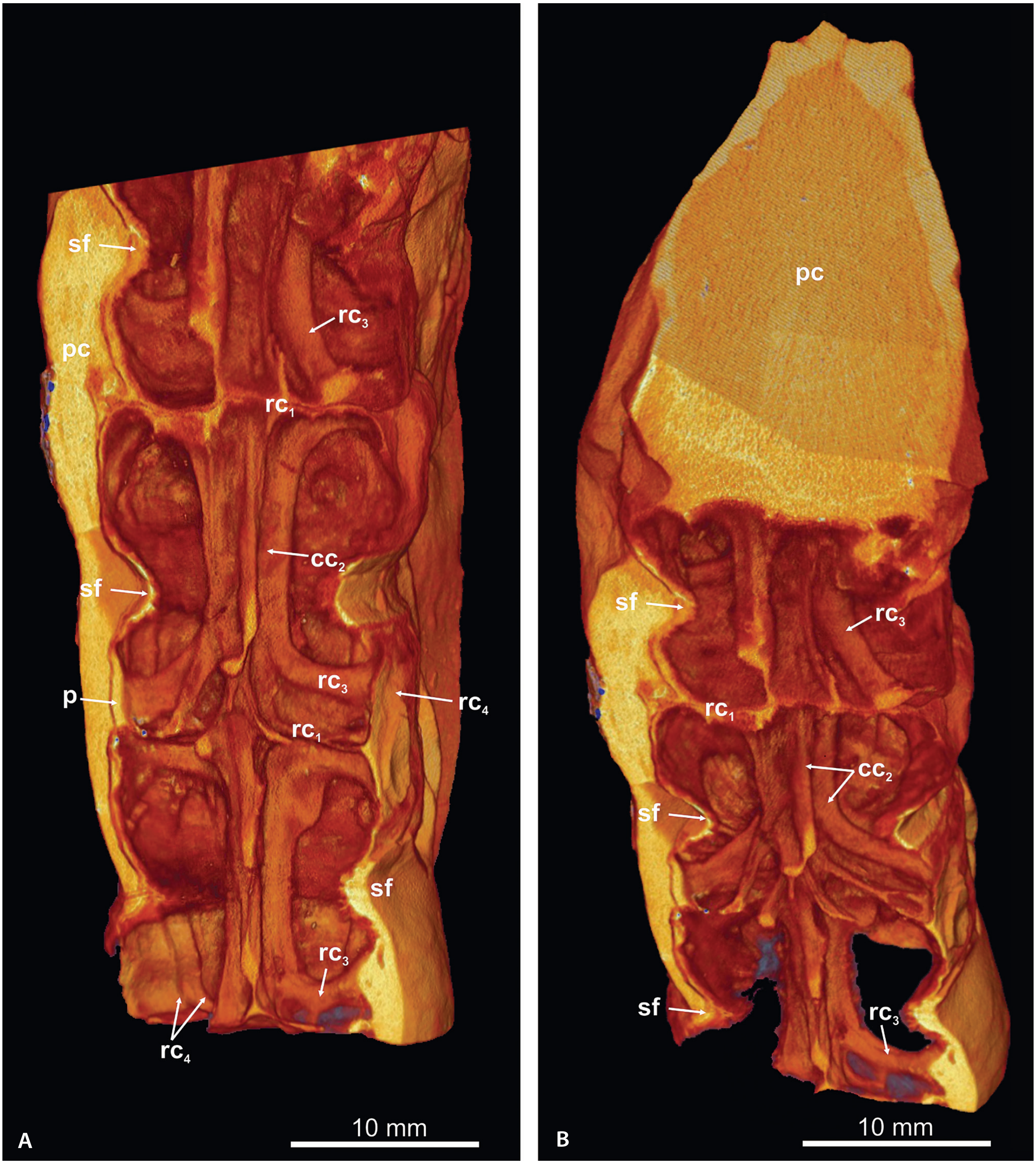


Figure 5. Segments 9–6. A – longitudinal lateral section. B – inclined view on the lateral section. For abbreviations see Tab. 3.

Description. – Holotype NM-L46568 is a fragmented phragmocone, 80 mm in total length, with a central or subcentral siphuncle (NM-L46568a-b, Fig. 4). Siphuncular segments are circular in the transverse section (Figs 6, 7, 9, 10, 12), quadratic or slightly broadened (SCR ~ 1.20), and slightly or strongly expanded (RSS ~ 1.50) (Tab. 4). Based on the shape of the narrowest part of the siphuncular segments, the septal necks were suborthochoanitic or cyrtochoanitic with free brims (connecting ring not adaperturally adnate, Figs 4, 8, 11).

The endosiphuncular structures are highly irregular in shape and distribution in all segments. The only indication

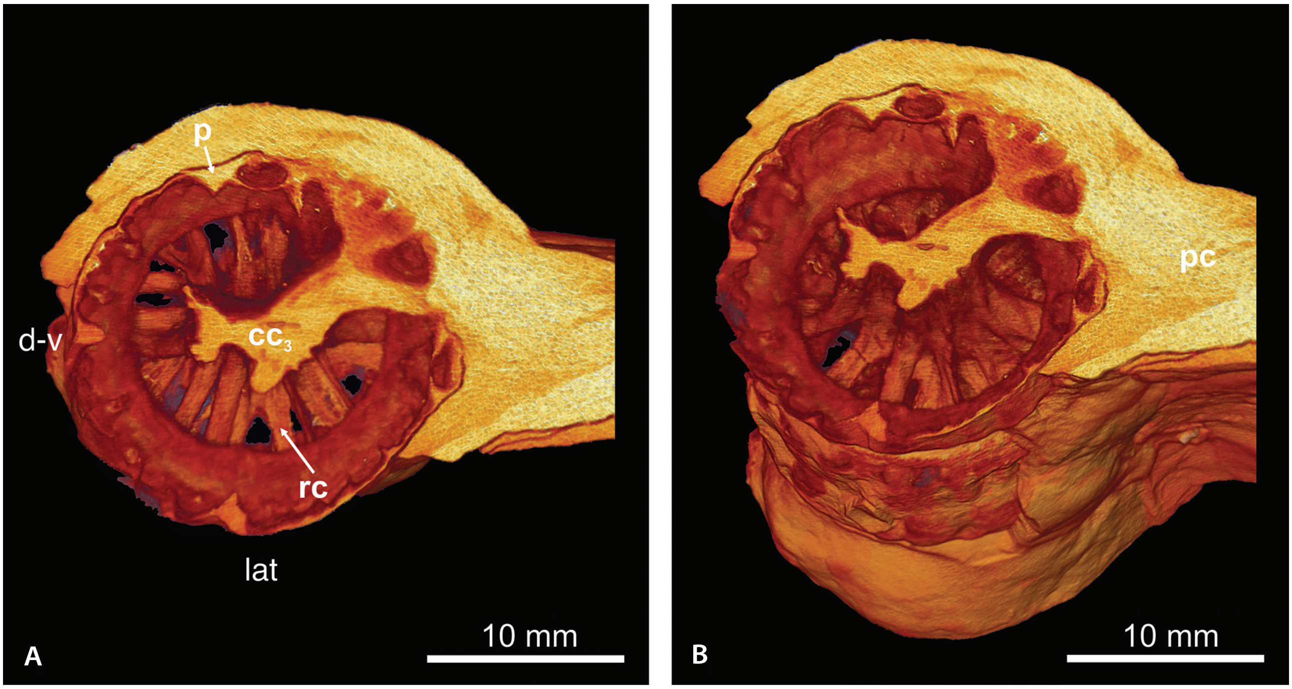


Figure 6. Segment 8. A – transverse section in the adapertural quarter of the segment length. B – inclined view of the same. For abbreviations see Tab. 3.

of any bilateral symmetry is the central canal, which is flattened in a longitudinal "lamella" with irregularly distributed, variably large openings (Figs 4–12). Therefore, in the longitudinal dorso-ventral section, the central canal is irregularly wide and appears locally shifted off the median plane of the siphuncle (Figs 4B; 8E, F) but very narrow and nearly straight in the longitudinal lateral section (Figs 8; 11B, C). In some segments, it is visible that the central canal consists of multiple, fused canals, which are also arranged in a flattened form (Figs 5, 7, 11C).

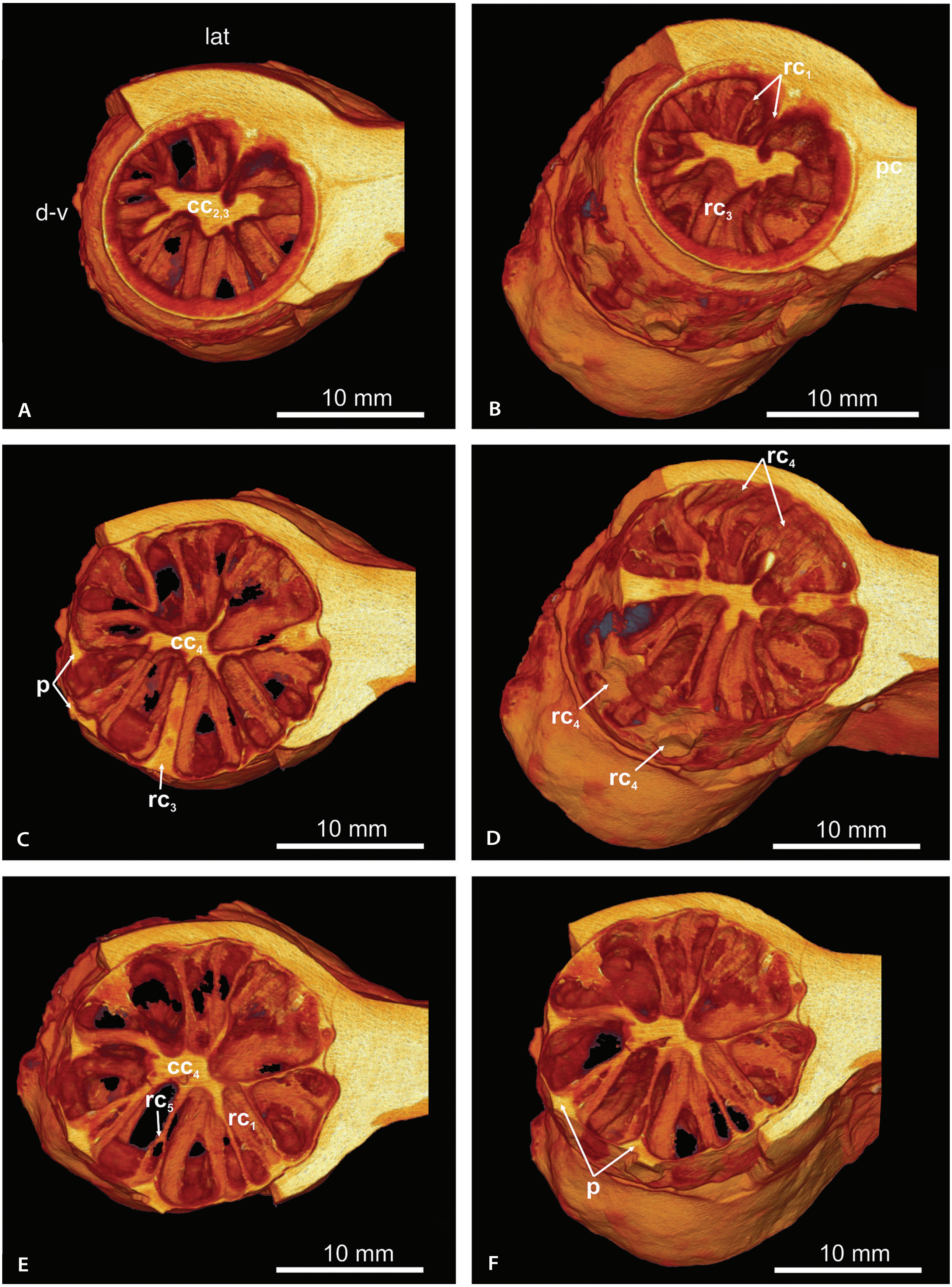
The cross-section of radial canals varies between circular and flattened. They branch off under right angles from the central canal at about the middle part of each segment (Figs 4; 7E, F; 8B–F; 9E, F). In addition, however, some radial canals extend randomly from the central canal in the first or last quarter of the segments; some of the latter radial canals are comparatively wider (Figs 4; 5; 8E, F; 9C, D; 11E), sometimes exceeding in width the central canal (Fig. 7C, D). Radial canals may bifurcate as they get closer to the perispatium (Figs 7E, F; 9; 12C).

After leaving the central canal, the radial canals extend towards the perispatium, where they widen in a shovel-like (fan-shape) form (Figs 8C–E; 10A–C; 11C, D). On the outer surface of the studied fragments, *i.e.* the inner surface of the perispatium, these widenings are manifested as longitudinal insertions of material of a different colour representing different density (Figs 4A, 7B, D, F). These insertions correspond to spaces between the tongue-shaped annulosiphonate deposits. The distribution of spaces between the deposits is indicated also by longitudinally extended ridge-like structures (Figs 4B, 5A, 8B, 9F) preserved around the inner circumference in some segments. In transverse sections, these ridges are manifested as sharp extensions delineating wide lobate spaces (Fig. 10A, B).

Remarks. – Because of the specimen's incomplete preservation, not much can be reliably said about the external shell morphology. The largest fragment NM-L46568a along with NM-L46568b indicate that the shell was probably orthoconic or weakly cyrtoconic with a circular or subcircular cross-section and angle of expansion of at least five degrees; the siphuncle was subcentral or central. The maximum preserved diameter of the strongly compacted adapertural part of the shell is 63 mm; however, the original shell diameter was higher because the phragmocone is clearly broken off from both sides.

The micro-CT image of the median section through the fragment NM-L46568a (Fig. 4B) shows changes in the density of the sediment infilling and indicates the shape and position of two septa; the length of the phragmocone chambers was moderate (about four chambers are estimated to correspond to the shell diameter).

The shape of the largely intact remains of the vascular system inside the siphuncle implies that deposits filled in most of the endosiphuncle. This, combined with the unreduced length of adapertural segments and the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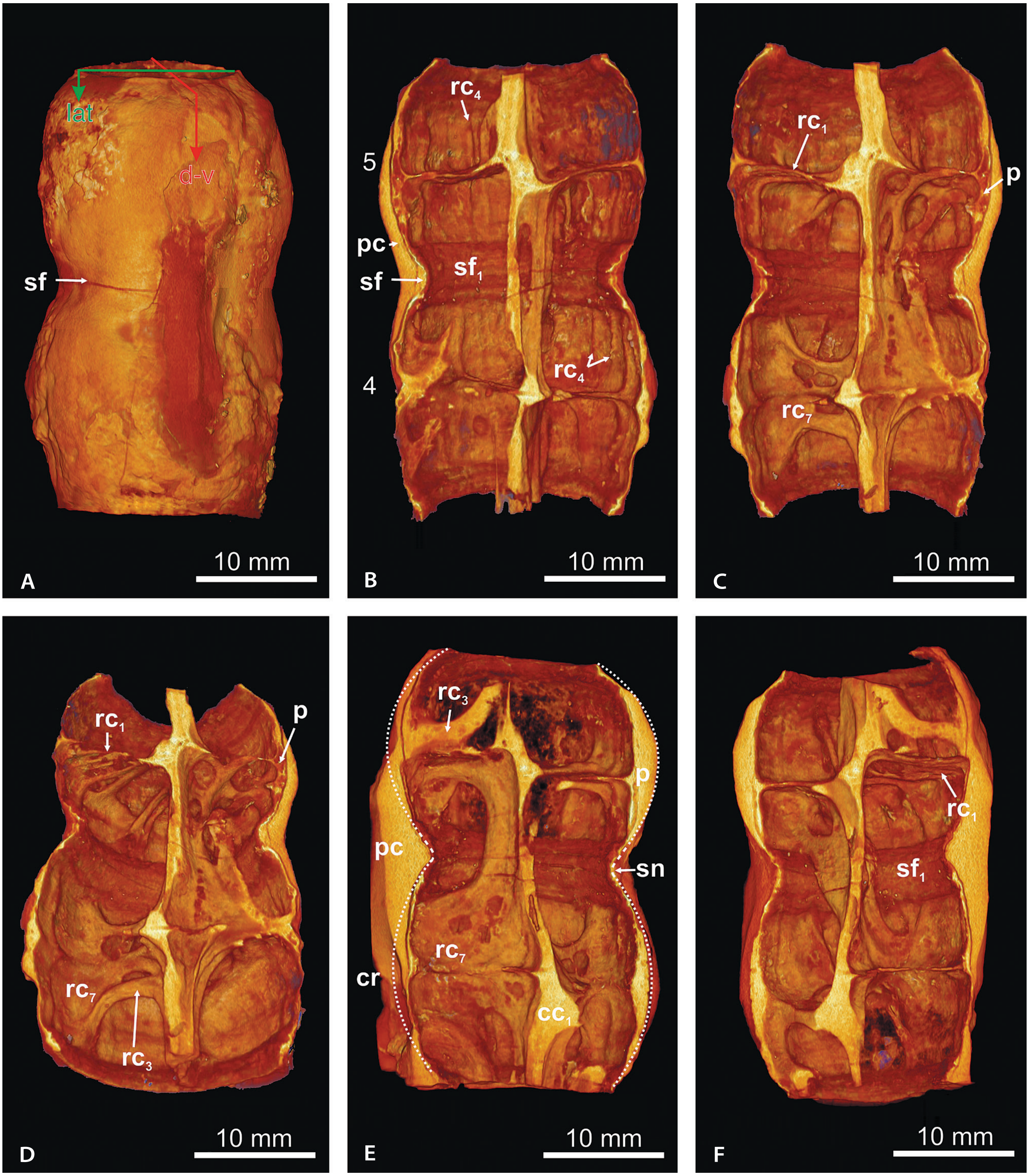
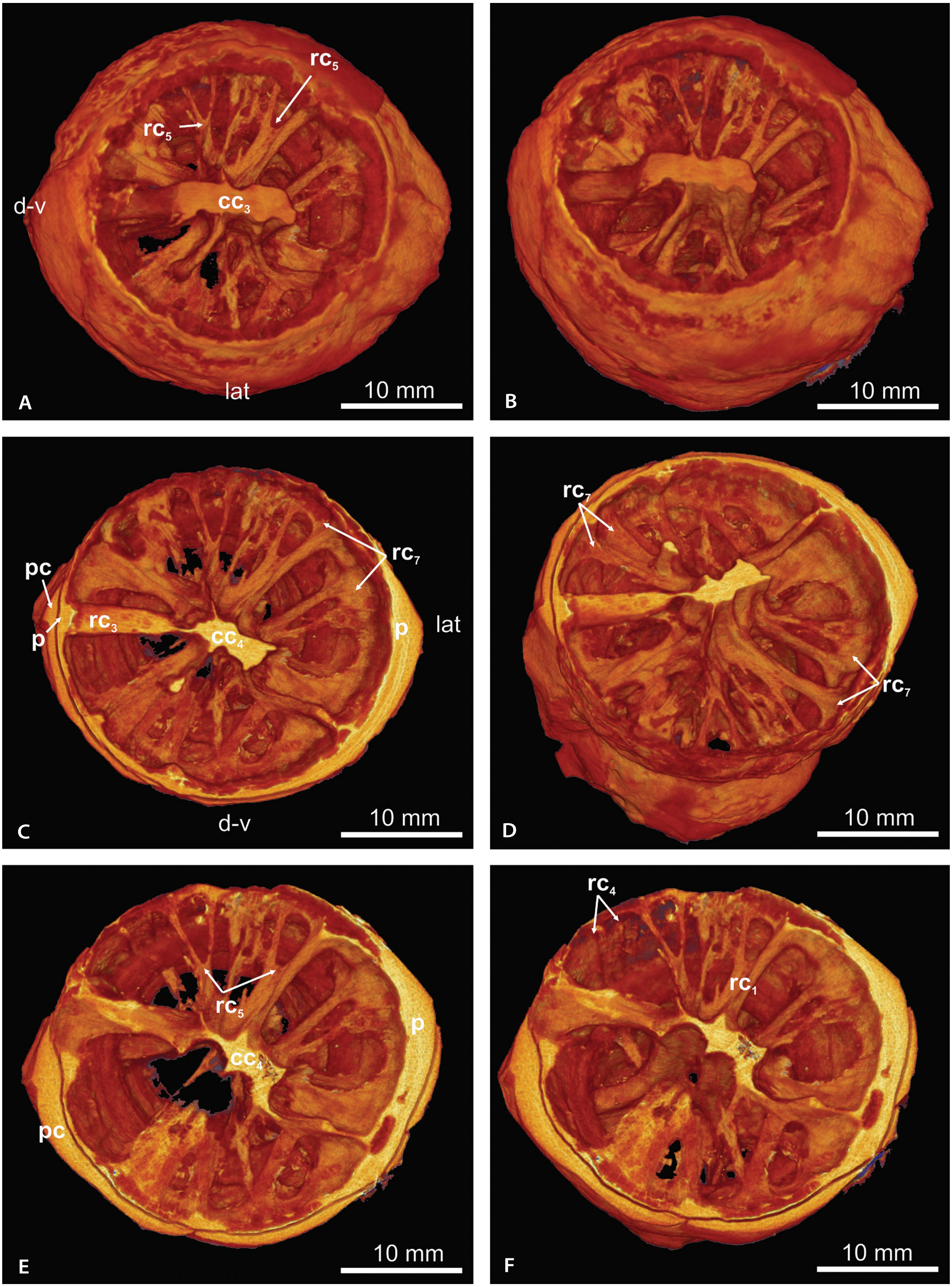


Figure 8. Segments 5–4. A – outer view with arrows indicating the positions of dorso-ventral (red arrow) and lateral (green arrow) sections. B–D – near-median longitudinal sections in the lateral direction; B, C – one and the other half of the siphuncle in directly upright orientation; D – inclined view of C; note branching of thin radial canals (rc1) perpendicularly to the central canal. E, F – near-median longitudinal sections in the dorso-ventral direction (directly upright); E – one half with reconstruction of septal necks (sn), connecting rings (cr) and exceptionally complete perispatium (p); F – the other half of E. For abbreviations see Tab. 3.

< Figure 7. Segment 7. A, C, E – transverse sections at the level of septal necks (A), adapertural quarter of the segment length (C) and mid-segment level (E). B, D, F – inclined views of A, C, E, respectively. For abbreviations see Tab. 3.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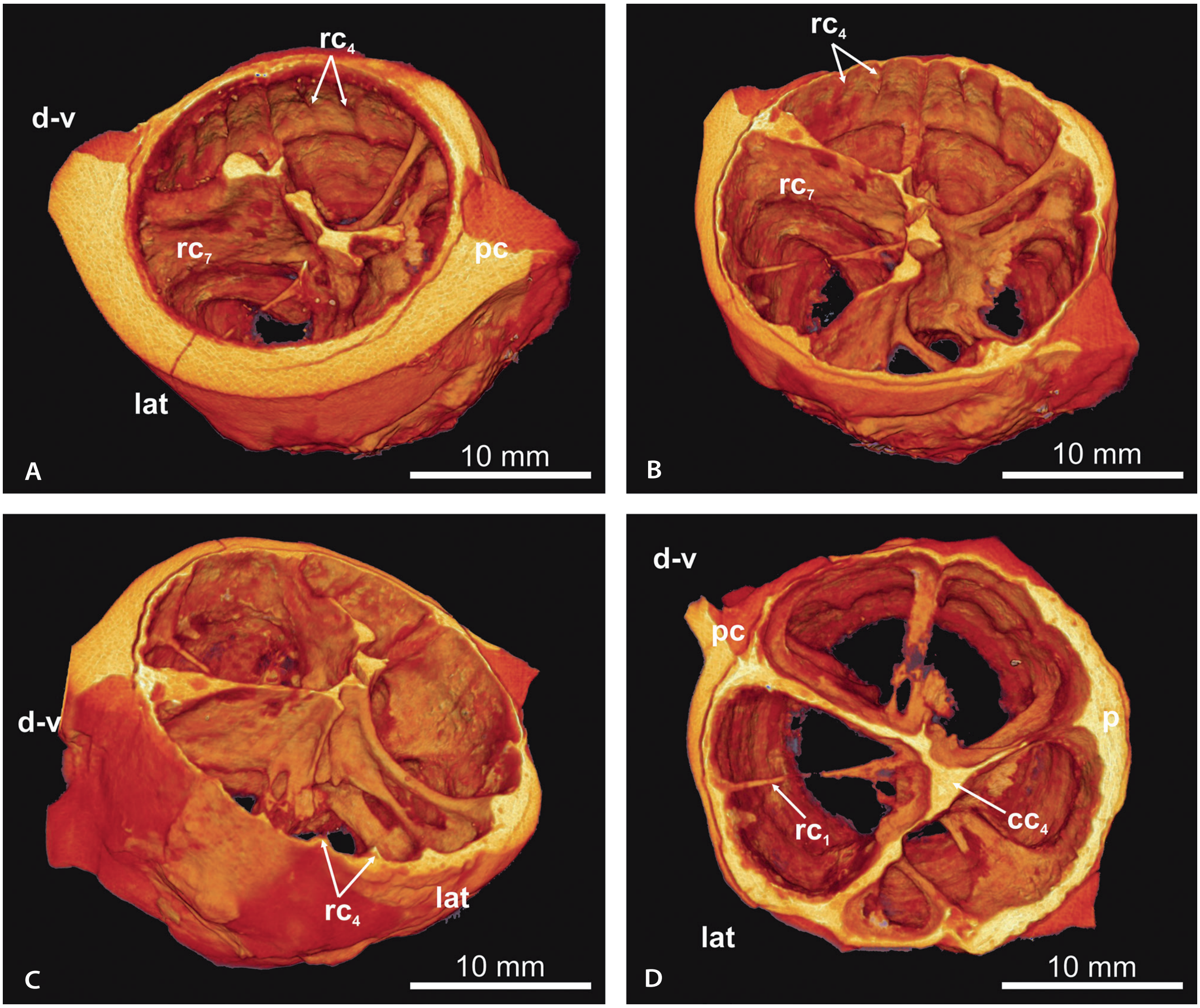

Figure 10. Segment 4 (radial canals partially broken off). A–C – inclined views at the septal foramen (A) and adapertural quarter of the segment length (B–C). D – transverse section at the mid-segment level. For abbreviations see Tab. 3.

relatively large size of the specimen, indicates a late (but not the latest) growth stage of the studied shell fragment (see *e.g.* Flower 1957, 1964; Teichert 1964).

The reconstructed shell morphology and character of endosiphuncular structures suggest two possible systematic positions of the specimen at the family level. First, the specimen is similar to the representatives of the Wademidae Özdikmen, 2008 in the possession of adaperturally suborthochoanitic or cyrtochoanitic septal necks with free brims, in the presence of multiple central canals and irregularly thick and branching radial canals; also, structures resembling engrafts are present (*e.g.* Figs 4A, 7D). The family was established based on specimens from the Floian of Australia (Wade 1977a, b), which have much shorter siphuncular segments than the studied specimen (SCR > 2 *vs*. 1.2). However, Ebbestad *et al.* (2019) described specimens from the Katian of Morocco with a central siphuncle and markedly elongated segments (SCR ~ 0.50), which they assigned to the Wademidae. If the latter classification is correct, then the herein studied specimen would fall within the variation of that family. However, it is not entirely clear whether the structures diagnostic for the Wademidae cannot reflect only the preservation of the material on which the family was

Figure 9. Segment 5. A, C, E – directly transverse sections at the level of septal necks (A), adapertural quarter of the segment length (C) and mid-segment level (E). B, D, F – inclined views of A, C, E, respectively. In A and B, note flattening of the central canal in the lateral direction and its extension in the dorso-ventral direction. For abbreviations see Tab. 3.

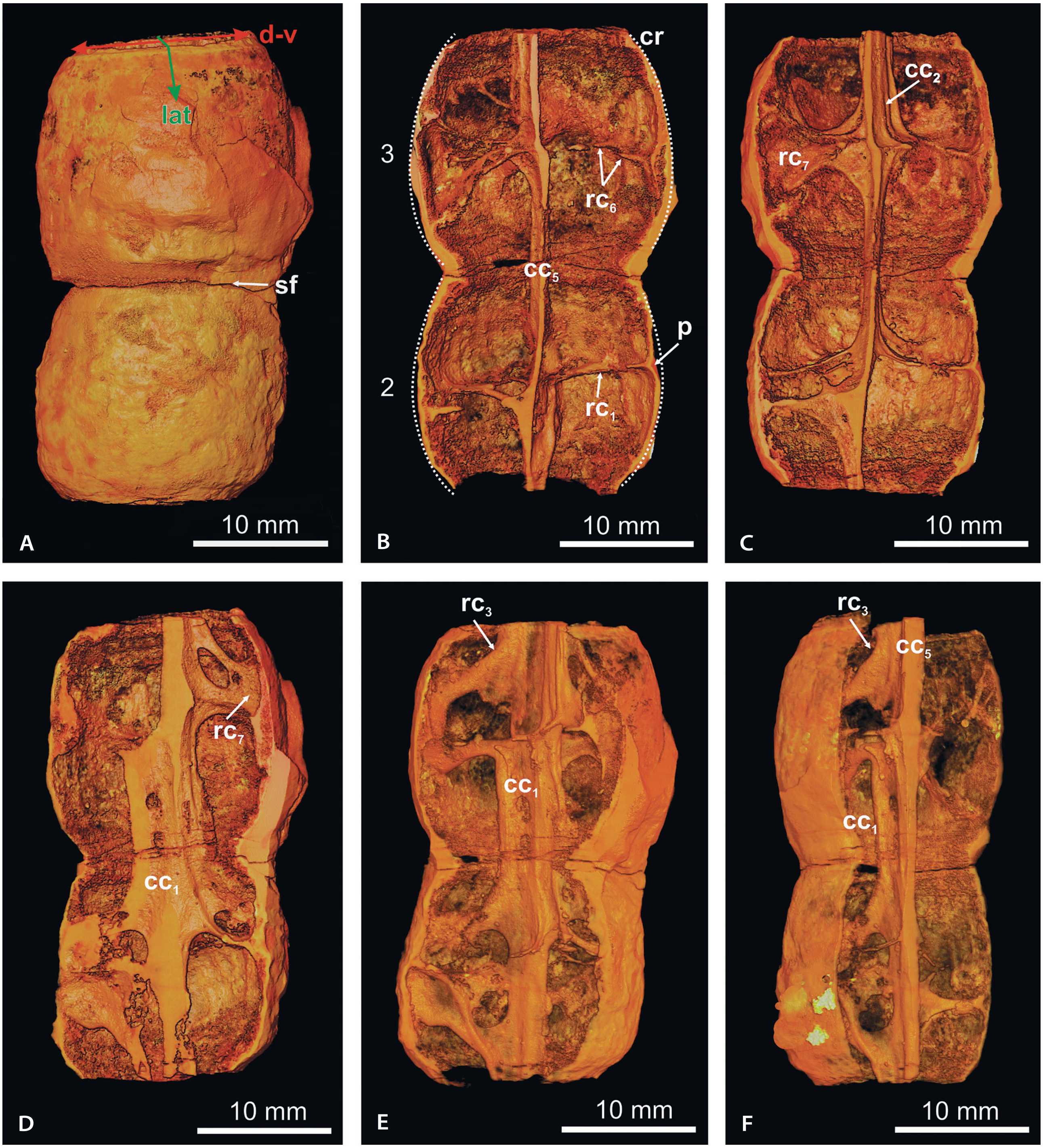

Figure 11. Segments 3–2. A – outer view with arrows indicating the positions of dorso-ventral (red arrow) and lateral (green arrow) sections used in subsequent images. B – longitudinal, median, slightly rotated (counter clockwise) lateral section with reconstruction of connecting rings (cr) and perispatium (p). C – longitudinal, slightly off-median, lateral section. D – slightly off-median longitudinal section in dorso-ventral view. E – sagittal section of D. F – near-median longitudinal section of F (rotated counter clockwise by *c.* 45°). For abbreviations see Tab. 3.

established by Wade (1977a, b) and also whether these structures are unambiguously present in the herein studied specimen.

Second possibility, and the one favoured here, is that the specimen represents the Ormoceratidae. Among the members of this family, the specimen most closely resembles representatives of the Middle Ordovician genus *Adamsoceras* because the connecting ring is not adaperturally adnate around the whole circumference of the septal foramen, siphuncular segments are wider than long,

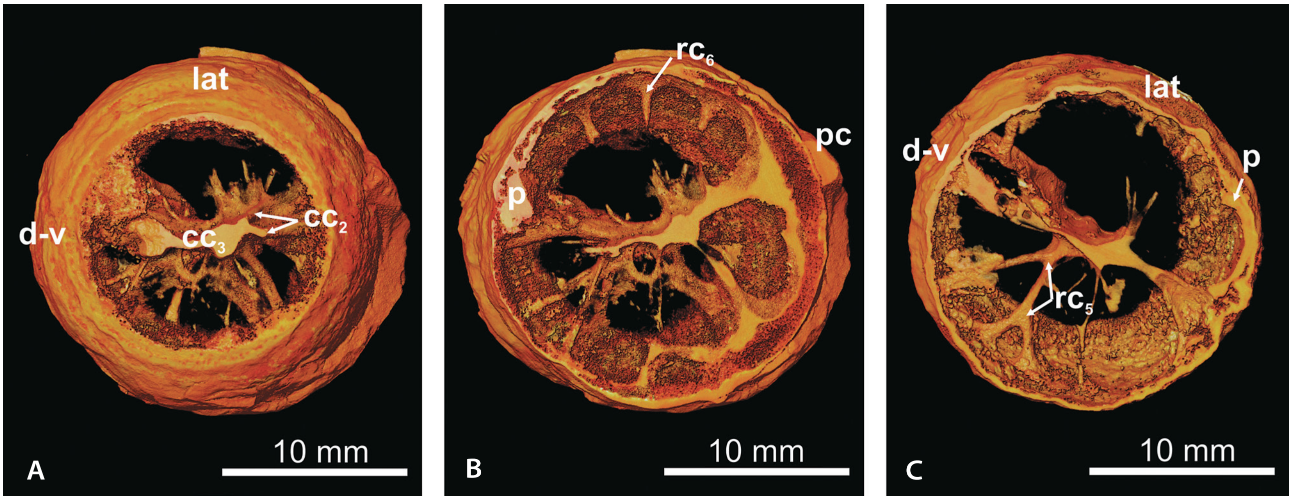

Figure 12. Segments 3–2 (radial canals partially broken off). Transverse sections at the level of the septal foramen (A) and segment mid-length (B) in segment three, and adapertural quarter of the segment length (C) in segment two. For abbreviations see Tab. 3.

the shell is slowly expanding and the endosiphuncular canal system is of reticular or straight type. Most similar among *Adamsoceras* species is *A. holmi* (Troedsson, 1926) (see Mutvei 2016, fig. 1a) from the early-mid Darriwilian of Estonia. However, the herein studied specimen differs by longer (SCR ~ 1.20 *vs*. 1.46) and much less expanded (RSS ~ 1.50 *vs*. 2.50) siphuncular segments in the late growth stage. Also, the siphuncle in *Adamsoceras*, including *A. holmi*, tends to be submarginal (Troedsson 1926, Flower 1957), while in the herein studied specimen it was probably subcentral or even central.

Due to the incomplete preservation of the holotype, it cannot be excluded that the specimen represents some other genus of the family Ormoceratidae. The representatives of *Orthonybyoceras* and *Treptoceras* are similar in the shape of the endosiphuncular system and siphuncular segments in later ontogeny but the septal necks are dorsally recumbent. In the species of the genera *Aluveroceras* and *Deiroceras*, the siphuncular segments are longer than wide (SCR < 1 *vs*. 1.22) and the endosiphuncular system appears to be less complex. *Ormoceras* has a higher angle of expansion (7–9 degrees *vs*. ~5 degrees), simpler endosiphuncular system (Flower 1957) and much higher SCR (1.75–2.0 *vs*. 1.22).

Occurrence. – Only the type horizon and type locality.

Discussion

Taphonomic interpretation

Preservation of the specimen. – The single specimen described above consists of a flattened internal mould of several phragmocone chambers and an undeformed infilling of the siphuncle. Presumably, this is because the siphuncle was protected against compaction by the thick primary annulosiphonate deposits. Siphuncular segments were most fragile at the septal necks. However, the segments six and nine were broken off in their middle parts, *i.e.* at the position, where annulosiphonate deposits are in contact.

The adapertural part of the shell including the body chamber is missing. Given the off-shore, deep-water environment and soft sediment in which the specimen was deposited, the loss of adapertural part of the shell at the sea floor due to wave action is unlikely (Štorch & Mergl 1989). This breakage rather occurred earlier, possibly in the water column, during the drift of the empty shell. Further breakage into individual fragments originated during the specimen collection.

Taphonomic history. – Based on the character, distribution and deformation of the specimen, we have reconstructed its taphonomic history as follows:

After the death of the cephalopod, soft tissue began to decompose and the shell was buried in the fine-grained sediment of the seafloor. However, the sediment invaded only the phragmocone chambers. The preservation of perispatium, central canal and radial canals was facilitated by early diagenetic pyritization. According to previous studies, this might have happened in two ways:

1) Martin (1999) argued that the solidification of material in narrow spaces happened through permineralization – early infiltration of cavities by fluids in fine-grained sediment enriched by organic material from decomposed soft tissues. Local dissolution of calcium carbonate from the shell raises pH and enables the precipitation of iron sulphides.

2) Another pathway of decay processes and pyritization was suggested by Wilkin & Barness (1997) to play a role in the deep-water, low energy marine environments. According to them, the formation of authigenic pyrite can occur very early in diagenesis of the sediment and can be initiated only a few centimetres below the sediment-water interface. As long as the environment is aerated, microorganisms present in the sediment break down organic carbon and respire aerobically. With increasing depth of burial, the diffusion of oxygen into the sediment is impeded and microorganisms start to respire anaerobically. This leads to sulphate reduction and origin of pyrite (Berner 1984) through metastable precursor phases – iron monosulphides (Wilkin & Barness 1997).

As the compaction of the sediment progressed, the phragmocone (by contrast to the relatively rigid siphuncle) was compressed. All calcareous structures of the shell were gradually dissolved; only minor differences in sediment density indicate the position of two septa in the fragment NM-L46568a (Fig. 4B). Massive annulosiphonate deposits were possibly among the last structures to dissolve in the diagenetically consolidated rock. At the end, internal moulds of phragmocone chambers, perispatium and central and radial canals were preserved, while cavities (hollow spaces) were left behind after the siphuncular wall and annulosiphonate deposits. Brown colour of the material infilling the central canal and radial canals is the result of post-diagenetic oxidation of pyrite, which turned into more or less hydrated iron oxides (limonite).

Endosiphuncular system in actinoceratids

There are two main interpretations regarding the structure, origin and function of endosiphuncular system in actinoceratid cephalopods:

1) Teichert (1933, 1935, 1964, 1967) and Flower (1955a, 1957, 1964) assumed the existence of a regularly shaped vascular system consisting of a central canal and variously complex network of radial canals, all surrounded by calcareous annulosiphonate deposits. In this concept, the radial canals served as a connection of the central canal with the perispatium – a narrow space between the connecting ring and outer surface of the annular deposits. It is in the perispatium, where the interchange of fluid and gas between the soft tissue of the sipho and phragmocone chamber took place (Teichert 1933, 1935, 1964; Flower 1957) through the porous walls of the connecting rings (Teichert 1935; Mutvei 1996, 2002).

2) Contrary to the above, Mutvei (1964, 1996), following *e.g.* Barrande (1855a, b; 1877) and Troedsson (1926), rejected the presence of a regular system of radial blood vessels and argued that the radial canals described by Teichert and Flower are in fact only interspaces between irregularly growing bodies of annulosiphonate deposits.

The structures preserved inside the siphuncle of the specimen studied herein show that at least in some actinoceratids, the primary connection between the central canal and perispatium happened through radial canals that branched off the central canal(s) at about the mid-length of the segment (Flower 1964, Teichert 1964). However, the shape and course of the supposedly soft and elastic radial vessels (Shimanski 1961) was modified by the shape and distribution of the calcareous deposits, irregularly growing around the inner surface of the septal neck (Mutvei 1964, 1996). The radial vessels bifurcated as they approached the perispatium (Shimansky 1961; Teichert 1933, 1935, 1964). Occasionally, sharp, spike-like structures are found on the inner surface in the central part of the siphuncular segments (Fig. 12B). The acute shape of these structures does not appear to reflect breakage of canals during taphonomy but rather indicates that the growth of the deposits sometimes interrupted the radial vessels; this would hamper the liquid interchange in the perispatium. Generally, however, the soft tissue of the siphuncle did not allow the deposits to fully fill in the endosiphuncle, as seen also in apical parts of some specimens with fully developed deposits (Teichert 1964). This means that even in the late growth stage, the siphuncle could have retained some, although decreased, function via vessels running through interannular spaces (*cf.* Crick 1988). Growth of perispatial deposits in latest ontogeny reduced the size of the perispatium and thus further limited the siphuncular function (Flower 1964).

Our investigation supports the observation of Shimansky (1961) and Wade (1977a, b) that the central canal contained not one but a bundle of multiple blood vessels closely attached to one another (Figs 5A, B; 7A; 11C; 12A); thus, the central canal is irregular in shape in the transverse section. Also, the tubular form of some canals in the herein studied (*e.g.* Figs 5B, 7D, 8D, 9) or previously described specimens (*e.g.* Teichert 1933) may indicate that the walls of the vessels were more rigid (see also Shimansky 1961) than the rest of the soft tissues in the endosiphuncle (note that the siphuncular cord in the extant *Nautilus* has vessels surrounded by additional soft-tissue; Stenzel *in* Moore 1964).

Remarks to palaeoecology of actinoceratids

The herein studied shell fragment is interpreted to represent the late growth stage. Generally, the (sub)adult individuals are considered to have been horizontally (*e.g.* Flower 1955b, Westermann *in* Savazzi 1998) or vertically (Peterman *et al.* 2019) oriented nectobenthic predators,

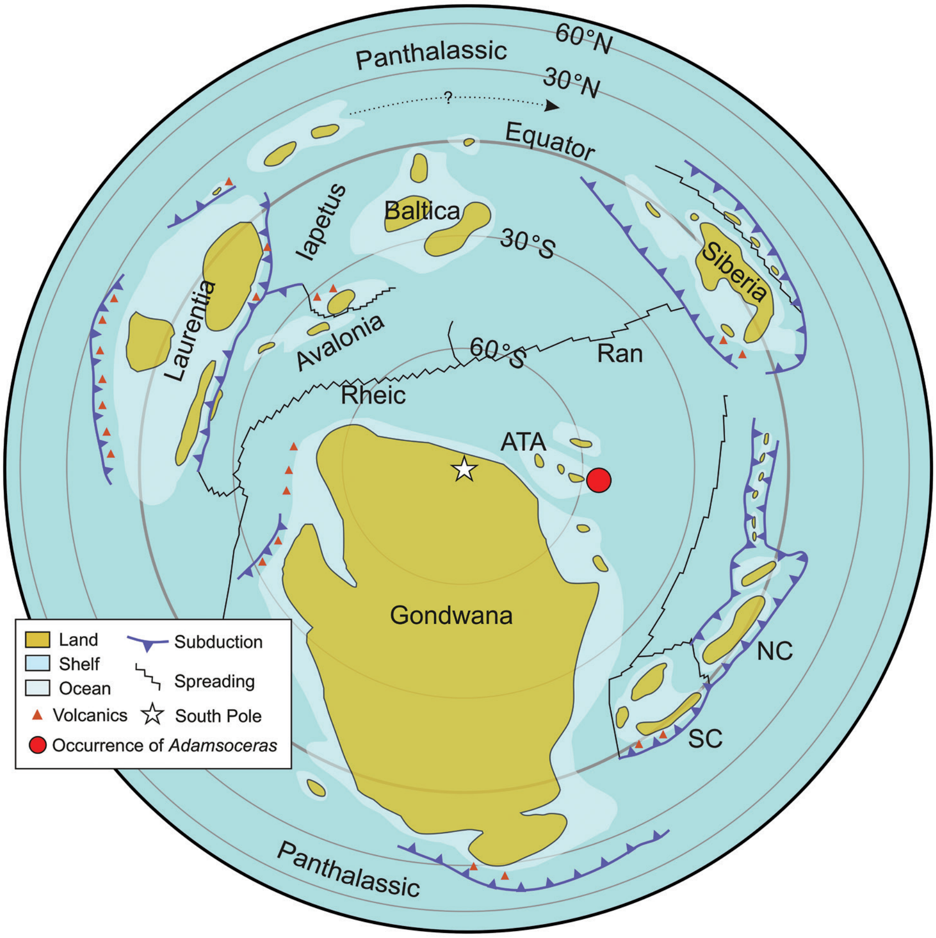

Figure 13. Palaeogeographic reconstruction for the Late Ordovician (Katian, 450 Ma) and the occurrence of *Adamsoceras*? *hanusi* in the high-latitude Prague Basin. Map redrawn and modified from Cocks & Torsvik (2021, fig. 2). Abbreviations: ATA – Armorican Terrane Assemblage; NC – North China; SC – South China.

which were, however, limited to shallow depths because of their thin and wide connecting rings and thin septa (*e.g.* Westermann 1973, Crick 1980, Evans 2000, Kröger *et al.* 2009, Kröger & Yun-Bai 2009, Kröger & Ebbestad 2014, Kröger & Rasmussen 2014). Nectobenthic lifestyle and relatively active swimming was argued for also in (sub) adult actinoceratids with comparatively narrow siphuncles and shells with circular or compressed cross section and lacking cameral deposits, such as ormoceratids (Teichert 1935, Barskov *et al.* 2008). Benthic lifestyle is supposed for strongly depressed actinoceratids and forms with large and heavy siphuncles (Teichert 1935, Westermann *in* Savazzi 1998, Barskov *et al.* 2008). By contrast, Mutvei (2002, 2016) refused jet-powered swimming in actinoceratids and argued that the calcified inner layer of the connecting ring with numerous pores implied that actinoceratids were capable of rapid, possibly diurnal, changes of volume of cameral liquid, which made it possible to migrate vertically in the water column.

In addition to their shallow-water preference, the actinoceratids are known to have been palaeogeographically restricted to regions located in low palaeolatitudes (*e.g.* Crick 1980, 1993; Kröger & Yun-Bai 2009; Kröger *in* Harper & Servais 2013; Niko & Sone 2014; Kröger & Ebbestad 2014; Kröger & Rasmussen 2014; Fang *et al.* 2018). Their occurrence in mid- and high latitudes, like the Prague Basin (Fig. 13), was only occasional and rare (Evans 2000, 2005). Previous studies of faunal assemblages of the late Katian part of the Králův Dvůr Formation indicate some palaeobiogeographic relationships to mid- and low palaeolatitudes, especially Baltica and to a lesser extent also to Avalonia and Laurentia (Havlíček *et al.* 1994, Fatka & Mergl 2009, Kraft *et al. in* Harper *et al.* 2023). These connections are supported by the rare occurrence of otherwise low-latitude cephalopod taxa: the single representative of the oncoceratid *Diestoceras* and fragments of an endoceratid siphuncle reported above. The only unambiguous representative of the Actinoceratida in the Prague Basin described herein provides additional support to certain low-latitude connections. Note, however, that the dominance and taxonomic composition of orthoceratoid cephalopods (Marek 1999) still point at prevailing relationships with other peri-Gondwanan assemblages (Ghavidel-Syooki *et al.* 2015).

Conclusion

The anatomy of the endosiphuncle in actinoceratid cephalopods has long been a matter of differing opinions. Herein, we have studied a specimen, which offers a possibility to address these views. The specimen consists of several undeformed siphuncular segments and some strongly flattened phragmocone chambers. All original calcareous structures of the shell (outer wall, septa, ectosiphuncle, annulosiphonate deposits) were completely dissolved. Empty spaces, left behind after these dissolved structures, reflect their original shape and distribution. Inside the siphuncle, remains of the endosiphuncular vascular system are preserved.

The system is asymmetric and highly irregular in shape. Its irregular organisation was formed by the uneven growth of annulosiphonate deposits around the inner surface of the septal foramen (Mutvei 1964). The growth of the deposits influenced not only the distribution of the central and radial blood vessels but also their shape in the transverse section. As a result, the endosiphuncular system appears to be of straight type from one longitudinal view but of reticular type from another (perpendicular) longitudinal view.

The shape of the preserved endosiphuncular system in the studied specimen supports the views of Teichert (1933, 1935, 1964, 1967) and Flower (1957, 1964), widely accepted by most cephalopod workers, that there was a vascular system inside the siphuncle of actinoceratid cephalopods. Our observations indicate that this system was pushed to interannular spaces by the growth of annulosiphonate deposits (Mutvei 1964, 1996). The communication between the central blood vessels and free space along the inner side of the connecting ring (= perispatium) remained functional even in the case of fully developed deposits. The blood vessels probably had elastic and soft walls with higher preservation potential compared to the rest of the soft tissues of the siphuncle (Shimanski 1961).

As a consequence of the above, the appearance of the endosiphuncular system in longitudinal sections depends not only on the precision of the median sectioning but also on the section orientation and rotation (see Pohle *et al.* 2024). Thus, the distinction between several types of endosiphuncular systems *sensu* Teichert and Flower and the taxonomy inferred from these distinctions might be, at least in some actinoceratids, artificial (see also Dzik 1984 and Mutvei 1996). It is also important to note that the internal shell structure in many actinoceratids changed substantially during ontogeny. This further adds to the probable oversplitting of the group due to establishment of taxa based on short fragments and comparison of non-corresponding growth stages. Any future revision or establishment of taxa should thus (in ideal cases and where possible) include 1) studying the siphuncle in at least two perpendicular longitudinal sections (*i.e.* dorsoventral and lateral) or by micro-CT or serial grinding tomography, and 2) studying longer fragments that allow consideration of ontogenetic changes.

The studied cephalopod specimen is the first unequivocal representative of the order Actinoceratida in the Ordovician of the Prague Basin. It was tentatively assigned to the genus *Adamsoceras*, although it differs from its representatives by the relatively less expanded siphuncular segments. *Adamsoceras* is one of the most widely distributed actinoceratids in the Middle Ordovician strata of North America and Baltoscandia; the holotype is late Katian in age, which would make it the stratigraphically youngest representative of *Adamsoceras* globally. The shell expansion rate, shape of siphuncular segments, reticular to straight type of the endosiphuncular vascular system justify the establishment of a new species, *Adamsoceras*? *hanusi*.

The holotype of *Adamsoceras*? *hanusi* sp. nov., along with the recently described holotype of the tarphyceratid *Trocholites chaloupkai* Aubrechtová *et al.*, 2023 and specimens of the ellesmeroceratid *Ellesmeroceras humahuacaensis* Cichowolski *et al.*, 2023, are the first Ordovician cephalopods, in which micro-CT scanning was successfully applied to study the internal shell structures. In addition, Pohle *et al.* (2024) showed in some Cambrian cephalopods that using only 2D sections might lead to incorrect interpretations of shell morphology, result in oversplitting of taxa and artificially inflating diversity. The information and data obtained from three-dimensional images convincingly demonstrate that the applied method can be used to obtain information on the anatomy of organisms from fossils, in which such a preservation is usually not present.

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