Ontogeny, muscle scars, colour pattern and predation marks in a Silurian orthoceratid cephalopod

ŠTĚPÁN MANDA and VOJTĚCH TUREK

Muscle scars, embryonic shell, colour pattern and intraspecific variation are known together in a very limited number of straight shelled cephalopods, leading to uncertainty in the classification of the subclass Orthoceratoidea. The newly described genus *Lepidoceras* from the Silurian of Bohemia, interpreted as a demersal orthoceratid similar to *Kionoceras*, shows all relevant diagnostic characters. The earliest late Wenlock populations of *Lepidoceras* have a weakly curved endogastric shell, but the shell becomes increasingly more curved throughout the Ludlow. The sculpture is characterized by distinctive longitudinal lirae or ridges, the number of which is variable and maintained during ontogeny. The embryonic shell of *Lepidoceras* is one of the largest in orthoceratids; it is conical or weakly curved in shape beginning with a smooth non-accretion initial shell. Hatching is manifested by growth walls in some specimens; hatchlings were apparently demersal. Adults are usually characterized by mature modifications of the shell: septal crowding and shell wall thickening. A high proportion of adult specimens indicates low mortality in palaeopopulations. Healed repairs indicate a lower predation pressure, which decreases after the juvenile stage. Extensive shell repair in juveniles demonstrates high regenerative capacity. Orthoceratomorph muscle scars found only in adults show a pair of dorsal retractor imprints that gradually expanded laterally. The colour pattern consists of irregular transverse bands, which have never been detected in orthoceratids before. The pattern, which is similar to that in curved oncocerids, is probably an expression of adaptive convergence of this feature in both groups. Shell pathologies, which have been observed in juvenile orthoceratids for the first time, are rare; an extensive pathology in a mature specimen illustrates limit of survival in orthoceratids. *Lepidoceras* is an example of a demersal orthoceratid entering a niche inhabited predominantly by multiceratoids.

Key words: Cephalopoda, Orthoceratida, ontogeny, variability, palaeoecology, predation.

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Introduction

The low number of cephalopod species, for which all significant morphological characters and their intraspecific variation are known, has limited a better understanding of early Paleozoic orthoceratoid phylogeny and auteocology. The diagnoses of many families and genera are based on a combination of characters of different genera or species placed in a given taxon. Adaptive convergence or parallel evolution in the shell form of early Paleozoic cephalopods is thus difficult to detect. Therefore, there is currently no general consensus regarding the classification of non-ammonoid cephalopods with external shells, especially orthoceratoids (Dzik 1984; King and Evans 2019; Niko et al. 2020; Pohle et al. 2022). The common adaptive convergence of orthoceratid shells reinforces the importance of early ontogenetic development for classification, but this is limited because early growth stages are known for only a small number of species (e.g., Kröger 2006; Kröger and Isakar 2006; Manda and Turek 2024). The majority of known early growth stages cannot be identified with taxa, which are defined based on post-juvenile shells (e.g., Ristedt 1968, 1971).

Understanding of predator-prey interactions and their evolution throughout the early Paleozoic is limited by the lack of studies on shell repair and cephalopod associations. There are almost no data documenting how common healed injuries are in individual species, how their frequency varies among associations and through the early Paleozoic (Kröger

2004, 2011; Klug 2007). The Silurian cephalopod fauna of the Prague Basin is known for its species richness and good preservation (Barrande 1865–1877), yet the number of species for which all diagnostic characters or at least the most important ones are known, is small, especially in orthoceratids (Turek and Manda 2012). Any study based on material from historical collections is somewhat limited by collecting biases. The cephalopod shells from limestones in the collections have been carefully removed from the rock matrix and their faunistic and taphonomic context is thus lost (Stridsberg 1985). The apical portion in smaller orthoceratid shells is almost always broken off.

The orthoceratid *Lepidoceras* gen. nov. from the middle Silurian of the Prague Basin is described herein. The material studied comes from historical collections, mainly the collection of Joachim Barrande, supplemented by the findings of one of the authors (ŠM) providing biostratigraphic control and taphonomic context. Endogastric, moderately expanding shell, distinct reticulate sculpture and thin siphuncle clearly differentiate the new genus *Lepidoceras* from all co-occurring taxa and make it possible to describe its morphological variability. The type species of *Lepidoceras*, *Cyrtoceras lepidum*, was described by Barrande (1866) and has since been mentioned only by Dzik (1984), who placed it in the family Sactoceratidae Troedsson, 1926.

The new findings of the apical parts of the shell allowed the study of the whole ontogeny from the embryonic shell to the shell with mature modification, which is only possible in a limited number of orthoceratid species (e.g., Barrande 1870, 1877; Marek 1971; Kolebaba 1977). In several individuals, muscle imprints are preserved and allow to study variability in the extent of retractors. Orthoceratoid muscle scars have so far been documented only in some species and based on single specimens (Mutvei 1957; Marek 1971; Kröger et al. 2005; Turek and Manda 2012).

The good preservation of relatively complete shells with the shell wall allowed the quantification of sublethal shell repairs. The pattern of shell coloration described here in *Lepidoceras* is new in orthoceratids, which are usually coloured by longitudinal bands. A pathological shell is also described here; the degree of the malformation is among the most striking yet known in early Paleozoic cephalopods (Kobluk and Mapes 1989; Kröger et al. 2009; Manda and Turek 2015).

Institutional abbreviations.—CGS SM, Czech Geological Survey, Prague, Czech Republic; MCZ, the Shary's collection of the Museum of Comparative Zoology, Harvard, USA; NM L, palaeontological collection of the National Museum, Prague, Czech Republic.

Nomenclatural acts.—This published work and the nomenclatural act it contains have been registered in ZooBank urn:lsid:zoobank.org:act:47BD78E7-F127-48E5-8B91-152D0A55557A.

Geological setting

The Paleozoic of the Barrandian area (Central Bohemia) represents the sedimentary cover of the pre-Cadomian Teplá-Barrandian Unit of the Bohemian Massif. The unmetamorphosed Silurian rocks are preserved in the central part of the Prague Synform, SW of Prague. The Prague Synform formed during the Variscan orogeny which substantially modified the sedimentary and volcanic infill of the former Early Ordovician–Middle Devonian marine basin, called the Prague Basin (for summary see Havlíček 1981, 1998). The facies distribution, the geometry of basin infill and the geochemistry of the volcanic rocks indicate a rather continuous marine deposition in an intra-plate linear rift basin divided into several sub-basins by synsedimentary faults (Kříž 1998b). There is no indication of a continental shoreline after the early Middle Ordovician. The preserved Silurian rocks represent an erosional remnant of the offshore part of the basin without a significant amount of continental siliciclastic input (Kříž 1998b).

The Silurian part of the Prague Basin infill consists of five formations. The herein studied material comes from the upper part of the Motol Formation and the Kopanina Formation, the lower boundary of which coincides with base of the Ludlow. The upper part of the Motol (Homerian, Wenlock) and the lower part of the Kopanina (Gorstian, Ludlow) formations consist of volcano-sedimentary and shale dominated facies. Volcanic activity formed several bathymetric highs of a largely submarine volcanic archipelago with shallow-water domains surrounded by off-shore laminites (Kříž 1998b). The largest volcano, the Svatý Jan Volcanic Centre, occasionally reached above the sea level as documented by subaerial basalts, plant remains and spores occurring in sediments close to the island shore (Kříž 1992; Bek et al. 2022). A basalt sheet, formed in the lower part of the Kopanina Formation across the Svatý Jan Volcanic Centre in the total area of about several square kilometres, emerged above sea level and forms an island from earlier Ludlow until latest Přídolí (Kříž 1998b). Cephalopod fossils are known from several sites, usually from local limestone beds within volcano-sedimentary facies. Several local benthic communities inhabited upper and lower slopes of the volcanic archipelago (Havlíček 1995; Kříž 2008; Mergl 2024) and the cephalopod assemblages are also differentiated (ŠM unpublished data). Cephalopod limestones are recurrent, time-specific facies, consisting of skeletal accumulations of current-oriented cephalopod shells; the shells were deposited in areas, where the surface currents reach the bottom (Ferretti and Kříž 1995; Kříž 1998a; Histon 2012). Cephalopod limestones form thin beds in distal volcano-sedimentary facies. The cephalopod limestones contains a specific bivalve-dominated benthic community, as well as a specific cephalopod assemblage in the Lundgreni, Nilssoni, and lower and upper Scanicus biozones (Kříž 1998a, 1999; ŠM unpublished data). Shales that deposited in an oxygen depleted environment contain abundant pelagic cephalopods

accompanied by very occasional stray migrants from shallow water environment (Turek 1983; Manda et al. 2019).

The upper part of the Kopanina Formation (Ludfordian, Ludlow) consists of carbonate and shale-dominated facies. The carbonate facies occur on former volcanic bottom highs. The shallow, light-coloured limestones pass basin-ward into grey muddy limestones. The carbonate facies rapidly changes laterally, progradation or flooding of carbonate platforms reflects sea level oscillations and local subsidence or uplift of basinal segments or their parts. The shallow water domains were surrounded by off-shore shales (Kříž 1998b; Manda and Kříž 2006). Cephalopod limestones form up to several meters' thick succession deposited on a distal carbonate platform (Braník type of Ferretti and Kříž 1995). Locally, the cephalopod limestones deposition persisted throughout most of the Ludfordian (Kříž 1998a); the low thickness and faunal succession indicates condensation and a gap in sedimentation in the mid-Ludfordian (Manda and Kříž 2006). Thin beds of cephalopod limestones occur also in the shallow water succession (Kosov type of Ferretti and Kříž 1995). The cephalopod fauna is diverse and most taxa are known from the cephalopod limestones. Cephalopods are missing in the shallow-water subtidal limestones. There is a succession of cephalopod assemblages across the Ludfordian; a distinct assemblage occurs in the Leintwardinensis, Inexpectatus, Kozlowskii, upper Latilobus-balticus and Fragmentalis zones (Kříž 1998a; ŠM unpublished data). The cephalopod faunas of the distal and proximal carbonate facies are different; pelagic and nektonic forms disappear towards the shore (ŠM unpublished data). Off-shore shales contain cephalopod faunas resembling those from the Wenlock and lower Ludlow (e.g., Štorch et al. 2014).

The orientation of graptolite rhabdosomes and cephalopod shells indicate a stable surface current system directed from the south to the northwest, considering present structural position of the Prague Synform (Turek 1983; Ferretti and Kříž 1995). The gradual transition from shallow water limestones to off-shore shales and benthic fauna in shales suggests that the maximum depth of the basin of about 200 metres was attained (e.g., Manda et al. 2019).

Material and methods

The studied material originates mostly from Barrande's (1865–1877) collection. The material from the Motol and the lower part of the Kopanina formations was completed by material collected by the author (ŠM) in the last decades. Field revision of Barrande's (1865–1877) localities enabled precise age determination of historical collections. Specimens from cephalopod limestone of the upper part of the Kopanina Formation come, with the exception of a single new specimen, from Barrande's (1865–1877) localities embracing several sites within the Ludfordian, Ludlow, and lowermost Přídolí strata; the exact age determination is difficult in these specimens. A single, recently collected specimen from the lithologically distinct, light-coloured, rusty cephalopod limestone bed exposed in Koněprusy, Velký vrch (Big Hill) road cut enabled to determine age of specimens from Barrande's (1865–1877) locality Konieprus e2. The studied material is generally well preserved.

The fundamental morphological terminology follows that of Teichert (1964). The terms "exogastric" and "endogastric" are used as defined by Teichert (1964). According to that definition, the endogastric shell has the venter on the concave side. In *Lepidoceras*, the venter is determined by the hyponomic sinus on the concave side of the shell and the dorsal furrow on the convex side of the shell.

The longitudinal lirae on the shell surface of *Lepidoceras* correspond in extent to the distinctly raised growth lines of Pohle et al. (2022). Longitudinal ridges differ from lirae in a raised profile protruding from the surface of the shell; the width of the ridges roughly equals or exceeds their height (Manda and Turek 2025). Pohle et al. (2022) called this sculptural element ribs, but ribs form a number of growth lines or lirae, while longitudinal ridges are a single narrow raised
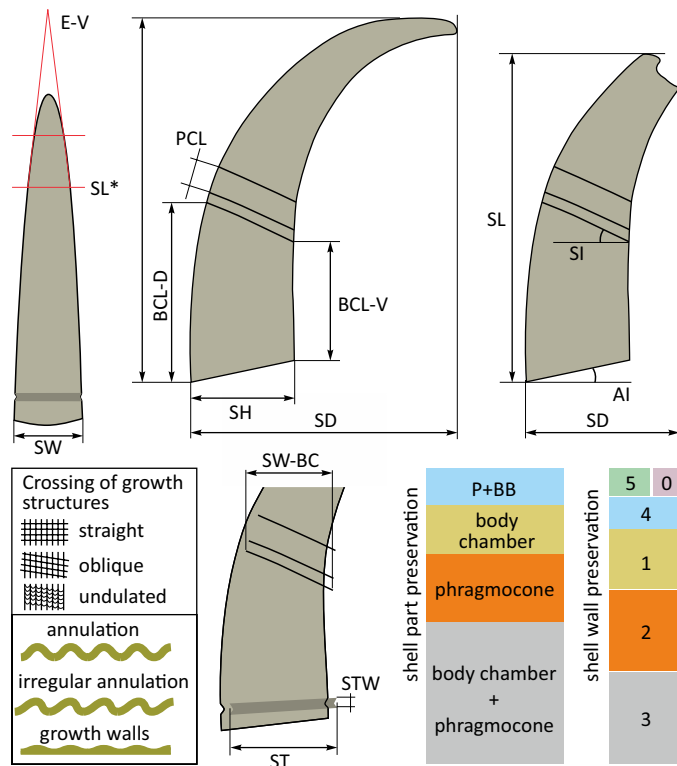

Fig. 1. Schematic drawing explaining the shell morphology of *Lepidoceras lepidum* (Barrande, 1866); the diagrams in the right lower corner show proportional representation of shell parts and shell wall preservation in the material studied; for categories see Material and methods. Abbreviations: AI, aperture inclination; BCL-D, body chamber length dorsally; BCL-V, body chamber length ventrally; E-V, shell expansion ventrally (in degree); SD, shell diameter; SL, shell length; SL*, shell lenght of complete shell; SH, shell height; SI, suture inclination, P+BB, phragmocone with base of body chamber; PCL, phragmocone chamber length; ST, shell wall thickening at aperture, shell height position of maximal thickening; STW, shell wall thickening width; SW, maximum shell width; SW-BC, shell width at the base of the body chamber. All dimensions in mm.

Table 1. Inventory numbers (type specimens in bold), locality, age, measurements and taphonomic characteristic of *Lepidoceras lepidum*. Abbreviations: AI, aperture inclination (in degrees); AP, aperture; B, body chamber; BB, base of the body chamber; BCL-D, body chamber length dorsally; BCL-V, body chamber length ventrally; E-L, shell expansion laterally (in degree); E-V, shell expansion ventrally (in degree); n, not observed; nd, not developed; NL, number of longitudinal lirae/ridges around shell circumference; P, phragmocone; p, present; SC, septal crowding; SD, shell diameter; SH, maximum shell height; SH-BC, shell height at the base of the body chamber; SI, suture inclination (in degrees); SL, shell length; SP, shell preservation; SR, shell repair; ST, shell wall thickening at aperture, shell height position of maximal thickening; STW, shell wall thickening width; SW, maximum shell width; SW-BC, shell width at the base of the body chamber; un, unmeasurable.

Specimen	Locality	Age	SP	SL	SD	SH	SW	BCL-D	BCL-V	SH-BC	SW-BC	E-L	E-V	AP	NL	SI	AI	ST	STW	SC	SR
NM L 646	Butovice	Nilssoni	P+BB	30.9	18	9.8	9.8					9	15		42	4				?	p
NM L 647	Butovice	Nilssoni	P+B	20.6	15	7.2	7.2	11	8.2	5.4	5.4	8	13	p		8		nd	nd	?	p
NM L 13820	Lochkov	Ludfordian	P+BB	33.1	30.4	11.3	11.3					10	8							?	p
NM L 13821	Vohrada	Ludfordian	P+BB	37.0	17	10.0				10			11							?	p
NM L 13822	Butovice	Nilssoni	P+B	37.9	17.2		11.2		15		11		9	p				11	2.6	?	n
NM L 13823	Butovice	Nilssoni	P+B	36.2	19.5	11.9	11.9	18	16	11	11	8	13	p		17.5		12	2.1	p	n
NM L 13824	Butovice	Nilssoni	P+B	51.9	13	11	10.8	19				7	8	p				10	1.9	?	n
NM L 15381	Lochkov	Ludfordian	P+B	59.9	13	11.9		20.6		9.2		5		p				11	1.2	?	n
NM L 15382	Kozel	Lundgreni	P+B	46.0	11.9	11.9	11.9	20.2	18.5	8.9	8.9	10	10	p		7.2		12	1.8	p	n
NM L 15385	Butovice	Nilssoni	P+B	42.0	11.4	9.8	9.8	17.1	15	8.9	8.9	8	6	p	28	14	2	9.2	2.1	p	p
NM L 63557	Kozel	Lundgreni	P+BB	30.9	8.9	7	7			7	7	10								?	p
NM L 63559	Butovice	Nilssoni	P+B	37.3	13.0	11.6	11.2	20	18	10.9	10.1	7	9	p	35			11	3.8	nd	p
NM L 63560	Lochkov	Ludfordian	P	31.0	17	12						14	16		42					?	n
NM L 63562	Vyskočilka	Lundgreni	P+B	44.9		10	9.9			8.80	8.8	10	16		42	16.5				?	n
NM L 63563	Butovice	Nilssoni	P+BB	21.7	10.1	8.1	8.1			7	7	17	18			16				?	n
NM L 63564	Butovice	Nilssoni	P+B	29.8	11.9		7.9	9.7		6.5	6	10	10	p		11		nd	nd	nd	n
NM L 63566	Butovice	Nilssoni	P+BB	32.0	15.0	8.6	8.5			8.6	8.5	10				17				nd	n
NM L 63567	Butovice	Nilssoni	P+B	35.4	16.9	12.9	12.9	19.6	13.8	11.1	11.1	13	13	p	34			nd	nd	nd	n
NM L 63568	Butovice	Nilssoni	P+B	45.0	10.4	9.8	9.8	20	17	8.1	8	7	7	p	45		4	9.7	2.5	?	n
NM L 63569	Konieprus	Ludfordian	P	27.9	22.0	12	10.1						17							?	n
NM L 63570	Kosorz	Ludfordian	P	32.2	17.0	10.5	10.5					14	13			4				nd	n
NM L 63571	Butovice	Nilssoni	P+B	39.0	19	10.4	10.4	14.1	11.1	10.1	10.1	11	15	p		18	5	10	0.9	?	n
NM L 63572	Butovice	Nilssoni	P	31.9	9.3	9	9			9	9	12	16		38	14.3				?	n
NM L 63573	Butovice	Nilssoni	P	22.6	12.2	8.2	8						14							?	n
NM L 63574	Kozel	Lundgreni	P+B	30.0	12.0	12	12	21.2	19.9	9	9			p	30	2	4	nd	nd	?	n
NM L 63575	Butovice	Nilssoni	B	18.0	10.0	10	10	18	14	7.9	7.8	13	13	p		21	10	nd	nd	?	n
NM L 63576	Butovice	Nilssoni	P+B	26.8	10.2	10.9	10.9			10	10	13	13		42	10				nd	n
NM L 63577	Butovice	Nilssoni	P+BB	25.8	17.5	7.1	7			7.1	7	14	15		52					nd	n
NM L 63578	Butovice	Nilssoni	P+B	21.9	8.4	7.4	7.4	9.9	8	6.9	6.9	17	13	p		16	2	nd	nd	nd	n
NM L 63579	Butovice	Nilssoni	P+BB	25.0		8.4	8.2					14	10		43					?	n
NM L 63580	Butovice	Nilssoni	P	16.0	7.6	5	3					15	15		40					?	n
NM L 63581	?Ischadites pit	Lundgreni	B	32.0	16.2	16		31	27.9	11.70	11	16	13	p	60	7.5		nd	nd	?	n
NM L 63582	Kozel	Nilssoni	B	25.6			9.5	25.6	23									nd	nd	?	n
NM L 63583	Kozel	Lundgreni	P+B	41.0	11.5	10.3	10.3	17.8	16.1	8.9	8.6	8	7.5	p			7	9.9	1	?	n
NM L 63584	Butovice	Nilssoni	P+B	26.1	10.2	9.9	9.8	16.9	11.3	7.6	7.6	9	8	p	40	14		9.3	2	nd	p
NM L 63585	Butovice	Nilssoni	P+B	37.9	14	12	11.1	24		9	8.4	9	10	p	37	12.6	9	11	3.4	nd	n
NM L 63586	Butovice	Nilssoni	P	28.1	8	7.1	7.1					12	14		46					?	n
NM L 63587	unknown	Ludfordian	P	25.0	14	8.9														nd	n

Specimen	Locality	Age	SP	SL	SD	SH	SW	BCL-D	BCL-V	SH-BC	SW-BC	E-L	E-V	AP	NL	SI	AI	ST	STW	SC	SR
NM L 63588	unknown	Ludfordian	P	25.0	22	10	10					11	11		45					nd	n
NM L 63589	unknown	Ludfordian	P+BB	29.1	13.6	10.8	9.8					16	15		39					?	n
NM L 63591	?Kozel	Lundgreni	P+B	42.6	11.1	11.1	10.9		17.2	9.2	8.8	9	9	p	31			11	1.7	?	p
NM L 63592	Kozel	Nilssoni	P	21.1	8.4	7.3	7.3					15	13							?	n
MCZ 132450	Butovice	Nilssoni	P+B	33	30.1	12.8	12.8	17.1	15	10.9	10.9	10	7	p	46	11		12	2.8	nd	n
MCZ 162299	Bubovice	Lundgreni	P+B	31.9	9.6	9.4	9.2	13.3	12.4	7	6.8	10	10	p	29	16	0	nd	nd	nd	p
CGS SM 197	Butovice	Nilssoni	P+B	34.1	9.8	7.9	7.7	13.3	12	7.1	6.9	11	9	p	39			nd	nd	?	n
CGS SM 450	Lištice 759, bn. 2A	Lundgreni	B	14.2		8	7	13	12.1	6.1	5.9		9	p	34			nd	nd	?	n
CGS SM 454	Butovice	Nilssoni	P	18.9	20.3		6.5			6.2		17	17		37					?	n
CGS SM 455	Lištice 759, bn. 2A	Lundgreni	B	32.0		15.7	15.6	30.2	26.1	10.9		12	10	p		13	8	16	2.6	?	p
CGS SM 461	Lištice 759, bn. 2A	Lundgreni	B	25.0		14.7	13.1	24.2			10.4		8	p						?	n
CGS SM 462	Lištice 759, bn. 2A	Lundgreni	B	26.4		14.3		26.2	25.1	11	10.9	9	8	p		5				?	n
CGS SM 463	Lištice 759, bn. 2A	Lundgreni	P	25.0		11.1	11.1					9			24	7				nd	n
CGS SM 464	Bubovice	Nilssoni	P+B	31.0	12.2	11.5	11											un	un	p	n

sculptural element on which no other sculptural element can be distinguished (Fig. 1). Longitudinal lirae can turn into ridges during shell growth. The transverse thickening of the shell wall that is not expressed on the internal mould is termed growth walls. Teichert (1964) also considered growth walls to be a less common type of annulation, but the distinction between the growth walls and annulation is useful for describing the ontogeny of sculpture. Pohle et al. (2022: appendix 1: 2) referred to growth walls by the term ribs, but in ammonites and nautilids the term ribs usually corresponds to what is called annulation in orthoceratoids. Therefore, the use of the term rib in orthoceratoids is confusing.

It is difficult to express the degree of curvature of the *Lepidoceras* shell because the apical part of the shell is preserved only exceptionally. The curvature of the shell is expressed here by the ratio of the shell diameter (SD) to the shell height (SH); this ratio is lower than it would be in completely preserved shells. In curved shells, the shell diameter equals shell height plus the projected distance to the apex. The main measured parameters are shown in Fig. 1, measurements are listed in Table 1.

The terminology of muscle scars follows Sweet (1959), Teichert (1964), and King and Evans (2019), while the terminology of annular elevation is after Mutvei (1957) and Mutvei et al. (1993).

The classification of shell repairs, minor, moderate, massive, is adopted from Bond and Sounders (1989). Minor damages span one to five growth lines (depending on spacing), but extend for only a short distance laterally. The repair is recorded in only a few growth lines immediately succeeding the injury. Moderate damages penetrate as much as 15% of the aperture. Such damages were probably somewhat traumatic, in that they would have required localized dedication of the mantle to generate repair, but the activity of the organism was probably not otherwise affected. Massive damages

probably represent traumatic events to the living organism, because a substantial portion of the animal's soft parts would have been exposed (for details see Bond and Sounders 1989: 418, 419). The proportion of preserved shell wall is expressed in six categories (0–5), where 0 represents the internal mould and 5 the fully preserved shell. The intermediate four categories include shell wall preserved to one-quarter (1, 25%), one-half (2, 50%), or three-quarters (3, 75%) of the preserved surface; category 4 includes individuals with shell preserved between three-quarters and fully preserved shell wall.

We recognize here four basic categories of shell preservation: body chamber + phragmocone, isolated phragmocone, isolated body chamber, phragmocone + base of the body chamber. Complete shell consists of a phragmocone with tip of apex and body chamber with preserved aperture. The number of specimens in each category indicates the degree of shell fragmentation. For each specimen, the preservation of aperture is indicated. The preserved aperture indicates that the specimen died in this growth stage. This is an implication for mortality in palaeopopopulations, i.e., proportionally high number of juvenile specimens with preserved aperture indicates high mortality of juveniles.

Graptolite biozone chart is used as defined by Štorch (2023).

Systematic palaeontology

Subclass Orthoceratoidea Teichert, 1967

Order Orthoceratida Kuhn, 1940

Family Dawsonoceratidae Flower, 1962

Genus *Lepidoceras* nov.

Zoobank LSID: urn:lsid:zoobank.org:act:47BD78E7-F127-48E5-8B91-152D0A55557A.

Type species: *Cyrtoceras lepidum* Barrande, 1866, Silurian of Bohemia; monotypic.

Etymology: The genus name is derived from the species name of the type species, lepidum meaning pleasant in Latin.

Diagnosis.—As for the type species, by monotypy.

Remarks.—The shell morphology of *Lepidoceras* corresponds to diagnostic features of the family Dawsonoceratidae as emended by Kröger and Isakar (2006). The presence of annulation is one of the typical characters of the Dawsonoceratidae. However, intraspecific variation exists in the type species of the genotype *Dawsonoceras annulatum* (Sowerby, 1818). In addition, annulation may be well developed, suppressed or eventually entirely missing in the evolutionarily younger representatives (*Dawsonoceras obsoletum* Barrande, 1874, in Horný 1956) from the Prague Basin (Barrande 1874; Horný 1956; Manda and Turek 2015, 2024). The annulation in *Lepidoceras* is usually developed in a short segment of juvenile shells but an indication of annulation may also occur in later ontogenetic stages. The changing distance of growth lines in the early shell of *Lepidoceras* and occasionally also in later stages resembles a similar pattern observed in the annulated shell of dawsonoceratids (Manda and Turek 2024). A reduction/suppression of annulation is a newly acquired character of *Lepidoceras*.

Dzik (1984) suggested a phyletic link between *Cyrtoceras lepidum* Barrande, 1866 (here the type species of *Lepidoceras* gen. nov.) and the pseudorthoceratid *Lyecoceras* Mutvei, 1957, but the comparison of the muscle scars and embryonic shells in the species of *Lyecoceras* (Mutvei 1957) and *L. lepidum* rules such a link out.

Lepidoceras differs from the very similar genus *Serpaglioceras* Gnoli & Serventi, 2008 (middle Silurian of the peri-Gondwana, Carnic Alps) in having a thinner siphuncle with less expanded connecting rings, short septal necks, and poorly developed annulation. Another similar orthoceratid, the Silurian *Metaspyroceras* Foerste, 1932 (Laurentia, northeast USA), differs from *Lepidoceras* in having well-developed annulation running obliquely to the sutures and a slightly constricted aperture. Many species were assigned to the genus *Metaspyroceras* in the past, but none of them have the similar shell shape and narrowing of the apertural part as the type species; the genus *Metaspyroceras* is probably monospecific. All three of these genera represent specialized cephalopods with small shells and limited geographic distribution that diverged from the ancestral lineage of dawsonoceratids.

Unlike *Lepidoceras*, the shell of *Calorthoceras* Chen in Chen et al., 1981, is long and slowly expanding, usually straight in the post-juvenile stages. The number of radial ribs increases as the shell grows. The shape of the embryonic shell of *Lepidoceras* corresponds to that of *Calorthoceras* (Ristedt 1968; Manda and Turek 2024). Both taxa share non-constricted, slightly curved, blunt, endogastric or conical embryonic shell. Fine longitudinal lirae appear already in the embryonic stage and pass into more pronounced ridges in the juvenile stage. *Lepidoceras* and *Calorthoceras* share well developed longitudinal ridges, the number of which markedly varies. In both genera, the reticulate sculpture is also variable, i.e., the distance of growth lines changes, forming growth sequences with densely and sparsely packed growth lines. In both genera, longitudinal ridges are occasionally intercalated with fine longitudinal lirae. *Lepidoceras* probably diverged from *Calorthoceras*.

The shell apex of *Lepidoceras* resembles the apical part of *Kionoceras* Hyatt, 1884, from which it is distinguished by the thinner siphuncle, the smooth non-accretion initial shell and the constant number of undifferentiated radial ridges. The shell cross section in *Lepidoceras* is never polygonal and the annular elevation is narrow. Both genera are endogastric, and in *Kionoceras* there are also specimens with a variably curved shell, especially in the apical part (Barrande 1868). The early stages of *Kionoceras* and *Lepidoceras* probably competitively filled the same niche as the juvenile stages of nautilids (Manda and Turek 2019). *Lepidoceras* and *Kionoceras* co-occur at all localities of the upper Wenlock and lower Ludlow strata, but *Kionoceras* is more widespread in this interval and its record is more continuous, which indicates *Lepidoceras* might have been a specialist.

Stratigraphic and geographic range.—Upper Wenlock (Homerian)–upper Ludlow (Ludfordian) of Prague Basin (Bohemia).

Lepidoceras lepidum (Barrande, 1866)

Figs. 2–9.

1866 *Cyrtoceras lepidum* Barr.; Barrande 1866: pl. 157: 31–34, pl. 168: 1–11.
1866 *Cyrtoceras acies* Barr.; Barrande 1866: pl. 168: 12–15.
1866 *Cyrtoceras fragile* Barr.; Barrande 1866: pl. 168: 16–21.
1867 *Cyrtoceras lepidum* Barr.; Barrande 1867: 637, 638.
1867 *Cyrtoceras fragile* Barr.; Barrande 1867: 636.
1867 *Cyrtoceras acies* Barr.; Barrande 1867: 473.
1868 *Orthoceras mimus* Barr.; Barrande 1868: pl. 279: 9–16.
1874 *Orthoceras mimus* Barr.; Barrande 1874: 202, 203.
1984 *Cyrtoceras lepidum* Barrande; Dzik 1984: 125, 127, fig. 49.

Type material: Lectotype of *Cyrtoceras lepidum* Barrande, 1866, designated herein: NM L 646, Butovitz (Barrande 1866: pl. 157: 31–33; refigured here as Fig. 5A). Paralectotypes: NM L 647, Butovitz (Barrande 1866: pl. 157: 34); NM L 13820, Lochkov (Barrande 1866: pl. 168: 1–3; refigured here as Fig. 2F); NM L 13821, Vohrada (Barrande 1866: pl. 157: 4–5); NM L 13822, Butovitz (Barrande 1866: pl. 157: 6–9); NM L 13823, Butovitz (Barrande 1866: pl. 157: 9, 10). Types of *O. mimus* Barrande, 1868: NM L 15384, Kozel (Barrande 1868: pl. 279: 15, 16; refigured here as Fig. 3B), NM L 15381, Lochkov (Barrande 1868: pl. 279: 9, 10); NM L 15382, Kozel (Barrande 1868: pl. 279: 11; refigured here as Fig. 3A); NM L 15383, Kozel (Barrande 1868: pl. 279: 12; refigured here as Fig. 3C); NM L 15384, Kozel (Barrande 1868: pl. 279: 13). All from Silurian of the Prague Basin, Czech Republic.

Type locality: Czech Republic, Central Bohemia, Praha-Butovice, Na břekvici (Butovitz).

Type horizon: Middle Nilssoni Zone, Gorstian, Ludlow, Kopanina Formation.

Material.—Seventy-four specimens (including type material): NM L 646, 647, 13820–13824, 15381–15385, 63557, 63559–63589, 63591, 63592, 63652, 63655, 63657; MCZ
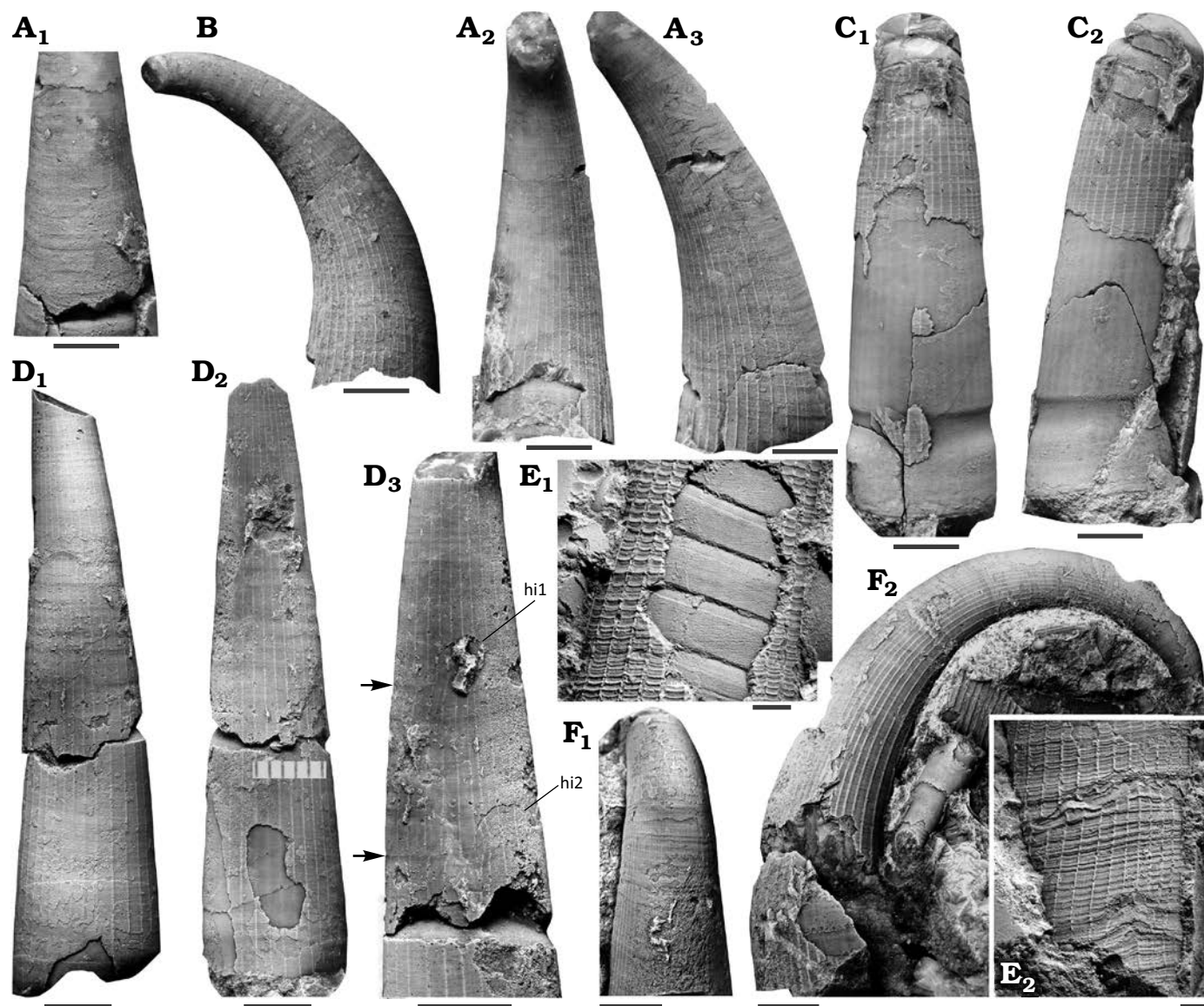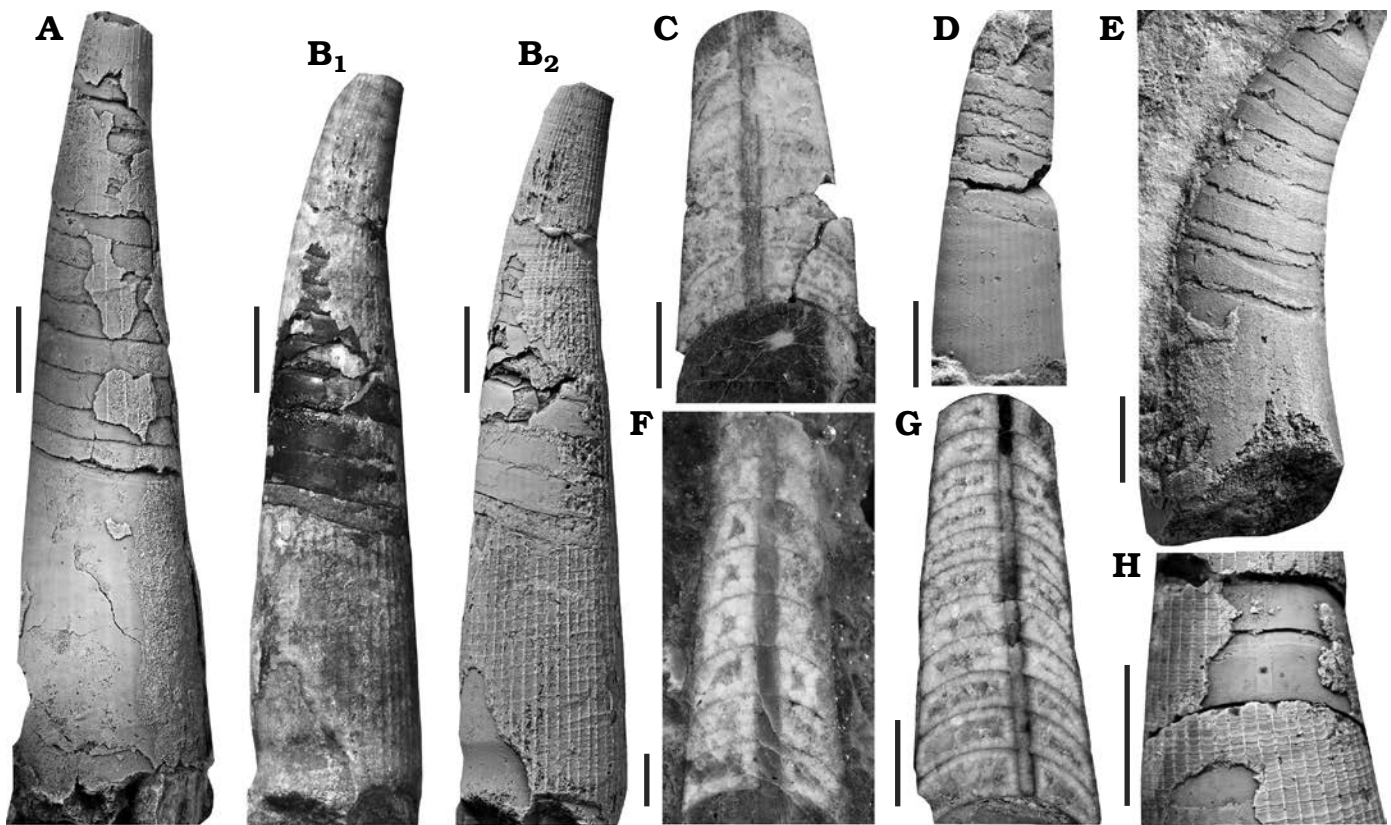
Fig. 2. General morphology of the orthoceratid cephalopod *Lepidoceras lepidum* (Barrande, 1866), Silurian of the Prague Basin (Czech Republic, Central Bohemia), Motol (D) and Kopanina (A–C, E, F) formations. **A**. NM L 63589, locality unknown (SW part of Praha), Ludfordian, Ludlow, dorsal (A_1, see reduced longitudinal lines dorsally), ventral (A_2) and lateral (A_3) views. **B**. NM L 63588, locality unknown (SW part of Praha), Ludfordian, Ludlow, lateral view (see Fig. 10C). **C**. NM L 63585, Praha-Butovice, Na břekvici, Nilssoni Zone, Gorstian, Ludlow, dorsal (C_1) and lateral (C_2) views. **D**. NM L 63591, Kozel (i.e., Lištice 759), Lundgreni Zone, Homerian, Wenlock, lateral (D_1), dorsal (D_2), and dorsolateral (D_3) views, two healed repairs h1, h2, arrows indicate the position of repairs on the shell edge. **E**. MCZ 11009 (see also Fig. 7B), Praha-Butovice, Na břekvici, Nilssoni Zone, Gorstian, Ludlow, lateral view, a detail showing wrinkle structure on internal mould (E_1) and two massive healed repairs close to the aperture (E_2). **F**. Most curved specimen, NM L 13820, paratype (Barrande 1866: pl. 168: 1–3), Praha-Lochkov, Ludfordian, Ludlow, apical-dorsal (F_1) and lateral (F_2) view. All specimens coated with ammonium chloride. Scale bars 5 mm.

11009, 132450, 162299; CGS SM 197, 446–466, all from upper Wenlock (Homerian)–upper Ludlow (Ludfordian) of Central Bohemia, Czech Republic (for localities see chapter Stratigraphic and geographic range).

Four categories of preservation are recognised. Relatively complete shells with broken apex represent 48% of the specimens (n = 29). Isolated phragmocones make up 23% (N = 22) of the studied shells. Phragmocones with preserved base of the body chamber and isolated body chambers are less frequent, 17% (n = 9) and 13% (n = 6) of all specimens, respectively (Fig. 1). The aperture is preserved in more than

half of the studied shells. The shell wall is usually well preserved, nearly half of the studied shells retained more than half of the shell wall with visible sculpture.

Emended diagnosis.—Orthoceratid with variously curved endogastric shell, cross section circular or slightly compressed. Apex gradually expanding without constriction, longitudinal lirae appear already on the embryonic shell. Body chamber short. Sculpture variable, consists of a combination of longitudinal lirae/ridges and growth lines/ridges; the distance of longitudinal elements is higher than that of transversal elements. Annulation either not developed, or

Fig. 3. Orthoceratid cephalopod *Lepidoceras lepidum* (Barrande, 1866), Silurian of the Prague Basin (Czech Republic, Central Bohemia), Motol (A, C, D, F) and Kopanina (B, E, G, H) formations. **A**. NM L 15382, paralectotype (*Orthoceras mimus*, Barrande 1868, pl. 279: 11), Kozel (i.e., Lištice 759), Lundgreni Zone, Homerian, Wenlock, lateral view. **B**. NM L 15385, type (*Orthoceras mimus* Barrande, 1868: pl. 279: 15, 16), Praha-Butovice, Na břekvici, Nilssoni Zone, Gorstian, Ludlow, lateral view (uncoated and coated with ammonium chloride). **C**. NM L 15383, type (*Orthoceras mimus*, Barrande 1868: pl. 279: 12), Kozel (i.e., Lištice 759), Lundgreni Zone, Homerian, Wenlock, lateral median section, left side. **D**. CGS SM 452, Lištice 759 (bed no 2a), Lundgreni Zone, Homerian, Wenlock, lateral median section, right side. **E**. NM L 63578, Praha-Butovice, Na břekvici, Nilssoni Zone, Gorstian, Ludlow, lateral view. **F**. CGS SM 455, Lištice 759 bed no 2a), Lundgreni Zone, Homerian, Wenlock, lateral median section, right side. **G**. CGS SM 464, Praha-Butovice, Na břekvici (bed no 10), Nilssoni Zone, Gorstian, Ludlow, lateral view. **H**. NM L 63584, Praha-Butovice, Na břekvici, Nilssoni Zone, Gorstian, Ludlow, dorsal view. All specimens coated with ammonium chloride, except for B_1, C, F, G. Scale bars 5 mm, except F 1 mm.

slightly indicated or restricted to the early juvenile stage. Siphuncle subcentral, thin, tubular, shifted ventrally, septal necks cyrtochoanitic. Colour pattern irregular with prevailing undulated, transverse bands.

Description.—The shell is endogastric, very slightly to strongly curved (Fig. 2); the ratio of shell diameter/shell height is 8–30.4 (median 13, n = 42). The shell is more curved dorsally than ventrally. The shell expansion is variable, usually decreases with shell growth. The angle of expansion (laterally) ranges from 5° to 17° (median 10°). The ventral angle of expansion varies from 6° to 18° (median 11°). The angle of expansion is the same laterally and dorso-ventrally in less than one third of the specimens (n = 13); the number of shells expanding more rapidly dorso-ventrally or laterally is equal; the maximum difference in lateral and ventral expansions in the same specimen is 6°. The ratio of the shell height at the aperture and the shell height at the body chamber base ranges from 1 to 1.4 (median 1.2, n = 32).

The shell wall is thin. It consists of the wrinkle layer (Fig. $2E_1$), nacreous layer and delicate outer prismatic layer; the maximum shell thickness is 0.3 mm. The wrinkle struc-

tures are very delicate, anastomosing, with about 12 ridges per millimetre; the wrinkles are perpendicular to the shell axis and oblique to the suture (Fig. $3E_1$). The outer shell layer is commonly exfoliated giving the shell a smooth look (e.g., Fig. $5B_2$). The shell cross section is circular or very slightly compressed, Barrande's (1866) form *Cyrtoceras acies* (Barrande, 1866).

The siphuncle is circular in cross section, thin, subcentral and shifts towards the venter during ontogeny (Fig. 3C, F, G). The ratio between the diameter of the siphuncle and the shell height and is about 0.1. The thin-walled connecting rings are very slightly convex, more vaulted dorsally. The septal necks are cyrtochoanitic. Intrasiphonal deposits are unknown. Phragmocone chambers are short; the chamber length is three to five times lower than the respective shell height. The last chamber may be shortened. The chamber length in the early growth stage is relatively longer than in the later growth stages. Cameral deposits are unknown. Septa are moderately concave with the maximum depth sub-centrally, slightly shifted towards the dorsum. The mural part of the septum is short. The dorsal furrow on con-
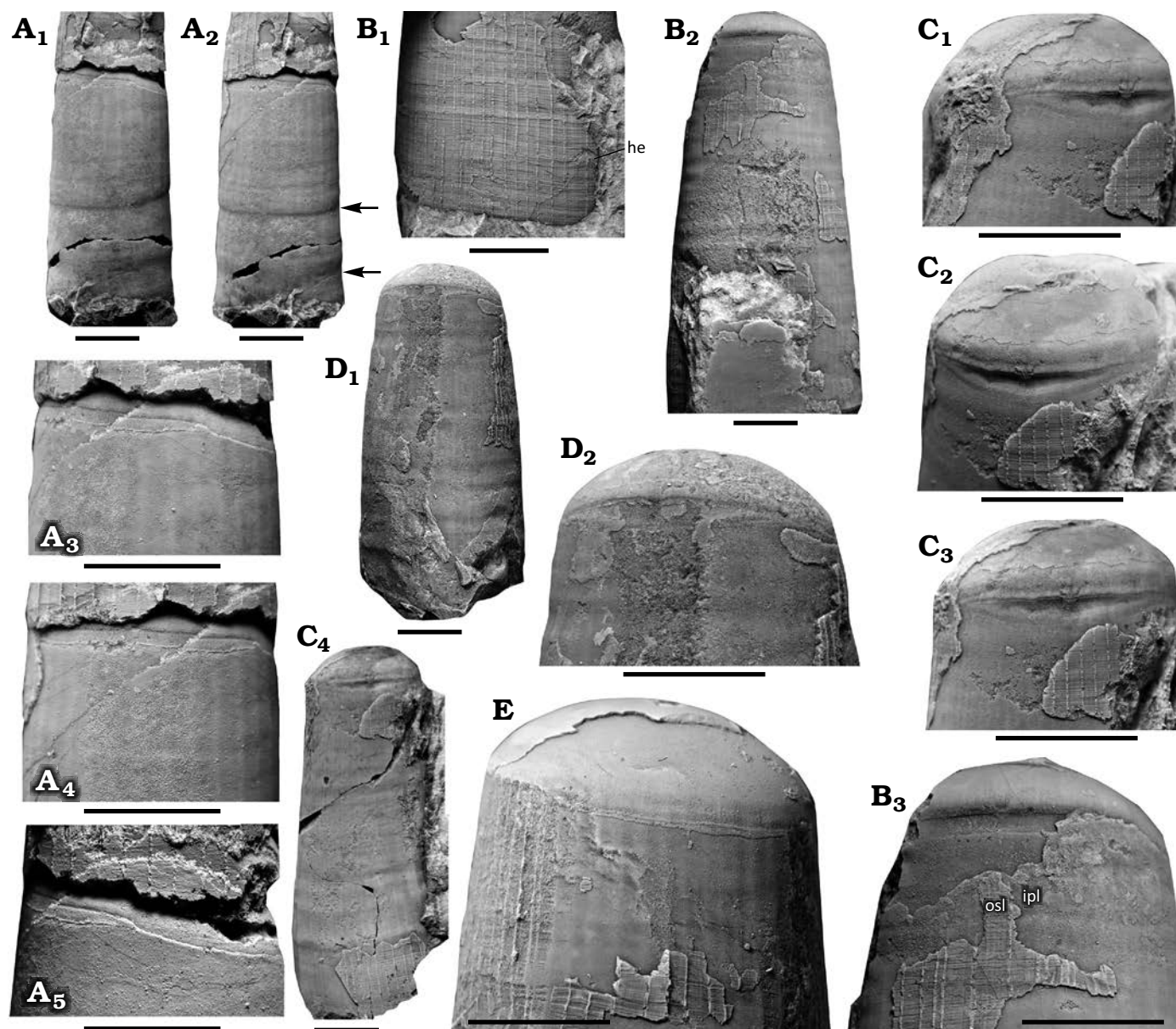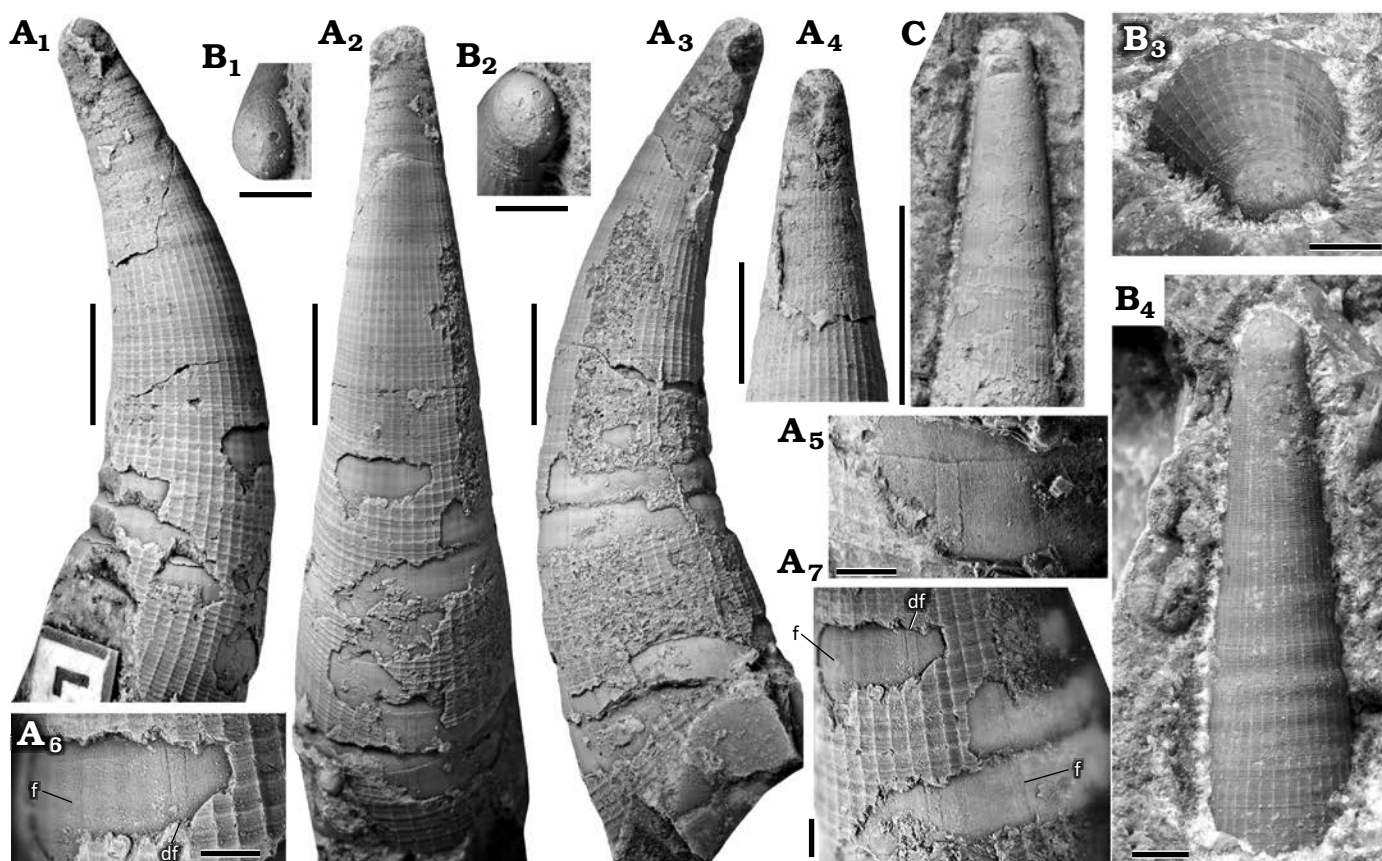
Fig. 4. Muscle scars of the orthoceratid cephalopod *Lepidoceras lepidum* (Barrande, 1866), Silurian of the Prague Basin (Czech Republic, Central Bohemia), Motol Formation; Kozel (A, C) and Lištice 759, bed no 2a (B, D, E), Lundgreni Zone, Homerian, Wenlock. **A**. NM L 63583, lateral (A_1) and dorsal (A_2) views, detail of muscle scars laterally (A_3), dorsolaterally (A_4) and ventrolaterally (A_5); arrows indicate two shell wall thickenings. **B**. CGS SM 463, dorsal view (B_2), detail of muscle scars (B_3) and ventrolateral detail of aperture (B_1) showing hyponomic sinus; osl (outer shell layer), ipl (inner shell layer). **C**. NM L 63582, detail of muscle scars, dorsolateral (C_1) and dorsal (C_2, C_3). **D**. CGS SM 458, dorsal view (D_1) and detail of muscle scars (D_2). **E**. CGS SM 461, ventrolateral detail of muscle scars. All specimens coated with ammonium chloride. Scale bars 5 mm.

vex shell side is straight, formed by two parallel lines, in apex the furrow is very narrow, later the furrow width is about 1/13 of the shell width. The ventral furrow was not observed. Sutures are straight, oblique, with an angle of inclination between 2° and 21°, the median is 13° (angle of inclination increases with increasing curvature). A dorsal shallow lobe can be indicated in the early stage (Fig. 6A).

The body chamber is short. The ratio between dorsal and ventral body chamber length ranges from 1 to 1.5 (median 1.1 which is also the most common value found in 13 specimens; n = 22). The ratio between the body chamber length (dorsally) and the shell height is 1.4–2 (median 1.7,

n = 25). The length of the body chamber increases linearly during ontogeny. The shell wall thickening is parallel to the aperture. The aperture is oblique, inclined dorsally with an angle of 2–11°. The hyponomic sinus, if present, is wide and very shallow. The annular elevation of the orthoceratomorph type is situated around the base of the body chamber (Fig. 4). Ventrally, the elevation is narrow and its width slightly fluctuates. The width of the elevation increases dorsally and reaches its maximum mid-dorsally; in one specimen, the width increases mid-ventrally (Fig. 5E). A shallow lobe may be developed mid-dorsally in the adoral band of the elevation. The adapical margin of the elevation is slightly bent

Fig. 5. Juvenile shell of the orthoceratid cephalopod *Lepidoceras lepidum* (Barrande, 1866), Silurian of the Prague Basin (Czech Republic, Central Bohemia), Motol (D) and Kopanina (A–C) formations. **A**. NM L 646, lectotype (Barrande 1868, pl. 157: 31–34), left lateral (A_1), dorsal (A_2), right lateral (A_3), ventral (A_4) view, details (A_5–A_7) of the dorsal furrows (df) and two parallel furrows (f), Praha-Butovice, Na břekvici, Nilssoni Zone, Gorstian, Ludlow. **B**. NM L 63657 (see Fig. 8B), apical (slightly inclined towards the dorsal side B_1, ventral side B_2 and lateral side B_3) and lateral view (B_4), Tachlovice, Prostřední mlýn, section 713, Nilssoni Zone. Gorstian, Ludlow, **C**. CGS SM 466 (see Fig. 7E), lateral view, Praha-Butovice, Na břekvici (bed no 10), Nilssoni Zone, Gorstian, Ludlow, lateral view. All specimens coated with ammonium chloride. Scale bars 5 mm, except A_5–A_7, B, 1 mm.

towards the aperture at the contact with the dorsal furrow, or perhaps in one case towards the apex. The maximum width of the elevation is ca. 1.1 mm. The onset of the widening of the elevation varies from dorsolateral to ventrolateral. The widening of the elevation is either abrupt, or gradual towards the middle of the dorsal side. The elevation bears a pair of retractor muscle impressions separated in the middle of the dorsal side by a narrow crest. The retractor scars disappear between the dorsolateral and ventrolateral side.

The reticulate sculpture is highly variable. It consists of a combination of longitudinal lirae/ridges and the usually more densely spaced and less distinct transversal growth lines and ridges. Their crossing is straight and perpendicular, straight and oblique, or undulating (U-shaped growth ridges intercalated between longitudinal elements). The number of longitudinal ridges around the entire circumference of the shell varies between 24 and 60 (n = 29, Q1: 34, median: 39, Q3: 42.5). Their number is retained during the whole shell growth. Sometimes one or several finer longitudinal ridges are intercalated between the more distinct ridges. The longitudinal ridges can be suppressed or disappear dorsally in the subadult-adult shell, e.g., in some Ludfordian specimens (Fig. 2F) of *Cyrtoceras fragile* Barrande, 1866. The

density and prominence of growth ridges varies markedly. During growth, the shell portions with more or less distinct growth structures are sometimes present. Low, transversal growth walls or annuli can be developed in any post-juvenile growth stage of the shell. Typically, four growth walls in the shell portion close to the apex are developed.

The smooth initial portion of the shell at the tip of the apex is slightly elliptical, dorsoventrally elongated with the maximum length of about 1 mm (Figs. 5, 6). There is a relief fold at the margin of the initial shell and growth lines and fine longitudinal ridges appear concentrically around the smooth initial shell area. The apical part of the shell is conical or slightly curved. The dimensions and morphological changes are summarised in Table 2. The shape of the shell apex and sculpture varies within a small range. A short part of the shell with four, more or less elaborate growth walls is usually present in the apical part of the shell; in one specimen the walls are missing (Fig. 6C).

The shell colouration has been observed in six specimens, where it is present over the entire surface in all ontogenetic stages. The colour pattern is irregular, bilaterally asymmetrical and different in each specimen. The proportion of pigmented and non-pigmented shell is roughly equal.
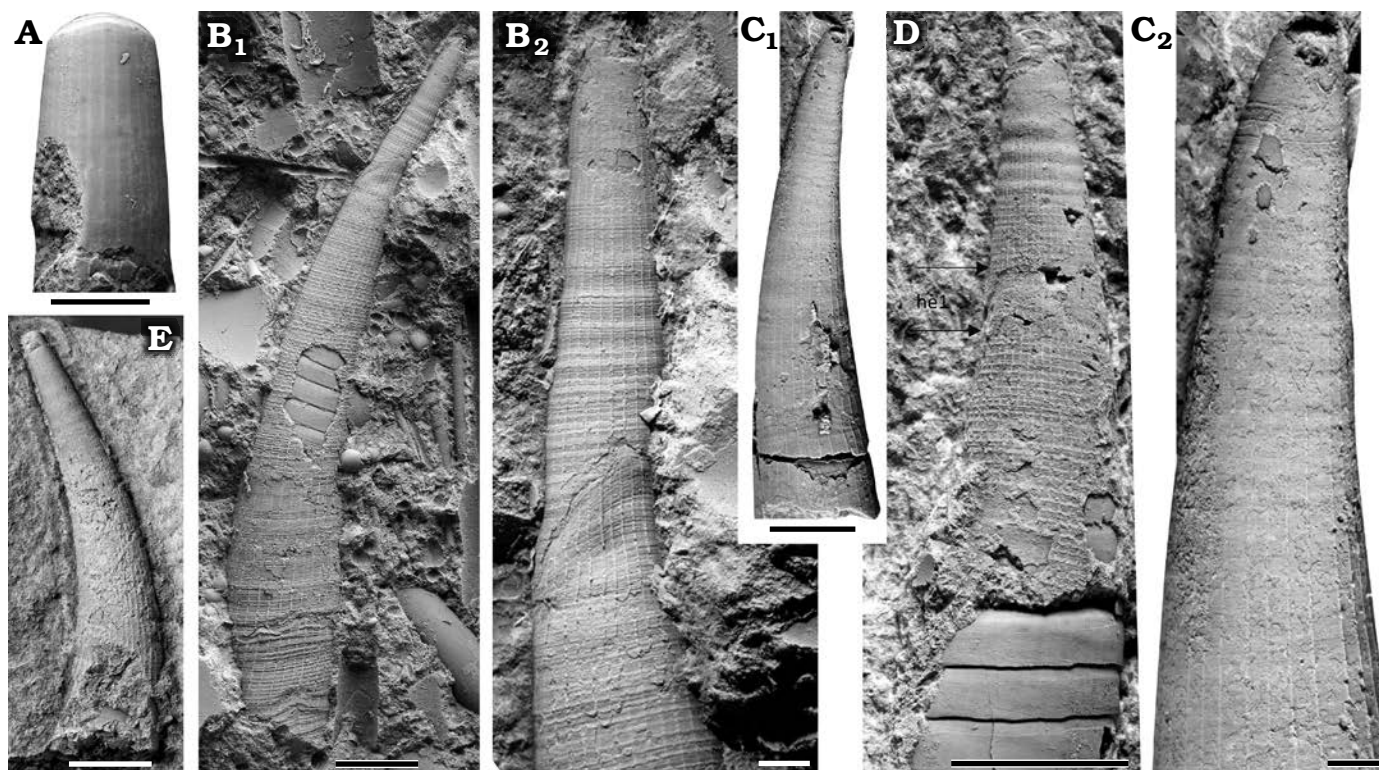
Fig. 6. Juvenile shell of the orthoceratid cephalopod *Lepidoceras lepidum* (Barrande, 1866), Silurian of the Prague Basin (Czech Republic, Central Bohemia), Kozel (i.e., Lištice 759), Lundgreni Zone, Homerian, Wenlock, Motol Formation (A, C) and Praha-Butovice, Na břekvici, Nilssoni Zone, Gorstian, Ludlow, Kopanina Formation (B, D, E). **A**. CGS SM450, dorsal view of a juvenile body chamber, longitudinal ridges already expressed on the internal mould. **B**. MCZ 11009, lateral view (B$_1$) and detail of the apex (B$_2$). **C**. NM L 63557, lateral view (C$_1$) and detail of the apex (C$_2$), see also Fig. 3E. **D**. NM L 63655, lateral view. **E**. CGS SM 466, lateral view (see Fig 6B). All specimens coated with ammonium chloride. Scale bars 5 mm, except B$_2$, C$_2$, 1 mm.

Table 2. Dimensions (in mm) and morphology of a juvenile of *Lepidoceras lepidum*. Abbreviations: AE, angle of expansion; DI, diameter of initial shell laterally; SD, shell diameter; SH, shell height, SH1: at SL 2 mm, SH2: at SL 4 mm, SH3: at SL 6 mm; SL, shell length.

| Specimen	SL	SH	SD	DI	AE	SH1	SH2	SH3	Sudden changes in morphology
MCZ 11009 Butovice	44	6.4	14.6	1.07	6°	1.7	1.77	2.07	1. appearance of growth lines and longitudinal lirae; SH: 1.34; SL: 0.44 2. strengthening of growth lines, number of lines per millimetre decreases from 28 to 13; SH: 1.76; SL: 2.89 3. appearance of growth walls; SH: 1.78; SL: 4.16 (four walls) 4. disappearance of growth walls; SH: 2.07; SL: 6.38
NM L 63655 Butovice	26.63	6.25	8.25	≤1.6	10.8°	≥1.94	≥2.38	≥2.86	1. appearance of growth walls; SH: 2.38; SL: ≤3.38 (four walls) 2. disappearance of growth walls, strengthening of growth lines; SH: 3.13; SL: 6.75
NM L 646 Butovice	30.9	15	18	≤2	13°	≥3.07	≥3.49	≥4.13	1. appearance of growth walls; SH: 3.2; SL: ≤4.8 (four faint growth walls) 2. increasing shell expansion (ventr), strengthening of growth lines; SH: 4.47; SL: ≤8.93 3. disappearance of growth walls, appearance of hyponomic sinus; SH: 4.8; SL: ≤10.27
NM L 63657 Tachlovice	9.9	2.62	2.62	1.06	10°	1.51	1.89	2.28	1. appearance of growth walls, strengthening of growth lines, decreasing spacing of growth lines; SH: 2.4; SL: 5 (four walls) 2. disappearance of growth walls; SH: 2.54; SL: 7.48
NM L 63557 Kozel	30.9	7	8.9	1.31	22°	2.03	2.63	2.86	1. appearance of longitudinal lirae ventrally; SH: 0.18; SL: 1.25 2. appearance of irregular growth lines dorsally; SH: 1.9; SL: 1.37 3. appearance of regular growth lines; SH: 2.26; SL: 2.3 4. decreasing expansion (to 11°), appearance of longitudinal lirae all around the shell, fide of growth lines; SH: 2.34; SL: 2.68 5. strengthening of growth lines; SH: 2.68; SL: 4.9
CGS SM 461 Butovice	22.8	6	13	≥1	10.9	1.5	1.9	2.4	1. appearance of faint growth walls; SH: 2.2; SL: 5 (four walls) 2. disappearance of growth walls, a break in shell curve, strengthening of growth sculpture; SH: 2.6; SL: 7.2
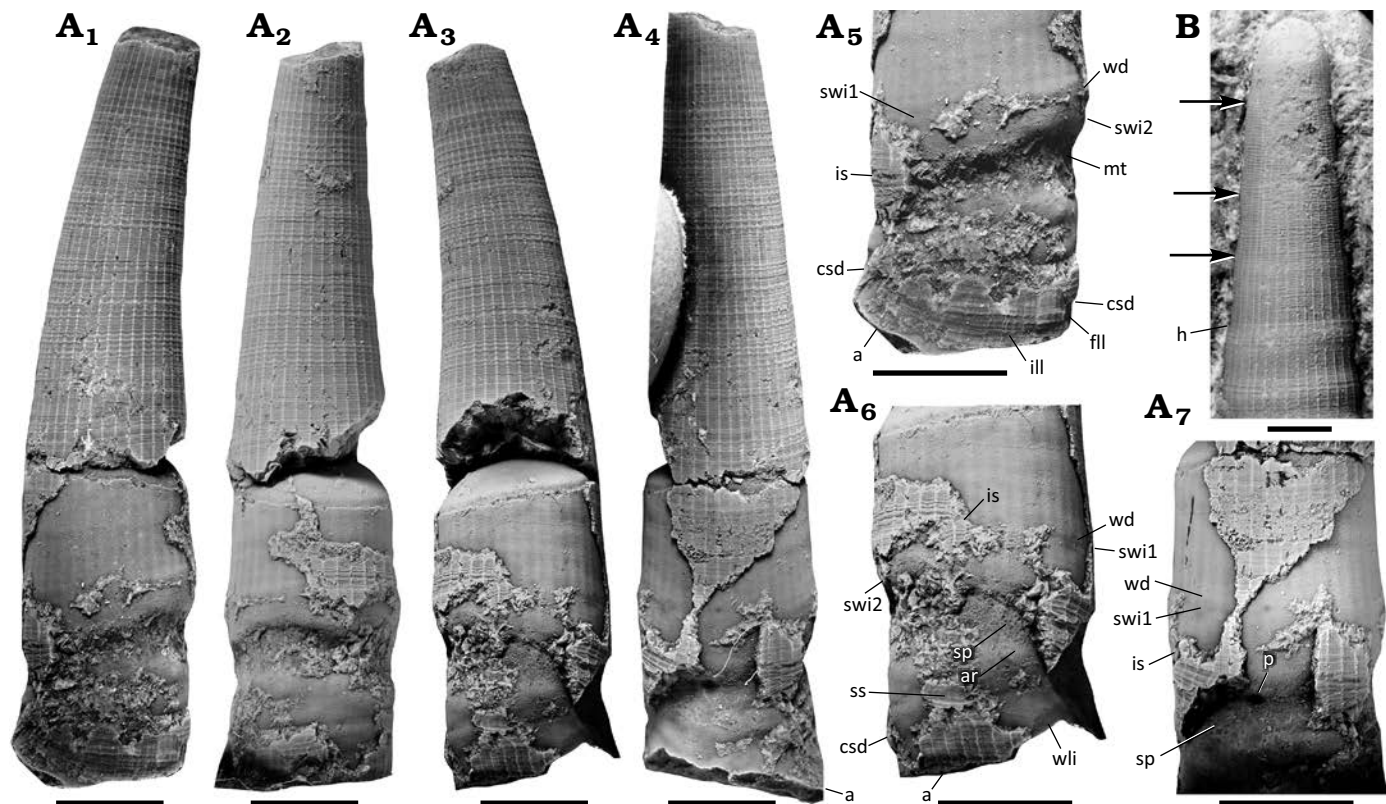
Fig. 7. Shell pathology in the orthoceratid cephalopod *Lepidoceras lepidum* (Barrande, 1866), Silurian of the Prague Basin (Czech Republic, Central Bohemia), Praha-Butovice, Na břekvici (A) and Prostřední mlýn, section 713 (B), Nilssoni Zone, Gorstian, Ludlow, Kopanina Formation. **A**. CGS SM 197, right lateral (A_1, A_5), ventral (A_2), left lateral (A_3, A_6), and dorsal (A_4, A_7) views, complete specimens and marked details. Abbreviations: a, aperture; ar, anastomosing ridges close to small pits; csd, changing shell growth direction at the aperture; fll, zone with several fine longitudinal lirae of second order intercalated between two adjacent first order lines; ill, irregular undulated growth of longitudinal lirae; is, irregular sculpture appearance; mt, maximum shell thickness; p, pit; sp, small pits; ss, anomalous smooth sculpture; swi1, slightly increased thickness of shell wall; swi2, rapidly increased thickness of the shell wall; wli, wrinkle layer indication in pathologic shell; wd, disappearance of wrinkle layer and traces of longitudinal ridges on internal mould. **B**. NM L 63657, detail of the shell apex with irregular growth lines indicated by arrows, dorsal side, appearance of growth wall corresponds to hatching (h) (see Fig. 6B). All specimens coated with ammonium chloride. Scale bars 5 mm.

Irregular and poorly distinguishable spots are seen on one juvenile shell (Fig. 10E). The post-juvenile part of the shell shows irregular transverse colour bands of variable width. Changes in band width are more pronounced in weakly curved shells (Fig. 9B, D, E) than in more curved shells with a more regular colour pattern (Fig. 9A, C). Transverse bands are occasionally connected by longitudinal or transverse pigmented zones. In one case, the dorsal strips are joined to form a broad longitudinal stripe flanked laterally by a longitudinal narrow, nonpigmented zone (Fig. 9C₁).

Remarks.—The vast majority of the studied specimens come from two localities in Praha-Butovice: Na břekvici section 584 and Beroun-Lištice section 579, where the species occurs in a thin part of the section consisting of a few beds. The shell preservation (no encrustation and corrosion, very fine preservation of delicate growth structures) indicates a rather rapid deposition at both sites. The relatively high intraspecific variation of the species thus rather reflects a variability of palaeopopulations than an effect of condensation in the sedimentary record.

Barrande (1866–1874) recognised four species, which are all synonymised herein. *Orthoceras mimus* and *Cyrtoceras*

lepidum differ in the shell form. The former species possesses a slightly curved shell and the latter one a more curved shell. However, there is continuous transition in the shell form between both co-occurring taxa. *Cyrtoceras acies* differs from the co-occurring *C. mimus* in having a slightly laterally compressed shell in the post-juvenile growth stage. However, this only represents the extreme case of subcircular cross section visible in several studied specimens (Table 1). *Cyrtoceras fragile* differs from *C. lepidum* by the suppression and eventual disappearance of longitudinal ridges on the dorsal side of the adult growth stage. This feature is slightly developed in more specimens from the upper Ludlow and is considered an intraspecific variation of evolutionarily younger populations.

Stratigraphic and geographic range.—Most of the studied specimens come from historical collections; the localities where the presence of the species has been recently confirmed are indicated below by an asterisk.

Motol Formation, Wenlock, Homerian, Lundgreni Biozone: Praha-Řeporyje, Arethusina Gorge, NW slope, section 687*, lower part of the biozone (a bed of cephalopod limestone embedded in shale, Kříž et al. 1993), SE slope
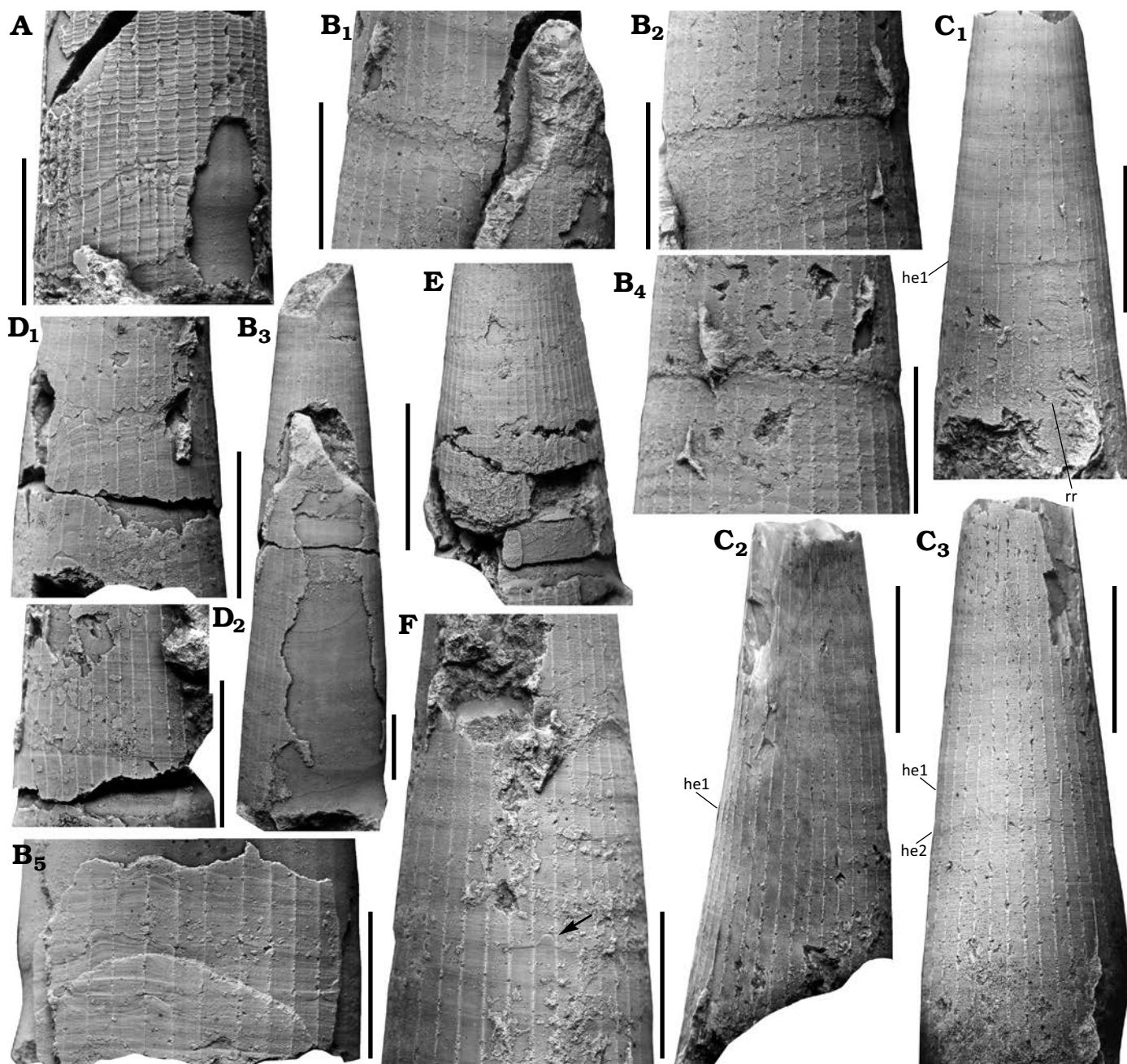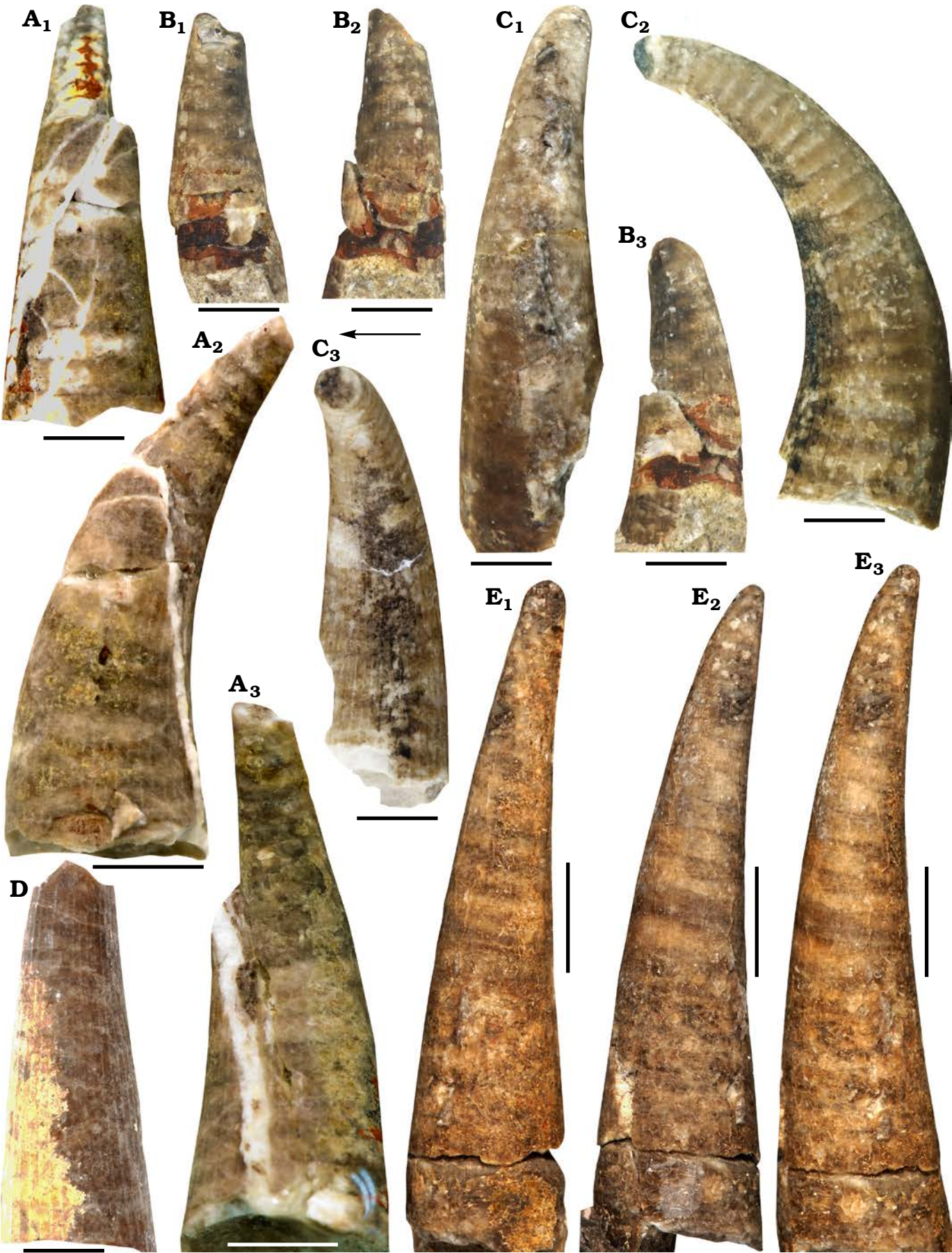
Fig. 8. Healed shell repairs in the orthoceratid cephalopod *Lepidoceras lepidum* (Barrande, 1866), Silurian of the Prague Basin (Czech Republic, Central Bohemia), Kozel, Lundgreni Zone, Homerian, Wenlock, Motol Formation (C, D) and Praha-Butovice, Na břekvici, Nilssoni Zone, Gorstian, Ludlow, Kopanina Formation (A, B, E, F). **A**. NM L 63584, ventrolateral view. **B**. NM L 63559, dorsal view (B$_3$) and details of a shell repair around the shell circumference in right lateral (B$_1$), left lateral (B$_2$), and ventral (B$_4$) views and of several repairs close to the aperture (B$_5$). **C**. NM L 63592, dorsal (C$_1$), lateral (C$_2$), and ventral (C$_3$) views; rr (reduction of longitudinal ridges after massive shell injury), he1, 2 (two healed repairs). **D**. NM L 63557, lateral (D$_1$) and dorsal (D$_2$) views. **E**. NM L 63586, dorsal view. **F**. NM L 63577, ventrolateral view, arrow indicates a small injury. All specimens coated with ammonium chloride. Scale bars 5 mm, except B$_3$, 10 mm.

of the gorge, upper part of the biozone (limestone beds with *Aulacopleura*, after Prantl 1936). Barrande's locality Bubovitz (Bubovice, exact site unknown, skeletal limestone, Havlíček 1995). Beroun-Lištice, U cestičky, section 759*, Barrande's locality Kozel (skeletal limestones; Kříž 1992; Manda 1996). Beroun-Lištice, Herinky, Barrande's pit*, limestone with *Plicocyrtia* Community and overlaying tuffites (Havlíček 1995). Barrande's locality Lodenitz

(Loděnice, Špičatý vrch-Černidla, Ischadites pit, skeletal limestone, Kříž 1992). Praha-Malá Chuchle, Vyskočilka locality (Wiskocilka in Barrande, limestone with juvenile molluscs; Vodička and Manda 2019, interval of beds 11 to 19). Tachlovice, Prostřední mlýn, section 713 (Barrande's locality Tachlowitz, skeletal muddy limestone, Kříž et al. 1993).

Lower part of the Kopanina Formation, Gorstian, Ludlow, middle Nilssoni Biozone: Praha-Butovice, Na břekvici

← Fig. 9. Shell coloration in the orthoceratid cephalopod *Lepidoceras lepidum* (Barrande, 1866), Silurian of the Prague Basin (Czech Republic, Central Bohemia), Motol Formation (E) and Kopanina Formation (A–D). **A**. NM L 63587, locality unknown (SW part of Praha), Ludfordian, Ludlow, dorsal (A_1), lateral (A_2), and ventrolateral (A_3) views. **B**. NM L 63586, Praha-Butovice, Na břekvici, Nilssoni Zone, Gorstian, Ludlow, lateral (B_1), dorsal (B_2), and ventral (B_3) views. **C**. NM L 63588 (see Fig. 3B), locality unknown (SW part of Praha), Ludfordian, Ludlow, dorsal (C_1), lateral (C_2), and ventral (C_3) views. **D**. NM L 63652, Praha-Butovice, Na břekvici, Nilssoni Zone, Gorstian, Ludlow, lateral view. **E**. NM L 63557 (see Fig. 7C), Kozel (i.e., Lištice 759), Lundgreni Zone, Homerian, Wenlock, dorsolateral (E_1), lateral (E_2), and ventrolateral (E_3) views. Scale bars 5 mm.

section 584*, beds 10, 11 (cephalopod limestone, Kříž et al. 1993, Barrande's locality Butovitz).

Upper part of the Kopanina Formation (the cephalopod limestone biofacies, see Kříž 1998), Ludfordian, Ludlow: historical collection material come from Barrande's (1865–1877) localities Dlauha hora (Beroun, Dlouhá hora), Konieprus* (Koněprusy), Kosorz (Kosoř), Hinter Kopanina (Praha-Zadní Kopanina), Lochkow (Praha-Lochkov), and Wohrada (Praha-Malá Ohrada); *Inexpectatus inexpectatus* Biozone: Koněprusy, road-cut near Velký vrch (light coloured cephalopod limestone).

Results and discussion

Evolutionary path of shell form.—Most orthoceratids, including the stratigraphically oldest species (Evans 2007), have a straight shell and a tubular siphuncle, and are considered to have been pelagic cephalopods (Kröger et al. 2009). Demersal orthoceratids have also evolved and often possessed an annulated shell (Marek 1971; Holland 1984; Manda and Turek 2015). Orthoceratids with a slightly curved shell are relatively common but more strongly curved shells have evolved only rarely (e.g., Dzik 1984; Kröger and Isakar 2006). The best-known case is the Silurian demersal orthoceratid *Cyrtocycloceras* Foerste, 1936, with an annulated, moderately curved shell (Marek 1971). *Lepidoceras* has a stratigraphic range of about seven million years. During that time, populations consisting of specimens with a slightly curved and finally strongly curved shell (Figs. 2, 10) developed. The body chamber/phragmocone ratio is a prominent factor in the shell hydrostatic properties (Petermann et al. 2019). The mode of preservation (fragmentation) does not allow an accurate measurement of the ratio between the length of the phragmocone and the length of the living chamber. However, considering the best-preserved shells, the ratio is about 1.5. The actual length of the phragmocone was probably greater in more curved shells than in slightly curved shells. Unlike the shape of the shell, proportions of the living chamber show very little variance (see ratios shell height at the aperture/shell height at the base of the body chamber, dorsal body chamber length/ventral body chamber length, shell height at the aperture/body chamber length; Table 1, Fig. 11).

Although there has been an increase in the shell curvature of *L. lepidum* throughout Ludlow, there are still specimens with a less curved shell. The question is whether this is a phenotypic (response to the environment) or genetic issue. The Silurian species of *Cyrtocycloceras* from the Prague Basin always have a very similar shell shape, but in this case the shape of the shell determines the swimming pattern, i.e., it allows rocking movement of the shell (Marek 1971). *Cyrtocycloceras ibex* (Sowerby in Murchison, 1839), on the other hand, is characterized by a variable shell curvature (Holland 2007). Similarly, in the related species *Dawsonocerina dulce* (Barrande, 1868) from the Ludlow/Přídolí boundary interval in the Prague Basin, the shell is curved in variable ways (Barrande 1868). For example, the material from about 40 cm thick set of cephalopod limestone beds, Praha-Lochkov, Nad ubikacemi section, contains specimens with straight to moderately curved shells (ŠM unpublished data). *Lepidoceras* exhibits highest variation in shell curving among orthoceratids.

Specimens of *Lepidoceras lepidum* with the most curved shell are convergent in shell form with co-occurring oncocerids with slowly expanding curved shells. This is a case of orthoceratids entering the morphospace usually occupied by
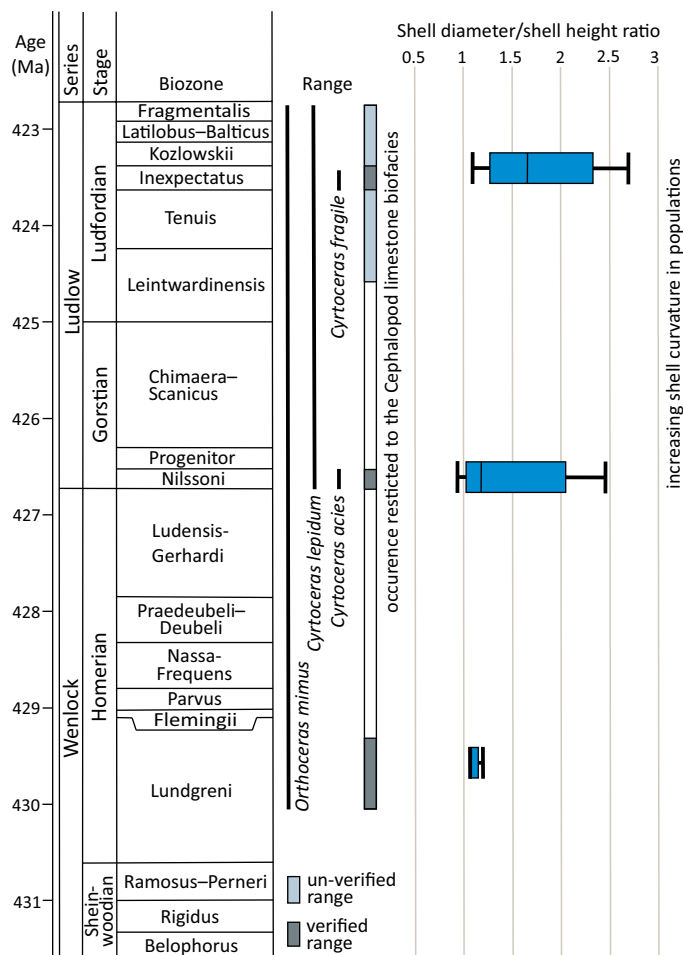

Fig. 10. Range of *Lepidoceras lepidum* (Barrande, 1866) and former Barrande's (1866, 1867) taxa in the Silurian of the Prague Basin and shell diameter/shell height ratio.
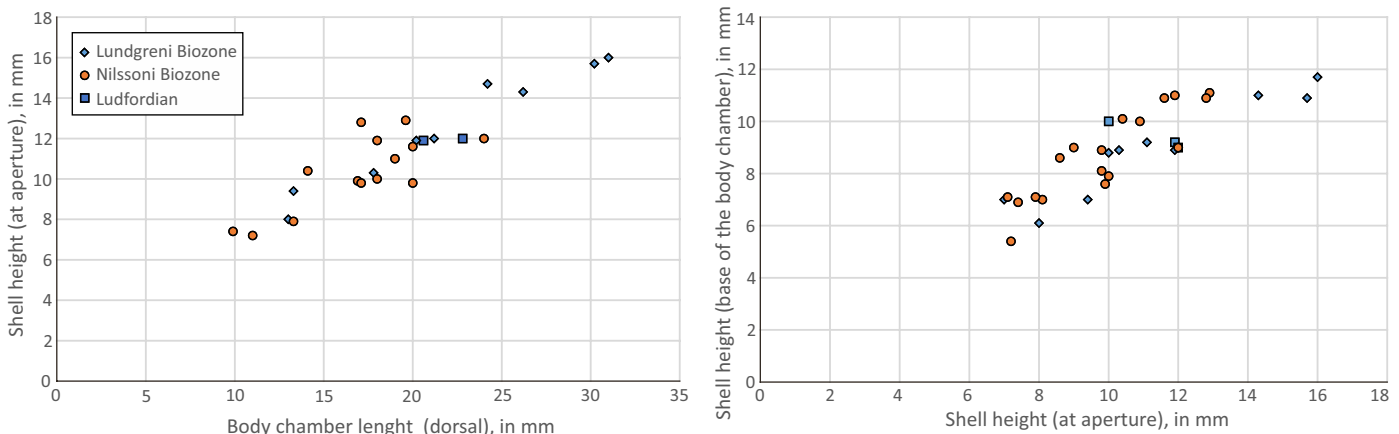
Fig. 11. Ratio of dorsal body chamber length/shell height and shell height/shell height at the base of the body chamber in *Lepidoceras lepidum*.

demersal oncocerids. The limited geographic dispersion of *Lepidoceras lepidum*, along with its locally high abundance in a specific community and its absence in oxygen depleted facies with pelagic fauna also corresponds with the distribution pattern of demersal cephalopods.

Apex, non-accretion initial shell.—The cicatrix region (cicatrix sensu Erben and Flajs 1975), well known in *Nautilus*, represents the initial part of the shell and is formed by secondary calcification of an initial organic plate/disc. Thus, this region does not show growth structures but there is a central bar and grove/s and a relief fold on the margin of cicatrix region (e.g., Arnold et al. 1987; Mutvei and Doguzhaeva 1997). Cicatrix region of similar type is known to have developed in actinocerids (Doguzhaeva et al. 1999; Kröger and Mapes 2007) and pseudorthoceratids where it is one of the diagnostic characters (e.g., Niko et al. 2020; King and Evans 2019). In the present concept, orthoceratids are distinguished from pseudorthoceratids by the absence of cicatrix and radial divisions of annulosiphonate deposits. Somewhat lost in the present discussion is the fact that Ristedt (1971) also described cicatrix in species that are currently classified as orthoceratids (see also Erben and Flajs 1975). Ristedt (1971: 168) described apex of Silurian *Merocycloceras declivis* Ristedt, 1968 "with a large smooth cicatrix area on initial calotte clearly delimited by marginal furrow and growth lines". Ristedt (1971) distinguished several other types of apex tips and non-accretion initial shells without growth lines in orthoceratids ("Schalenanfang" or "Initialkalotte"). For bactritids, Doghuzayeva (2002) used the term primordial dome. However, the smooth apex of the initial chamber encircled by the growth lines, the so-called "bald spot", is also known in Devonian ammonoids (for summary see Klofak et al. 1999). In orthoceratids, the margin of the smooth area may or may not coincide with the relief fold. Unlike the nautilids, however, the orthocerids do not have a central bar. We refer to this non-accretion portion of the shell by the term non-accretion initial shell.

The very tip (initial portion of the shell) of the apex in *Lepidoceras lepidum* is very slightly convex, dorsoventrally elongated, and smooth without any growth structures

(Figs. 5B, 6C). The size of the non-accretion initial shell is variable with a dorsoventral diameter between one and two millimetres (Table 2). Length of the initial shell of *Lepidoceras lepidum* is moderately higher than in closely related *Calorthoceras butovitzense* Chen in Chen et al., 1981 (Manda and Turek 2024). The non-accretion initial shell of the apex is poorly known in orthoceratids probably due to the very small size of the apex and the smooth surface of the juvenile shell in many species. The variable size of the non-accretion initial shell in orthoceratids is consistent with the size variation of cicatrix region in pseudorthoceratids (cf. Blind 1988; Kröger and Mapes 2004) and nautilids.

Early shell form variability.—The understanding of the rate of evolution and intraspecific variation of juvenile orthoceratids is limited by the fact that most juvenile orthoceratids cannot be assigned to species based on specimens in adult/subadult growth stage. In *Lepidoceras lepidum*, juvenile individuals can be unambiguously identified by specific sculpture. The five juvenile specimens available (Table 2; Figs. 5, 6) suggest high variation in shell shape, size and sculpture. The shape and overall dimensions of the embryonic shell in *Lepidoceras lepidum* are not uniform. The embryonic shell is conical and either straight, or slightly endogastrically curved. The annulation on the early juvenile shell is not always developed, and the size of the annuli also varies. Similar shape variability of the embryonic shell is documented (Manda and Turek 2024) in the closely related Silurian orthoceratid *Calorthoceras* Chen in Chen et al., 1981. Generally, the intraspecific variability in embryonic shells of Silurian orthoceratids is poorly known, and there are species for which only moderate variability in the shape and size has been documented (e.g., Serpagli and Gnoli 1977). Kolebaba (1973) described forty forms of orthoceratid embryonic chambers from a very thin bed at a single locality (Praha-Pankrác, upper Lundgreni Zone, lower Homerian, Wenlock), a number far exceeding the number of orthoceratid species known from upper Wenlock of the Prague Basin (ŠM unpublished data). This also suggests a high intraspecific variation in the early shell formation rather than a higher diversity than currently

known and detectable by subadult and adult shells only. The virtual absence of transitional forms between straight conical and curved embryonic shells and between annulated and non-annulated juvenile shells might indicate embryonic shell polymorphism in *Lepidoceras lepidum*. However, the data are still too limited at this point to further evaluate this possibility.

Hatching.—On the *Lepidoceras lepidum* shell, hatching is presumably manifested by a change in sculpture, most commonly by the appearance of annulation (Figs. 5, 6B, D; Table 2). However, the change in sculpture may be very subtle (Fig. 6C).

The shell of a freshly hatched individual of *Lepidoceras lepidum* reached a height (i.e., dorsoventral diameter) of about 2.5 mm and a length between 4–5 mm. Cephalopods with the embryonic shell/egg size of *Lepidoceras lepidum* have been suggested to be planktonic or nektobenthic (e.g., De Baets et al. 2012). Juvenile orthoceratids have so far been considered planktonic (Hewitt 1988; Kröger et al. 2009). In *Lepidoceras*, the shell shape is conical with a relatively large angle of expansion and in one case even resembles the shape of the juvenile shells of oncocerids. Pelagic orthoceratids, on the other hand, have shells with a lower angle of expansion (e.g., Ristedt 1968). The complete juvenile shells of *Lepidoceras lepidum* with preserved body chamber, which document juvenile mortality, are usually found together with adults. In one case, a juvenile shell comes from a locality from which no other *Lepidoceras lepidum* specimen is known. No juvenile *Lepidoceras lepidum* specimens have been found in association with juvenile orthoceratids in oxygen-depleted facies. The demersal mode of life of *Lepidoceras lepidum* juveniles would also correspond to the geographically limited occurrence of the genus so far known only from the Prague Basin. In summary, all indications are that the juveniles were nektobenthic, similar to adults. The shell of the early juvenile stage is usually characterized by four growth walls; a hyponomic sinus develops shortly after the disappearance of the last growth wall.

The juvenile shell of *Lepidoceras lepidum* is one of the largest among orthoceratids and probably the largest among post-Ordovician orthoceratids (Ristedt 1971; Aubrechtová et al. 2020). The size of the embryonic shell, i.e., egg and hatchling, of *Lepidoceras lepidum* moderately increased in comparison with the type species of *Dawsonoceras* (Kröger and Isakar 2006) and *Calorthoceras*, the assumed ancestor of *Lepidoceras* (Manda and Turek 2024). Thus, in *Lepidoceras lepidum*, there is an increase in egg size and a simultaneous decrease in the shell size, including the length of the living chamber, compared to its relatives. This implies a reduction in fertility and an increase in incubation time to a rate comparable to some K-strategy oncocerids. Thus, a correlation between adult shell size and egg size cannot be considered for orthoceratids. *Lepidoceras lepidum* is another indication that the evolution of reproductive strategies in cephalopods is rather complex (see Rocha et al. 2001; Pohle et al. 2020).

Fig. 12. Mature modifications in *Lepidoceras lepidum*, all specimens with preserved aperture included.

Mature modification, adult shell size range, and mortality.—*Lepidoceras lepidum* exhibits three morphological features considered to be mature modifications (Fig. 12): septal approximation, apertural shell thickening (Klug et al. 2015) and eventually the presence of muscle scars (Davis et al. 1996). Septal crowding and shell wall thickening might also result from pathologies (e.g., Hoffmann and Keupp 2015), but there is no indication of such an origin in the material studied here.

Septal crowding was observed in three specimens (Figs. 3A–C, 13). However, it is not present in three specimens with shell thickening. In one case, a shortened phragmocone chamber is followed by a chamber of standard length (Fig. 3E). Documentation of septal approximation in orthoceratids is very limited (e.g., Kröger and Landing 2007; the Middle Ordovician *Gangshanoceras* Zou, 1988). Septal crowding probably occurred in only some individuals and may have been followed by at least one non-shortened phragmocone chamber. Septal crowding itself is therefore
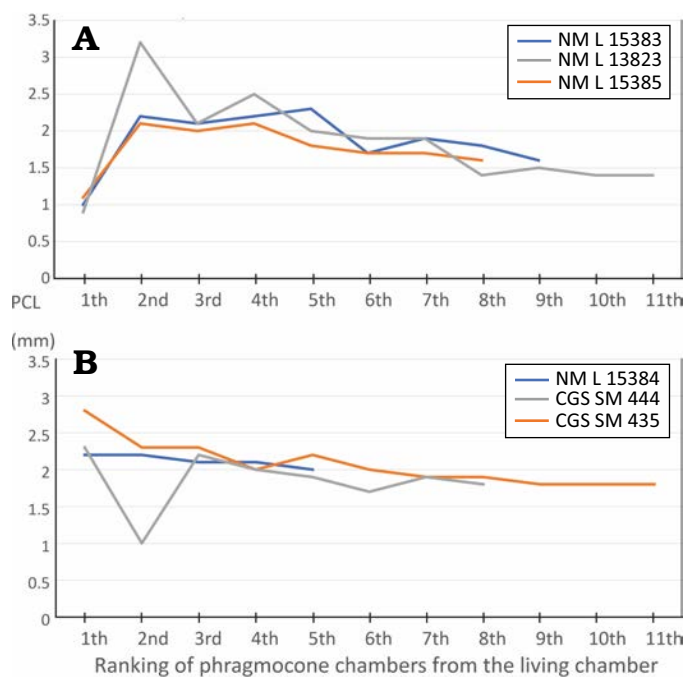
Fig. 13. Distance of septa calculated from last chamber in specimens of *Lepidoceras lepidum* with narrowing of the last chamber (**A**) and in specimens without narrowing of the chamber but with thickening of the shell at the aperture (**B**).

not sufficient to identify the adult growth stage (see Beck et al. 2021).

Shell wall thickening at the aperture was found in shells with a width between 9.2 and 15.6 mm (median 11 mm, n = 16, Table 1). The thickening was found immediately at the apertural edge or at distances of up to 4.2 mm from the apertural margin (Figs. 2D, 3A, B, 12). The width of the thickening varies between 0.9 to 3.8 mm (median 2.1 mm). In one specimen, two wall thickenings were observed in close proximity (Fig. 4A).

There is no general agreement on the preservation of muscle scars being an indicator of maturity, particularly in nautilids (Davis et al. 1996; Klug et al. 2015). Muscle attachment is known in pre-adult stages in oncocerids and discosorids (Barrande 1865–1877; Manda 2008; Manda and Turek 2009a). Muscle scars were observed in five specimens of *Lepidoceras lepidum*, four of which also showed the shell wall thickening (apertures of the other are broken off). The scars were observed only in adult specimens. Muscle scars preservation linked with a fully-grown specimen was observed also in the orthoceratid *Cyrtocycloceras semitectum* (Barrande, 1866) (Marek 1971). There is no known case of retractor muscle imprints in immature orthoceratids. The presence of muscle impressions may therefore indicate maturity in orthoceratids.

Shell wall thickening and septal crowding are not terminal adult modifications but show a degree of flexibility. If they really represent mature modifications and indicate maturity, the difference between the shell height of the smallest mature and the largest mature shell is six millimetres (maximum measured shell height is 15.7 mm). Environmental-

related variation in adult shell size is well known in multiceratoids (e.g., Silurian *Pentameroceras* and *Phragmoceras*; Barrande 1865, Stridsberg 1985, Manda 2008) but has not yet been investigated in orthoceratoids.

Of the thirty shells with preserved aperture (Table 1), nearly all have a shell height above 6 mm. More than half of the specimens fall in the shell height interval 9.6–12.8 mm. Only one shell belongs to a juvenile. Sixteen shells show an adult modification. Overall, this implies relatively low mortality in the populations (Fig. 12). Given the preservation of the shells, significant taphonomic bias can be ruled out.

The shell height (Fig. 1) of the mature shells with preserved aperture varies between 10–16 mm, which indicates the size variability of the fully-grown shell (Fig. 12). Intraspecific variation in shell size is well known in oncocerids (e.g., *Pentameroceras* Hyatt, 1884; Stridsberg 1985) and discosorids (e.g., *Phragmoceras* Broderip in Murchison, 1839; Barrande 1865) with an adult modification (constricted aperture). The smallest specimens can be three times smaller than the largest. *Lepidoceras* is the first orthoceratid with documented variance in the fully-grown shell size (Fig. 12).

Muscle attachment.—In orthoceratids, the annular elevation is developed around the base of the body chamber. It consists of an unpaired (or paired), low anterior lobe (or lobes) on the dorsal side corresponding to unpaired (or paired) retractor imprints (Mutvei 1957, 2002; Marek 1971; Kröger et al. 2005). The development of muscle attachments during ontogeny is unknown and intraspecific variability of muscle scars is poorly known.

Mutvei (1957: text-fig. 7e; 1964: figs. 3c, 6a–c; 2002) pointed out that the retractor muscles in orthoceratids did not form a roof over the ventral mantle cavity as in nautilids and tarphyceratids. The retractor contractions could therefore not have been used to expel water from the mantle cavity to allow jet-powered swimming. Mutvei (2002) also suggested that the area of the orthoceratoid retractor muscle scars relative to the size of the living chamber is often smaller than in *Nautilus* and tarphyceratids. However, the studies of Mutvei (1957, 2002) concern muscle scars in straight orthoceratids with long body chambers. The living chamber of *Lepidoceras lepidum* is relatively short but the annular elevation corresponds to that of orthoceratids with long body chambers. The body chamber of *Lepidoceras lepidum* is conical or slightly curved, its dorsal side is considerably longer that the ventral (oblique, dorsally expanded aperture, inclined septa). The retractor muscles are thus longer than the mantle cavity. The shape of the body chamber and its position in life produced an aperture that was oriented obliquely towards the shorter ventral side. The dorsal retractor muscles were thus relatively close to the ventral side of the mantle cavity. Consequently, the contraction of the retractor muscle expelled water from the mantle cavity more effectively than in the case of straight orthoceratids with a long body chamber. The swimming ability was probably slightly improved in the curved endogastric shell compared to the slowly expanding straight shell. This

may correspond to increasing of the shell curvature in *L. lepidum*. The species also exhibits well developed and relatively broad dorsal furrow, which according to Kröger et al. (2005) represents the most important zone for the attachment of the pallioviseral ligament.

Until now it has been assumed that retractor imprints on the annular elevation are established in a shape that does not change in adults. However, *Lepidoceras* shows an extension of the retractor scars. Retractors on the annular elevation were initially located in the middle of the dorsal side (about a quarter of the circumference of the base of the living chamber) and gradually extended laterally to more than half the circumference of the shell (Fig. 4). The muscle impressions are only known in adults. The growth slowed down upon maturation and the soft body probably remained longer in the same body chamber and became more firmly attached, which resulted in the expansion of the muscle attachment site. The gradual enlargement and lateral extension of the retractors certainly led to an increase in the propulsion efficiency.

We do not question the planktic life style of orthoceratids with a straight shell and a long living chamber (Mutvei 2002; Kröger et al. 2005). *Lepidoceras lepidum* is an example of an orthoceratid in which a change in shell morphology led to an adaptation to a demersal mode of life. The Silurian species of *Cyrtocycloceras* are other examples of a demersal orthoceratids (Marek 1971; Holland 1984) whose muscle scars do not differ in position and development from those of *Lepidoceras lepidum*. However, the well-developed hyponomic sinus of *Cyrtocycloceras* clearly demonstrates a relatively efficient jet propulsion.

Mid-dorsal furrow.—The mid-dorsal furrow is developed on the convex side of the shell of *L. lepidum* and along with the shallow hyponomic sinus on the opposite side demonstrates the endogastric character of the shell (Fig. 3H). Like in other orthoceratids, the mid-dorsal furrow is formed by an interrupted, paired, shallow groove on the internal mould. The furrow width relatively increases slightly during ontogeny and forms an elliptical depression on the inner surface of the shell (second type of preservation of Flower 1939: fig. 2b; Fig. 8E).

In cephalopods, the dorsal furrow originates from the inner part of the calcified shell apex, in line with the inner dorsal termination of the central linear depression of the cicatrix (Schindewolf 1933). The dorsal furrow in orthoceratids originates in the same position in the initial chamber (Ristedt 1971; Kolebaba 1973) and therefore synchronously with the ventral furrow appearing on the opposite side of apex (Chirat and Boletzky 2003; Kröger et al. 2005). In one specimen, morphological structures resembling the dorsal furrow are also developed dorsolaterally on both sides of the dorsal furrow in a symmetrical position (Fig. 5A). One groove is developed on the right side and two closely adjacent grooves are present on the left side. This demonstrates that the conditions leading to the formation of the dorsal furrow may have occasionally partially occurred in a sym-

metrical position at other locations on the margin of the developing initial shell. A parallel morphological structure corresponding to the ventral furrow has also been described in a Silurian oncocerid (Manda and Turek 2009a: fig. 7i).

Shell colouration.—Shell colouration was observed in six out of the 69 specimens retaining the shell wall and is recorded from the entire stratigraphic range of the species (Fig. 9). The colouration in embryonic shells is poorly preserved but in juvenile and adult shells, it is well recorded. This is one of the best documented shell colourations in the Orthoceratoidea.

The colour pattern described in the Ordovician, Silurian and Early Devonian orthoceratoids consists of regular longitudinal bands (Kobluk and Mapes 1989; Kröger et al. 2009; Turek and Manda 2012; Manda and Turek 2015; Kröger and Aubrechtová 2019). Regular chevron pattern appears in the Middle Devonian orthoceratids/pseudorthoceratids and is documented also from the Carboniferous (Kobluk and Mapes 1989). Shell colouration in the form of regular transverse bands is known in a single Carboniferous, flattened, straight specimen (Foerste 1930). Irregular transverse bands are described in a straight shell fragment from the earliest Devonian of the Prague Basin (Turek 2009). However, the taxonomic position of the two latter specimens is uncertain (?Orthoceratida, Pseudorthoceratida, Actinoceratida, Astroviida). The irregular, transversely oblique colour bands in *Lepidoceras lepidum* thus represent the first record of this type of colour pattern in the Orthoceratoidea. The colour pattern of *L. lepidum* corresponds to the shell colouration of some morphologically similar Silurian oncocerids (Turek and Manda 2020; Fig. 14). The moderately irregular trans-
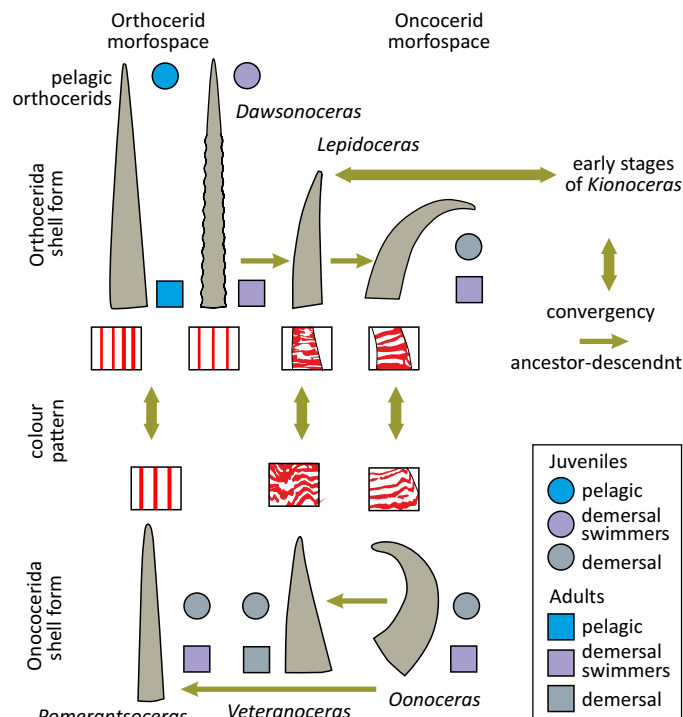

Fig. 14. Convergences in coloration and shell shape between Silurian orthoceratids, oncoceratids, and pseudorthoceratids.

verse colour bands have been observed in the most curved adult shells of *L. lepidum*, as well as in some oncocerids (a more strongly curved shell generally exhibits more regular colour bands that a less curved shell; Turek and Manda 2020). The most irregular colouration is present in slightly curved shells and the embryonic and juvenile shell of *L. lepidum*, which is also a feature observed in some moderately expanded and curved Silurian oncocerids (Turek and Manda 2020). The demersal orthoceratid *Lepidoceras* acquired the shell colouration characteristic of demersal multiceratoids as a result of adaptive convergence. This is the second case of convergence of shell colouration and shell form between orthoceratoids and multiceratoids (Fig. 14). The first case is a Silurian oncocerid with a slowly expanding and moderately curved shell exhibiting longitudinal bands like orthoceratoids (Manda and Turek 2009b).

The course of the colour bands, their width and shape are highly variable in *L. lepidum*, as in some Silurian oncocerids with a slightly curved shell. The variability of the colour pattern in *L. lepidum* is exceptional among Ordovician and Silurian orthoceratoids, which show a low variability of colouration restricted to the number of longitudinal bands and their width. However, the number of orthoceratoids with known colour pattern is limited so far.

Variability in longitudinal sculpture.—Longitudinal sculpture appeared in numerous orthoceratids. The density of longitudinal sculptural elements is often used as a diagnostic character at the genus level, even when only a small number of specimens is available.

Longitudinal ridges were calculated in 29 specimens of *Lepidoceras lepidum*. The number of these elements does not change during ontogeny including embryonic stage. In one case, two longitudinal ridges were lost after a massive, repaired shell damage (Fig. 8C_1). The number of longitudinal ridges varies from 24 to 60 (Fig. 15, Q1 = 34, median = 39, Q3 = 42.5) and shows a unimodal and slightly skewed right distribution, when plotted on a histogram (Fig. 15). Thus, there is a preference for a relatively lower number of longitudinal ridges rather than a higher number. The greatest range in the number of longitudinal lirae/ridges is shown by the upper Wenlock specimens. The average number of longitudinal lirae/ridges increases slightly in the Ludlow compared to the Wenlock. The variability in the number of ribs is smallest in the evolutionarily youngest specimens (Ludfordian, late Ludlow), and the number of ribs corresponds to the average number in preceding populations. The width and height of the longitudinal lirae/ridges is not related to the number of lirae/ridges, so individuals with fewer ridges do not have these elements more pronounced. No correlation was found between the number of longitudinal lirae/ridges and the origin of the respective specimens from shallower or deeper water environments (limestone facies). In summary, the above findings indicate that the number of the longitudinal sculptural elements cannot be considered a reliable diagnostic feature. A variable number of longitu-
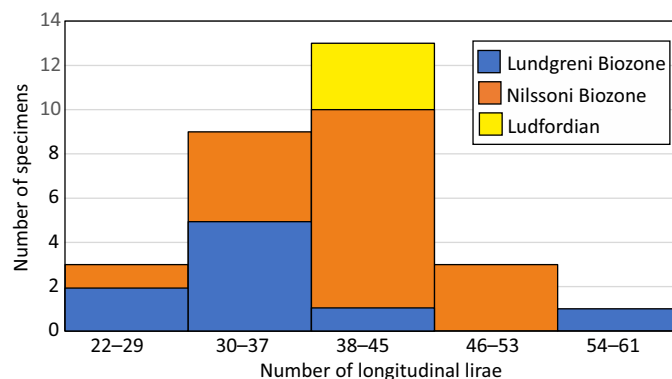

Fig. 15. Number of specimens of *Lepidoceras lepidum* in categories by number of longitudinal lirae.

dinal lirae/ridges has also been documented in the Silurian *Calorthoceras*, where it has been used as a character diagnostic for several species (Chen et al. 1981). However, in the latter genus, the differences in the number of longitudinal lirae/ridges clearly represent intraspecific variation (Manda and Turek 2024).

The appearance of distinct sculpture has been attributed to shell strength improvement, anti-predatory adaptation, shell hydrodynamics refinement, and camouflage (Chamberlain 1993; Barskov 2018; Jaitly et al. 2022). Regardless of its adaptive function, there wasn't a strong selection pressure for a particular number of longitudinal lirae/ridges in *Lepidoceras lepidum*.

Healed shell damages.—A healed shell damage was found in 18 of 74 individuals (23%, Fig. 16, Table 3). Nine specimens had more than one injury. Minor damages were found in ten individuals, moderate in seven and massive in six.

Three types of shell repair were recognised. The first type (Figs. 2E, 8B) is characterised by an interruption of the shell secretion associated with a displacement of longitudinal ridges (number of observed repairs, n = 6). The interruption may be accompanied by a gentle constriction of the shell. The second type (Fig. 8C, E) represents a symmetrical, more or less deep, U-shaped breakage of the shell (n = 19). The third type (Fig. 2F) represents a broad, crested breakout of the shell followed by irregular growth lines gradually filling the breakout (n = 9). The combined shell repair (Figs. 2E, 8C, D) is represented by a combination of the first type with the second or third type (n = 3). One specimen exhibits a specific combined shell repair around the shell circumference manifested as transverse narrow break in the shell secretion with two U-shaped repairs located dorsally and ventrally (Fig. 8C).

Table 3. Quantification of shells with a healed repair in relation to the shell wall preservation.

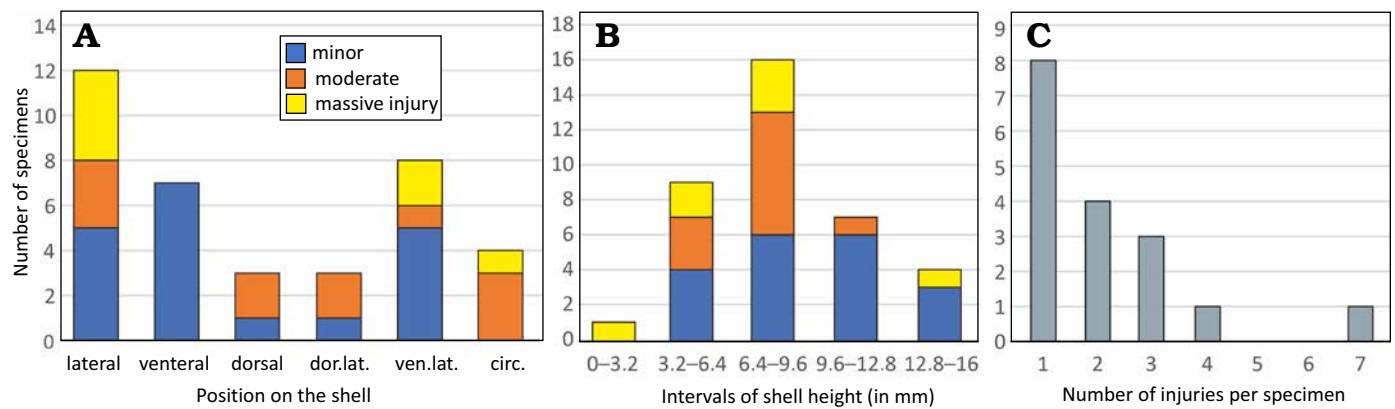| Shell wall preservation category	0	1	2	3	4	5
Number of specimens	3	15	20	23	8	4
Number of specimens with an injury	0	3	3	8	3	0
Specimens with a repair in %	0	20	15	35	38	0
Total number of repairs	0	4	5	17	9	0

Fig. 16. Shell repairs in *Lepidoceras lepidum* related to the position on the shell (**A**), shell height (**B**), and number of specimens with one to seven repairs on the shell (**C**). Abbreviation: circ., circumference; dor.lat, dorsolateral; ven.lat, ventrolateral.

Most healed shells exhibit a single shell damage, number of specimens displaying two, three, or four damages decrease; the exception being the apertural region of one adult specimen, which shows seven damages (Fig. 8E). Multiple massive repairs on the same specimen were not observed.

The distribution of shell damages on the shell surface is difficult interpret. A limited number of shell repairs occur on the dorsal side, while minor damages are most common on the ventral and ventrolateral sides. The types of healed damages found in *L. lepidum* are consistent with those found in other Silurian cephalopods from the Prague Basin and early Paleozoic cephalopods in general (Kröger 2004, 2011; Klug 2007). However, combined shell damages with deeper, narrow breaks on the opposite sides of the shell are rare in the Silurian of the Prague Basin and, if they occur at all, are mainly documented in Přídolí.

The number of damages in relation to the shell height varies. Most damages occur in the 6.4–9.6 mm height interval, while moderate and massive damages are rare as the shell height increases (Fig. 16, Table 3). One specimen (Fig. 6B) possessing extensive healed juvenile damages defines the limits of survival after an extensive shell breakage. This indicates that the maximum tolerated shell loss is about 25%, similar to the modern-day *Nautilus* (Arnold 1985). This is higher than has been previously reported (Kröger 2004) and indicates a high level of survivability even in juveniles. Kröger (2011) concluded that specimens of the Ordovician *Anthoceras* with conch diameters above 30 mm had a considerably lower risk of predation than smaller shells. Yomogida and Wani (2012) suggested a higher risk of fatality by predatory attacks in earlier ontogenetic stages of modern *Nautilus*. Although the shell of *Lepidoceras lepidum* is small, there is a higher frequency of sublethal damages in early ontogenetic stages, and the most serious damages occur in juveniles. The distinct sculpture makes it possible to identify *L. lepidum* even from shell fragments, which are, however, very rare. Thus, there is no evidence for massive crushing of shell of *Lepidoceras lepidum* in the studied section.

Quantification of healed damages is limited by the preservation of the shell wall (Fig. 16, Tables 1, 3). The number of specimens with a damage in the categories 3–5 with more than half of the shell wall preserved is 32% (n = 35), and the categories 0–2 with less than half of the shell wall preserved it is 15% (n = 38). The number of specimens with a shell damage repair in category 3 and 4 is 35% (n = 23) and 38% (n = 8), respectively. Four individuals with a well-preserved shell over the entire surface show no repairs. The total number of individuals with damages was certainly higher than preserved, but there is no indication that it was significantly higher. This is particularly valid for the large damages that can be recognized on the shell relics and often on internal moulds. Given the lack of quantitative data on healed damages in early Paleozoic cephalopods, it is difficult to compare predation rates. However, the proportion of individuals with damages roughly corresponds to that of Ordovician endocerids from the Baltic (Kröger 2011).

A more detailed study of the frequency of damages in different cephalopod groups is prevented by a lack of data, but it is a promising area of research. However, the study of the cephalopod collections from Lištice and Butovice (Na břekvici), i.e., localities with *Lepidoceras lepidum*, indicates that a higher number of damages are observed in demersal cephalopods, whereas healed damages are very rare in pelagic and nektonic cephalopods (e.g., *Sphooceras*; Turek and Manda 2012). No damage has been found on the small shells of the genus *Kionoceras* (i.e., corresponding in size to *Lepidoceras*), which are morphologically similar to *Lepidoceras* at sites where they occur together. However, *Kionoceras* appears to have been a better swimmer which is consistent with its significantly wider geographical distribution. The frequency of healed damages may serve as an indirect evidence of the lifestyle of Silurian cephalopods.

Shell pathologies.—Two specimens with a pathological shell interpreted as a result of parasitic infestation were recognised. One immature shell (Fig. 3D) shows a pathological septum (fourth from the aperture) with the suture slightly curved laterally towards the apex. The sutures of the following septa, which run diagonally to the axis of the shell, are straight. There is a circular depression on the internal mould of the phragmocone chamber following the anom-

alous septum, which may correspond to the pathological pit. A similar case of anomalous septa associated with pits has been described in an oncocerid coming from the same locality (Manda and Turek 2009b) and also in a discosorid from Upper Devonian of Russia (Mironenko 2018). It was considered to be the result of parasite infestation (De Baets et al. 2021). The anomalous course of septa has not yet been described in orthoceratids.

CGS SM 187 (for dimensions see Table 1) is a fully-grown specimen with pathologic development of apertural part of the body chamber showing irregular shell wall thickening with pits (Fig. 7). The shell wall thickness slightly increases around the shell circumference, where the shell is 9.8 mm in length and 8.4 mm in height. On the internal mould, the wrinkle layer and low longitudinal ridges suddenly disappear. This is followed by a sudden increase in the thickness of the shell wall around the entire circumference; the thickening of the shell is irregular with a ventrolateral maximum of almost 2 mm. Subsequently, the shell thickness decreases again adaperturally until it reaches almost the normal thickness. The wrinkle layer is again indicated. The shell axis direction shifts towards the dorsum for a length of about 2.8 mm just at the aperture. The line of a sudden increase in the shell thickness is reflected on the shell surface by an irregular sculpture persisting to the aperture. However, this is not accompanied by a change in shell expansion. The radial ridges and growth lines are irregular and wavy; thin radial lirae appear in some places, while the shell is smooth in others. On the thickened shell there is a large dorsal pit, followed dorsolaterally by small pits; the area of small pits is surrounded by gradually disappearing fine ridges forming an irregular network.

The described specimen CGS SM 187 (Fig. 7) shows one of the most striking pathologies ever described in an early Paleozoic cephalopod shell. The anomalous growth and secretion of the shell is likely a response to an ultimately lethal parasite infestation, probably located between the mantle and the shell (for discussion see De Baets et al. 2021). Pit-like pathologies on internal moulds are known from several Silurian cephalopods but have not yet been recorded in association with a change in sculpture.

Anomalous growth line development was found in one embryonic shell (Fig. 7B). It is manifested by a repeated irregular course of growth lines, their insertion and duplication. The causes of the anomalous sculpture development are uncertain. Similar embryonic shell anomalies have not yet been detected in orthoceratids, but are known in nautilids (Chirat 2001).

The frequency of pathologies in the studied collection shows that some kind of lethal or survivability-reducing pathology caused by parasites affected at most a few percent of the population. The pathologies found on the *Lepidoceras lepidum* shells correspond to those found in multiceratoids and nautilids (see De Baets et al. 2021). So far, the fossil record from the Silurian of the Prague Basin contains pathologies exclusively in demersal cephalopods.

Conclusions

Lepidoceras lepidum is a small endogastric orthoceratid with a prominent reticulate sculpture. From the late Wenlock to the late late Ludlow, there is a tendency for the curvature of the shell to increase. Number of longitudinal ridges did not change during life and there is a prominent intraspecific variation in their number. The distribution pattern and shell morphology of the only species of the genus, *Lepidoceras lepidum* (Barrande, 1866), suggest that it was a specialized demersal cephalopod since hatching.

The embryonic shell reached a height of about 2.5 mm and a length of 4–5 mm and started with non-accretion initial portion of the shell. Its shape varies between straight conical and curved. The hatching is usually manifested by more or less distinct growth walls. There is an increase in egg size and a simultaneous decrease in shell size and length of the body chamber, compared to its relatives. This implies a reduction in fertility and an increase in incubation time to a rate comparable to some K-strategy oncocerids. There is no correlation between body and egg size. Septal crowding and thickening of the apertural margin of the shell wall are adult modifications found. The modifications are not necessarily quite terminal either, but can generally be regarded as indicative of maturity or near-maturity. The adult modifications illustrate a variation in the size of the fully-grown shell which has not been found in orthoceratids before. Orthoceratomorph muscle scars consist of a pair of retractors appears mid-dorsally and gradually expand over half the shell circumference. Longer convex dorsal side and shorter straight ventral side of the body chamber influenced the muscle function, the efficiency of jet propulsion was probably higher than in straight-shelled orthoceratids. The colour pattern consists of irregular transverse bands; this is the first time such a colour pattern has been detected in orthoceratids. Slightly curved shells exhibit irregular colour bands while more curved shells show less irregular bands. This is the second reported case of adaptive convergence between orthoceratids and oncocerids and support for the protective function of colouration.

Shell repairs in *L. lepidum* were quantified with respect to the repair size and position on the shell. In juvenile stage, there is a higher frequency of repairs, especially massive ones. Juveniles were able to survive even extensive shell loss of around 25%. The relatively high frequency of shell repairs probably indirectly illustrates the demersal habit because shell repairs are generally very rare in Silurian pelagic cephalopods. The study of the frequency and extent of shell repair and preliminary examination of co-occurring species points at the possibility of a comparative study of predation marks. However, there is a lack of data on the frequency and extent of cephalopod shell repairs allowing comparisons of individual morphotypes across the early Paleozoic, which should be a part of future research. Pathological shells representing about four percent of available specimens. Anomalous growth of the embryonic shell is described for

the first time in orthoceratids. The morphology and its intraspecific variation in *L. lepidum* is among the best known among orthoceratoids, although the internal structure of the embryonic shell has not been determined. *Lepidoceras lepidum* is a model example of the evolution of a demersal orthocerid known from only one peri-Gondwanan basin over a period of about 5 million years.

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