“An endocochleate experiment” in the Silurian straight-shelled cephalopod *Sphooceras*

VOJTĚCH TUREK & ŠTĚPÁN MANDA

Sphooceras truncatum (Barrande, 1860), a Silurian straight-shelled cephalopod with a short finger-shaped shell, is one of a few cephalopods in which natural truncation of the apical part of the phragmocone from the rest of the conch is confirmed. Periodic natural removal of the apical part of the shell (4 to 5 phragmocone chambers) preceded formation of a terminal callus and a calcareous plug closing the septal foramen. The apical callus probably originated by fusion of the truncation septum with episeptal deposits. These structures temporarily formed the new apex on which two additional calcareous layers had been secreted. A unique specimen preserves a colour pattern in the convex apical region, which proves that the shell in *Sphooceras* was temporarily completely surrounded by mantle extending from the body chamber, *i.e.* the cephalopod was at least temporarily endocochleate. The co-occurrence of different growth stages of *S. truncatum* together with one type of short juvenile orthoceracone shell, with a maximum of eight phragmocone chambers and a very small subglobular initial chamber indicates that these embryonic shells may belong to *Sphooceras*. Two other genera are discussed, both previously included in the family Sphooceratidae: *Disjunctoceras* Gnoli *in* Kiselev, 1992 and *Andigenoceras* Gnoli *in* Kiselev, 1992. The newly discovered thickening of the apex in “*Disjunctoceras*” *disjunctum*, the type species of *Disjunctoceras*, indicates that this species does not differ substantially from *Sphooceras* and should be reassigned to this genus. Similarly, representatives of *Andigenoceras* also possess characteristic features of *Sphooceras*. *Sphooceras* has many features characteristic for modern cephalopods: short, thin-walled, semi-internal shell; phragmocone reduced to only a few chambers; uncalcified connecting rings; apical callus (a structure analogous to the belemnite rostrum); retractor muscle scars situated dorsally; very small protoconch without cicatrix. In some exceptionally well-preserved cephalopods with orthoceracone shell radula with seven rows of teeth were observed. All these features support the thesis that some straight-shelled cephalopods are evolutionarily closer to coleoids than nautiloids and their separation from nautiloids is legitimate. Vascular imprints on the surface of the cameral deposits provide further support for their primary origin and the existence of a cameral mantle. The character of cameral deposits in *Sphooceras* demonstrates that the systematic value of these structures in other straight-shelled cephalopods, a subject of controversy, has limited value. The morphology of *Sphooceras* also demonstrates that the boundary between endocochleate and ectocochleate cephalopods is not sharp, *i.e.* internalisation of the shell in cephalopods occurred repeatedly.

• Key words: Cephalopoda, Angusteradulata, Silurian, shell truncation, colour pattern, mantle extension, internal shell, embryonic shell.

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“Endocochlia”, frequently used as an older synonym of the Coleoidea (Shevyrev 2005), represents a derived clade of cephalopods, the history of which is reasonably well documented from the Carboniferous onward (Flower & Gordon 1959, Gordon 1964, Fuchs 2006, Doguzhaeva *et al*. 2010, Mapes *et al*. 2010). The problematic middle Cambrian *Nectocaryx pteryx* fossils from the Burgess Shale, showing affinity to coleoids (Smith & Caron 2010), are neither cephalopods nor do they belong to the stem group of cephalopods (Mazurek & Zatoń 2011, Kröger *et al.* 2011).

From a formal standpoint, appearance of an external mantle cover of the shell is considered a fundamental feature for classifying a cephalopod among coleoids. However, to find solid proof of the presence of an external mantle in Palaeozoic cephalopods is very complicated (Dzik 1984, Drushchits *et al.* 1978, Korn 2000). To regard a cephalopod as a coleoid, one needs to look for the

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internalisation of the phragmocone. The presence of additional shell layers secreted on the outer surface of the primary shell wall by encasing soft tissues can provide evidence of this. There are, however, some other characters such as the narrow ventral siphuncle and some aspects of the aperture, which may be of great importance for the proper assignment of cephalopods to the coleoids.

The Silurian cephalopod *Sphooceras truncatum* (Barrande, 1860), by its shell shape markedly resembling some Mesozoic belemnites, displays such shell features. It demonstrates that the boundary between the endocochleate and the ectocochleate state has been crossed by more than one group of cephalopods convergently. Morphological similarity of some non-ammonoid cephalopods with orthoceracone shell to some early coleoids (such as belemnites) is remarkable, demonstrating convergence in both groups. The shell of *Sphooceras* is short during the entire ontogeny owing to periodical truncation – the natural removal of the apical part of the shell during ontogeny. This interpretation was first expressed, extensively discussed and supported by precise illustrations by Barrande (1855, 1860, 1868, 1870, 1874, 1877) in *Orthoceras truncatum* Barrande, 1860. This phenomenon was also found in some other cephalopods and was widely accepted by other cephalopod workers (*e.g.* Blake 1882; Schröder 1888; Flower 1941, 1964; Furnish *et al.* 1962; Teichert 1964; Gnoli & Kiselev 1994).

Teichert (1964, p. 48) summarised Barrande's ideas (1855, 1860, 1877) concerning the mechanism of truncation in *Sphooceras*: "The truncation was preceded by formation of a calcareous plug in the siphuncle at the septum of truncation. The posterior portion of the phragmocone was thus cut off from metabolic processes, resulting in progressive (dis)solution and final destruction of the deciduous portion." Barrande (1860) supposed that the new apical end was formed by the septum on which new calcareous material was deposited. Thus, the less convex shape of the septum changed into the domelike form of the apex. According to him, the reconstruction was done by means of two special and longer tentacles capable of massive and precisely controlled secretion of calcareous material. He substantiated their existence by the presence of a groove in the median plane of the conical part of the shell, as well as the presence of transversal grooves. Such a mode of shell secretion is known in recent argonauts (Naef 1923, Hewitt & Westermann 2003).

Blake (1882, p. 35) accepted Barrande's conclusion and wrote: "These features are best accounted for on the supposition of Barrande, that the animal had the power of breaking off the end of its shell at the septa, and of depositing shell matter on the truncated end. Of course this involves the assumption that the animal could reach so far outside the shell, which must have been therefore more nearly internal than in the *Nautilus*." Schröder (1888) explains the varying appearance of the apex in *Sphooceras* as truncation in different portions of the shell, but he regards *Sphooceras* as a close relative of *Nautilus*. Flower (1941) remarked that the structures on adapical septal surfaces of *Sphooceras* are open to very different interpretations. He saw the most probable way to explain them as the surfaces of hyposeptal deposits. He claims that the camerae have evidently been broken at the point of greatest weakness, namely in the region of the pseudoseptum. Movement of the animal and surrounding water caused separation of both parts of the shell. He offered no explanation for the concentric markings bearing fingerprint patterns (Flower 1941, p. 473). Tasnády-Kubacska (1962, p. 69) expressed an opinion that truncation of the last chambers in some orthoceratid may have been due to resorptive processes, activated by the siphuncle and the intracameral tissues and isolating deciduous portions, which finally broke off.

However, the existence of truncation was challenged by some authors (Dzik 1984, Doguzhaeva & Mutvei 1989). For everyone involved in these discussions, the crucial point was the mechanism of truncation. Dzik briefly discussed this problem (1984, p. 135) in context with *Sphooceras* as well as with the Ascoceratidae and concluded that "one cannot suggest any reasonable mechanism of shell truncation". Doguzhaeva & Mutvei (1989) saw the problem of finding conclusive evidence of truncation in Palaeozoic cephalopods in their poor structural preservation.

Turek & Marek (1986) provided other evidence supporting truncation, especially through the documentation of the ontogeny of the species. *Sphooceras truncatum* and closely related species were later studied by Gnoli & Kiselev (1994). According to the latter authors, the apical part was symmetrically sealed by the cameral mantle after truncation and the cameral mantle extended through siphonal opening could have left the fingerprint pattern on the truncation surface (comp. Gnoli & Kisselev 1994, p. 417).

In spite of the considerable attention *Sphooceras* received there is no consensus concerning the existence of periodic truncation and the mode of secretion of terminal callus, nor is the systematic position of the genus *Sphooceras* (*e.g.* Sweet 1964, Dzik 1984, Gnoli & Kisselev 1994, Zhuravleva & Doguzhayeva 2002, Kröger 2008). Also questions concerning internal structures, the mode of their secretion and the ecology of this species have not been sufficiently answered. For these reasons, the species *Sphoceras truncatum* has been revised, using both historical material and new discoveries. Preliminary report summarising main results of this research was published by Turek (2007).

Other cephalopods morphologically similar to *Sphooceras truncatum* have been taxonomically revised. "*Orthoceras*" *sarcinatum* Barrande, 1868 is newly assigned to this species. Median sections of five well preserved specimens of "*O*". *disjunctum* Barrande, 1868 allowed detailed study of their internal structure and discussion of the systematic position. The existence of an apical thickening (callus), not documented previously for this species, indicates it belongs in the genus *Sphooceras*. Muscle scars are also described here for the first time, and its stratigraphic range is refined.

Additional evidence for periodic truncation of the shell in the Silurian cephalopod *Sphooceras* and the discovery of a colour pattern on the "new" apex in *S. truncatum* are equally exceptional and of great importance. These features represent proofs for the temporary encasing of the whole shell of this cephalopod by soft tissue. Additionally, this evoked the question concerning systematic position of *Sphooceras* and some other closely related cephalopods with an orthoceracone shell. Similarity to coleoids is further emphasized by the very short phragmocone and a smooth or indistinctly sculptured shell surface. *Sphooceras* probably possessed a minute spherical initial chamber (protoconch), which is another specific character of endocochleate cephalopods and also of orthocerids, early ammonoids and bactritoids. This generic study brings additional support for separation of orthoceracone cephalopods with small spherical protoconch lacking a cicatrix from the nautiloids.

Material and methods

Most of the available specimens of *Sphooceras truncatum* have been collected in the Prague Synform (Bohemia, Czech Republic) during 19th century. More than 500 specimens come from Barrande's collection; about 20 revised specimens are deposited in the collection of M. Shary. These specimens come from the classic localities "Hinter Kopanina" (several collecting sites near Zadní Kopanina, *e.g.*, Draská Gorge section, early Ludfordian), Butowitz (Praha-Butovice: Na břekvici and Kovářovic mez sections; earlier Ludlow and early Ludfordian), Wohrada (Mušlovka Quarry near Praha-Řeporyje), Wiskočilka (Praha-Malá Chuchle, Vyskočilka Hillside; early and middle Ludlow), Kosorz (Praha-Kosoř; late Ludlow) and Lochkov (several localities south of Lochkov Village, Ludfordian). The exact stratigraphic position and collecting site of specimens from old collections is often uncertain, except for localities with a characteristic mode of preservation (Butovice – Na břekvici, Zadní Kopanina – Draská Gorge). More than 200 specimens have been collected during the last two decades by the authors, Ladislav Zedník and Antonín Čížek. These specimens come mostly from measured and numbered reference sections with a high biostratigraphical resolution, permitting dating into specific graptolite biozones. Many specimens have been found in new localities, which allows the more acurate description of distribution patterns, ranges and abundances of *Sphooceras*. Jiří Kříž assembled an extensive collection containing 136 specimens, collected from the Homerian cephalopod limestones in the Arethusina Gorge section near Praha-Řeporyje. Specimens used in this study are usually not deformed; some are almost complete. Apical parts of phragmocones possessing three to five phragmocone chambers and probably representing deciduous parts of shells occur abundantly.

The study of *S. disjunctum* is based primarily on material from Barrande's collection. Around 40 specimens come from Butowiz (Praha-Butovice: Na břekvici, earlier Ludlow). The species was newly found in Praha-Butovice, Kační Quarry, late Wenlock, Praha-Malá Chuchle, Vyskočilka Hillside and Praha-Řeporyje (early Ludlow). Specimens are undeformed, with preserved internal structures, usually with the first phragmocone chamber missing.

To gather additional information about the internal structure of the shell, 38 specimens of *Sphooceras truncatum* and five specimens of *S. disjunctum* were cut in the median plane. Unfortunately, due to recrystallization and infilling of the phragmocone by sparitic calcite, internal structures are frequently completely destroyed. Nevertheless, about 25 specimens, primarily from the Praha-Butovice and Kosoř localities, are very well preserved internally, so characteristic features could be studied. Specimens were photographed with an Olympus Camedia 5050 digital camera, minute shells and details with an Olympus DP 700 digital camera attached to an Olympus SZX 12 microscope. Some polished sections were documented by scanner. To obtain better contrast, a specimen with a preserved colour pattern and median sections were photographed immersed in alcohol. Other specimens were coated in ammonium chloride prior being photographed. The resulting images were processed using Photo Paint software.

The basic morphological terminology is according to Teichert (1964). Due to some unique morphological features of *Sphooceras*, a schematic drawing is attached (Fig. 1); some terms used in this paper are explained in the chapter dealing with its morphology. Since the truncation process removes chambers, the most apical remaining chamber of the phragmocone (possessing the callus) is called the first.

Studied specimens are deposited in the Palaeontological collection of the National Museum, Prague (prefix NM L) and in the collection of the Geological Survey, Prague (prefix CGS SM). Some specimens from the Silurian of Central Bohemia, which significantly contributed to our knowledge about this species, are deposited in Shary's collection, Museum of Comparative Zoology, Harvard (prefix MCZ), Natural History Museum, London (prefix NHM) and Naturhistoriska Riksmuseet, Stockholm (prefix RM Mo). The Stockholm collection includes a few Bohemian specimens and four specimens from the Silurian rocks of Gotland, Sweden.

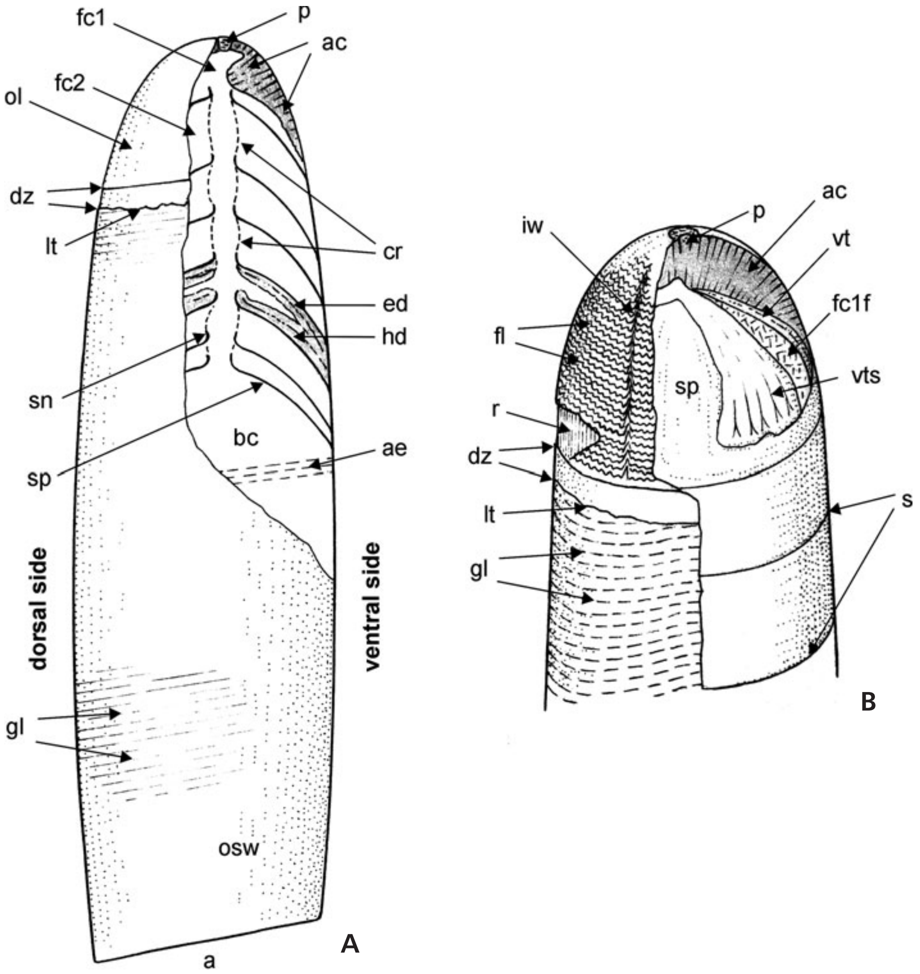

Figure 1. Schematic drawing of *Sphooceras* explaining terminology used in this paper. • A – adult specimen with partially removed shell. • B – apical region and adjacent part of phragmocone, showing external and internal features of shell. Based on specimen illustrated in Fig. 20. Abreviations: a – aperture, ac – apical callus formed by episeptal cameral deposits fused with septum, ae – annular elevation, bc – body chamber, cr – connecting ring, dz – detachment zone, ed – episeptal deposits, fl – finger-pattern layer, fc1 – first phragmocone chamber, fc1f – empty space of first phragmocone chamber filled with sparitic calcite, fc2 – second phragmocone chamber, gl – growth lines, hd – hyposeptal deposits, iw – invagination of wrinkles, lt - line of truncation, ol – outer shell layer, osw – outer shell wall, p – plug, r – radial sculpture on surface of cameral deposits (below partially removed wrinkle pattern layer), s – suture, sn – septal neck, sp – septum, vt – replica of vascular tissue on concave surface of cameral deposits (seen on calcite camera filling), vts – vascular tissue impression on convex surface of septum. Not in scale.

Morphology of *Sphooceras*

Barrande (1860, 1868) described "*Orthoceras*" *truncatum* in detail, including shell structures and the process of truncation. Special attention has been paid here only to features not mentioned by J. Barrande or to features having special importance for the systematic assignment of *Sphooceras* within the Cephalopoda and for palaeobiological interpretations.

Variability

Our study of the intraspecific variability of *Sphooceras truncatum* is based primarily on specimens collected by us at the Draská Gorge section near Zadní Kopanina. About 200 non-deformed specimens of this species, both fragments as well as "complete" shells, come from a 20 cm thick bed of yellow-grey strongly weathered dolomitic cephalopod limestone, that corresponds with the late *S. linearis* Zone

Figure 2. *Sphooceras truncatum*, Ludlow, Kopanina Formation. • A–E – specimen MCZ 160328, locality Kosoř, specimen with preserved colour pattern in apical part of shell. A – apical view; B, C – detail of apical part of shell; oblique and lateral views; D, E – lateral views. • F, G – almost complete adult specimens with preserved apertural margin; F – specimen NM L 40959, Praha-Butovice; G – specimen NM L 9201 illustrated by Barrande (1868, pl. 343, fig. 17), Zmrzlík. • H – specimen NM L 9180 illustrated by Barrande (1868, pl. 343, figs 1–5), Zmrzlík; apical part of shell; imprint of soft tissue on concave surface of cameral deposits preserved on sparitic infilling of first chamber; dark colour is probably owing to primarily high content of organic matter in cameral deposits, × 1.3. • I – specimen NM L 9193 illustrated by Barrande (1868, pl. 343, figs 1–3), Zadní Kopanina; apical part with partly exfoliated layer with finger-print pattern; surface of cameral deposits having radial structure is exposed; lateral view, × 1.7. • J, O – specimen NM L 9197 illustrated by Barrande (1868, pl. 342, figs 11–13), Zadní Kopanina; apical view (× 1.7) and detail of the border area between cameral deposits and shell, × 10. • K – specimen NM L 40960, Kosoř; almost complete adult growth stage. • L – specimen NM L 9190 illustrated by Barrande (1868, pl. 342, fig. 9), Kosoř; almost complete internal mould with only four phragmocone chambers; cameral deposits in apical region slightly developed. • M, N – lectotype NM L 9184, illustrated by Barrande (1868, fig. 15, and 1868, pl. 341, figs 15–18), Praha-Butovice; the first phragmocone chamber showing finger-print pattern and sudden change in course of roughly concentric ridges (invagination), × 0.9. Scale bar: 30 mm, details with magnification.


A
B
D
E
C
F
G
H
I
J
N
M
K
L
O

Table 1. Measurements of complete specimens of *Sphooceras truncatum* in mm. * Measured at the boundary phragmocene/body chamber.

Specimen	Sagital lenght	Body chamber lenght	Phragmocone lenght	Dorsoventral diameter *	Width	Dorsoventral diameter max	Dorsoventral diameter at aperture	Ratio bl/f l	Ratio dv/w
L 9201	112	62	50	24	22	26	23	1.2	1.1
L 9202	100	55	45	19	19	20	19	1.2	1.0
L 9180	130	74	56	33	31	35	33	1.3	1.1
L 9182	111	67	44	27	25	30	28	1.5	1.1
L 9185	86	52	34	25	22	26	25	1.5	1.1
L 17534	110	65	45	28	24	30	32	1.4	1.2
L 9191	140	77	63	30	28	30	30	1.2	1.1
L 9190	127	78	49	35	33	36	34	1.6	1.1
L 9186	76	44	32	25	22	26	26	1.4	1.1
L 9189	55	34	21	18	17	19	18	1.6	1.1
L 17533	82	46	36	20	19	23	23	1.3	1.1
L 9197	104	60	44	21	19	23	22	1.4	1.1
L 21467	78	44	34	17	16	20	20	1.3	1.1
L 9203	71	45	26	15	15	16	16	1.7	1.0
L 9183	92	55	37	19	19	24	24	1.5	1.0
L 41333	110	65	45	34	30	?	33	1.4	1.1
L 40960	143	78	65	41	39	43	40	1.2	1.1
L 40959	89	51	38	22	20	24	22	1.3	1.1
L 41334	95	56	39	30	30	32	30	1.4	1.0
L 41336	111	61	50	26	25	28	28	1.2	1.0
L 41337	95	55	40	25	22	28	24	1.4	1.1
L 40940	95	55	40	24	18	24	23	1.4	1.3
L 41335	125	75	50	31	29	33	32	1.5	1.1
L 41339	136	83	53	31	27	31	30	1.6	1.1
L 41338	101	61	40	25	23	26	24	1.5	1.1
L 40919	288	148	140	90	86	?	?	–	1.0
35050	119	75	44	22	22	23	22	–	–
L 40919	288	173	115	90	86	–	–	–	–
L 42163	24	15	10	6	4.1	7	7	–	–
L 40940	95	60	35	23	18	24	23	1.7	–

(early Ludfordian, *S. linearis* Zone, former "*Cromus beaumonti* trilobite horizon"). Different growth stages include specimens possessing a dorsoventral diameter of 2 to 30 mm (measured in the position of the first septum). This collection made a study of its variability within palaeopopulations across several depositional cycles possible.

S. truncatum collected from other localities exhibits a similar pattern of size classes. Specimens with large cross-sections are rare and come from the localities Praha-Butovice and Praha-Braník. Six were collected in Praha-Butovice: Na břekvici, *Neodiversograptus nilssoni* Zone, earlier Ludlow. They comprise isolated first phragmocone chambers, considerably infilled by cameral deposits. Three are almost the same size and attain a dorsoventral length of approximately 80 mm, the other three have dorsoventral diameters of 65, 49 and 48 mm. A recently found specimen from Praha-Braník (NM L 40919) has 80 mm diameter. However, it is much more complete, comprising the phragmocone and the adapical part of the body chamber. The eight-chamber phragmocone is about 110 mm long, its estimated total length is 270 mm. This specimen, preserved as a limestone nodule in shale was found about four meters below the cephalopod limestone bank in Školní vrch section (Praha-Braník); its exact age is unknown, but a co-occurring *Saetograptus fritschi*, a graptolite indicates *L. scanicus* or *S. linearis* Zone (Gorstian, early Ludlow). All large specimens are slightly stratigraphically older than specimens from the Zadní Kopanina locality.

Although the finger shape of the shell in *Sphooceras truncatum* is striking and characteristic, the shell may be slender and relatively long, or wider and shorter (Table 1, Fig. 2). In the pre-adult growth stage, both dorsoventral and lateral diameters frequently decrease, so that fully grown specimens show the maximum diameter in cross section is about midway through the last body chamber. In several internal moulds, a moderate constriction of the peristome is present. This shape of the shell, strongly shortened last or last two phragmocone chambers and heavily developed cameral deposits almost completely filling the first chamber are features considered to be indicators of the mature growth stage. Size variability of fully-grown specimens is extraordinary. Such variability in fully-grown longicone cephalopods was not previously known, although it had been commonly recorded in nautiloids (see discussion in Stridsberg 1985, Manda 2008, Manda & Turek 2011).

The cross section of the shell is subcircular or widely elliptic, with the dorsoventral diameter being larger than lateral. The aperture is oblique to the shell axis; the hyponomic sinus is shallow and broad. A shallow ocular sinus is present in some specimens. Both size and vaulting of the first phragmocone chamber are highly variable: short to long; moderately convex to highly vaulted, in some specimens almost pointed. Convexity of septa during ontogeny generally decreases. The last two or three septa in fully-grown specimens are very closely spaced (Fig. 3F, G, Table 2, App. 1, 2). The outer shell wall and septa are thin, the septa pass into markedly thickened orthochoanic to suborthochoanic septal necks. The shape of the slightly ventrally shifted siphuncle is not known, as only septal necks are preserved. Based on the presence of suborthochoanitic septal necks, moderately inflated connecting rings appear probable (Dzik 1984). Because no complete siphuncular segment has ever been found, their fully organic nature is assumed. In one specimen of *Sphooceras truncatum*, some traces in the form of secondary calcite lining are discernible, suggesting the lost connecting rings. The position of two graptolite rhabdosomes of *Saetograptus fritschi* within these traces (NM L 40919, Fig. 4) indicates that they were originally deposited within the siphuncle. The presumed connecting ring traces are slightly inflated within the phragmocone chambers; the substantially smaller diameter of the traces, compared with the diameter of septal necks, is interpreted as a result of post-mortem processes.

The surface of the shell is usually smooth or bears very fine, widely spaced growth lines; between these, even finer closely spaced growth lines may be discernible. In a few specimens, growth lines are rather distinct. Their course is laterally oblique to the shell axis; dorsally they form a shallow adapically convex saddle and ventrally a shallow and broad sinus. Some of the stratigraphically youngest specimens from the uppermost part of the Kopanina Formation (latest Ludfordian and earlier Přídolí) show more pronounced and densely spaced growth lines and a slightly larger apical angle (Fig. 5A, I). Transitional forms between these two morphotypes have been found. The great differences in surface patterns on the first chamber among individual specimens are the result of different factors connected with the process of truncation (see section dealing with truncation).

An interesting anomaly concerning shell size is that of palaeopopulations containing specimens with only small shells, found in the narrow stratigraphic level of the latest *Neocuculograptus kozlowskii* Zone (Ludfordian, Ludlow). This level corresponds with the onset of the Kozlowskii and Lau extinction event (Urbanek 1993, Calner 2008, Manda *et al.* 2012). Three paleopopulations were examined, from three thin beds with erosive surfaces, each representing a single depositional event: Zadní Kopanina – Nad Jirasovým lomem, bed No. 3, maximum dorsoventral diameter 14 mm; Koněprusy – Cesta section, bed No. 5,

Table 2. Phragmocone chamber lengths in *Sphooceras truncatum* and *Sphooceras disjunctum* in mm.

	Phragmocone chamber (from truncation) and presence of body chamber (bc)								
Specimen	1th	2th	3th	4th	5th	6th	7th		
Sphooceras truncatum									
L 40935	3.2	2.5	2.7	2	2	bc			
L 40940	6	6	8	6	3.4	2.5	bc		
L 40939	5.5	8	6	5					
L 40930	3.3	6	4.5	4.5	4.3	2.3			
L 40931	7.5	2.5	6	6	6.5	2.5	bc		
L 9199	12.5	8	7.1	5.8	5.8	7.4			
L 42164	4	7	8.5	8	5				
L 40929	9	7	7	7	6	6	6	bc	
L 40928	9	8.8	6.3	7	6.1	4.9	bc		
L 40925	7.8	7.6	6.1	6.6	4.7	bc			
L 40927	10.3	8.2	6.2	7.3	5.8				
L 40926	9	8.1	5.6	5.7	6.5	4.8			
L 40932	11.8	9.5	9.5	9.5	9.5	5.2			
L 40933	10.3	9.2	6.3	6.6	6.1	6.1	3	bc	
L 40919	17	16.5	16.2	14.8	16				
MCZ 160432	9.5	9.5	7	7	5.3	5	3	bc	
MCZ 160212	5.2	8.7	6	4.3	bc				
Mo 42807	6.2	6.8	8	6	6.2	6	2.5	2.5	bc
Mo 42808	4	5.8	6.3	6.4					
Mo 42813	2.7	4.5	3.7	4	bc				
Sphooceras disjunctum									
L 40937	2.6	5.3	5.2	3.2	bc				
L 40938	2.1	4.9	4.5	3	bc				
L 40936	1.2	1.8							
L 40944	?	8.5	6	5					
L 17550	?	3.5	3.5	2.8	bc				
L 41313	1.7	2.8	2.3	2.3	bc				

maximum dorsoventral diameter 9 mm; Nová Ves – Hradiště II section, bed No. 13, maximum dorsoventral diameter 10 mm. Most specimens had a much smaller dorsoventral diameter, *i.e.* 5–8 mm. The largest shell from these beds, 14 mm diameter, is markedly smaller than those in the underlying strata. Above this small-shelled population, a Lazarus gap occurs, then *Sphooceras truncatum* reappears in the latest *P. latilobus-Sl. balticus* Zone. The appearance of the palaeopopulation with small shells corresponds to the beginning of shallowing, increasing anoxia and instability of currents in the Silurian sea (Manda & Kříž 2006). The decrease in shell size (Lilliput effect) may be related to these harsh conditions (see Harries & Knor 2010).

In general, the intraspecific variability of *Sphooceras truncatum*, the sole well-known species of the Sphooceratidae is quite high (Fig. 6, App. 1, 2). Although the species ranges from the Wenlock to the earlier Přídolí, *i.e.* more than 8 Ma, neither a clear evolutionary trend nor changes in variability were traced.

A smaller species of *Sphooceras* – *S. disjunctum* – is fairly uniform, both in size and morphology. Specimens from Praha-Butovice, Na břekvici, *Neodiversograptus nilssoni* Zone, earlier Ludlow are perhaps from one palaeopopulation. Two other localities, Praha-Butovice, Kační Quarry, *C. lundgreni* Zone, *T. testis* Subzone and Praha-Malá Chuchle, Vyskočilka Hillside, *L. scanicus* Zone have yielded palaeopopulations with smaller shells. Lengths of shells from these three localities vary from 32 to 45 mm; dorsoventral diameter from 13 to 18 mm. There are 3 to 5 chambers in the phragmocones. Most internal moulds have a visible constriction of the peristome, which corresponds to a thickening of the external shell wall (Fig. 7B, C). Consequently, they are quite probably shells of adults. The shell wall near the aperture is unusually thin (0.2 mm). Thin deposits forming the apical callus correspond to very short phragmocones. They are similar to deposits in *Sphooceras truncatum* with similar phragmocone lengths. Short siphonal necks are suborthochoanitic or cyrtochoanitic, sometimes even both in the same specimen. Slightly asymmetrical septa are only moderately convex; marked differences in convexity were not observed.

Muscle scars

Dorsomyarian position of muscle scars, typical for orthocerids (Sweet 1957, Mutvei 2002a) has been ascertained in both studied species of *Sphooceras*. The annular elevation, found only in adult *Sphooceras truncatum* specimens, is very faint. It is located in the basal part of the body chamber, close to the last septum, forming a narrow stripe ventrally and ventrolaterally, becoming one distinct lobe on the dorsal side (Fig. 5G, H, J, K). A complete dorsal muscle imprint was observed in only one specimen. Several other specimens show a fine annular elevation only ventrally and laterally. A similar shape of the retractor muscle imprints is visible in one specimen of *S. disjunctum* (NM L 40976, Fig. 8C, D). The border of the adapical annular elevation indicates that the lobe was created by two retractor attachments merging. Small retractor muscle scars indicate relatively underdeveloped retractor muscles. From that, it may be concluded for active movement that the animal relied on its tubular hyponome musculature.

Detachment zone

The annular stripe, frequently present adapically on the outer surface of the shell, roughly above the mural part of the first septum is here named the detachment zone (Fig. 5B–E). It is the area where, during truncation, the mural part of the septum usually detached from the remaining part of the shell. There is often a visible step in shell diameter at the adapertural edge of the detachment zone. The adapical edge frequently has a shallow indentation, bordering the cameral deposits in the apex, which reach surface of the shell; they are different from the outer shell wall, in structure and sometimes in colour. While the shell wall is smooth and usually light gray, the apical callus deposits has longitudinal striations or dimples and is dark. The adapertural edge of this zone is the actual detachment boundary (line of truncation). Growth striations cover the remaining shell surface forward to the aperture. As long as the shell surface is not completely smooth, the striations do not

Figure 3. *Sphooceras truncatum* (Barrande, 1868). Ludlow, Kopanina Formation. Specimens sectioned in median plane. • A – NM L 40932, Zadní Kopanina; domelike first chamber with strongly developed cameral deposits ventrally, × 1.3; see also Fig. 14A. • B – specimen NM L 9199 illustrated by Barrande (1868, pl. 343, fig. 15), Praha-Lochkov; dome like first chamber with moderately developed cameral deposits showing their unusual growth in central part of apical region, × 1.2. • C – NM L 40925a, vicinity of Prague; marked shortening of phragmocone chambers during growth. Thick deposits ventrally, × 1.5; see also Fig. 14F. • D, N – specimen NM L 40929a, vicinity of Prague; third phragmocone chamber with episeptal deposits interpreted as possible initial stage of apical callus, × 1.6; detail of the chamber with episeptal deposits, × 4.1 (see also Fig. 9B). • E – NM L 40939a, vicinity of Prague; detail of apex showing infilling of siphonal opening forming the plug, × 2.3. • F – specimen MCZ 160432, Kosoř; progressive shortening of phragmocone chambers. 5th chamber filled with episeptal and hyposeptal deposits, × 1 (see also Figs 9D and 14H). • G – specimen NM L 40933a, Praha-Slivenec; progressive shortening of phragmocone chambers, × 1.2. • H – specimen MCZ 160212, Praha-Slivenec; growth stage early after truncation with very thin cameral deposits, × 0.9. • I–L – specimen NM L 40924a, Zadní Kopanina; strongly developed cameral deposits with radial lamellae (comp. also Fig. 9A); I × 1.2; J – the same specimen; detail of cameral deposits in dorsal part of shell, × 7.5; K, L – apical part; details (× 2.1 and 4.6). • M – specimen illustrated here in Fig. 3B, × 2.5.


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cross this boundary. The line of truncation abruptly disrupts the outer shell wall, as is clearly documented by the course of growth lines.

Cameral deposits

Only a few cephalopod workers have mentioned the cameral deposits in *Sphooceras* (Flower 1941, Dzik 1984, and recently Kröger 2008). Other authors (*e.g.* Sweet 1964, Kiselev 1993, Gnoli & Kiselev 1994) evidently distinguished in terminology the callus and cameral deposits and they characterised this genus as a nautiloid without cameral deposits. However, the callus in *Sphooceras* represents only a specific form of cameral deposits (probably fused with truncation septum) forming an apical part of the shell immediately after truncation, before secreting additional layers on its surface.

Cameral deposits forming the main body of the apical end of the shell (callus) represent a feature invariably occurring in all specimens studied. Their development (thickness of the callus) depends on the length of the phragmocone. Longer phragmocones possess thicker episeptal deposits while in shorter shells (with three or four phragmocone chambers, *i.e.* growth stages just after truncation) deposits forming the "callus" are very thin. In large, fully-grown specimens the deposits may occupy almost the whole volume of the first phragmocone chamber (Figs 3K, 4A, 9A, 10). The synchronous increase in callus thickness and in the number of chambers between body chamber and callus suggests an ongoing growth of the callus subsequent to truncation. The presence of the apical callus probably represented some kind of counterweight probably enabling the animal to keep its shell horizontal.

In specimens with slightly developed deposits, apical callus reach its maximum thickness around the sealed septal foramen (Figs 3H, 9C, E, 11A, D). Laterally, their thickness decreases more or less regularly. A crater-like depression in the convex side of the apical callus within the confines of the plugged septal foramen is frequently present; in medially cut specimens a trace of a very narrow channel in the septal foramen plug is sometimes discernible. In some specimens the colour and structure of the matrix infilling the septal foramen differs from neighbouring cameral deposits forming the callus (Figs 3D, G, 9B, E, 11A, D). In specimens with a longer phragmocone, cameral deposits are more developed ventrally. The central part of the callus is sometimes markedly thinner. This feature is very well seen in median sections as well as on some of Barrande's type specimens, in which infilling only of the empty space of the first chamber is preserved, so that a cast of the adapertural surface of the callus is exhibited. The callus is sometimes darker, due to the presence of organic matter. It may be a consequence of an originally high content of organic matter. The radial structure of the deposits is clearly visible close to the outer surface of the shell in well-preserved, medially cut specimens. Sometimes the structure is accentuated by pyrite or Fe-hydroxide. The deposits comprise lamellae or thin pillars interconnected through lateral anastomoses (Dzik 1984), sometimes arranged in rows, so that the outer surface looks like a pitting or fine longitudinal ribs. However, one large and strongly weathered specimen (NM L 40922) of *Sphooceras* shows a spongy character of these deposits. Their microstructure thus seems to be analogous to that observed in the cameral deposits of lamellorthocerids such as, *e.g. Arthrophyllum* Beyrich, 1850 (for summary see Zhuravleva & Doguzhayeva 2002). In specimens with massively developed deposits, their microstructure changes rapidly inward; their lamellar character disappears and becomes sparitic calcite. These specimens also exhibit slightly developed deposits on the convex surface of the first septum, documenting precipitation of calcium carbonate on the outer surface of the siphonal neck (Fig. 10A, B).

The fact that this material was deposited by the living animal is evident partly from the patterns of deposition and its characteristic structure resembling the radially arranged calcite prisms of belemnite rostra. Additionally, in a certain phase of ontogeny (just after truncation) it formed the only wall at the apical end of the shell. Its development and arrangement indicates that it also served to keep the shell horizontal.

Besides the apical callus, cameral deposits interpreted as a live-secreted structure have been found in three specimens of *Sphooceras*. The 4th phragmocone chamber of *S. truncatum* (specimen NM L 40929a, Figs 3D, N, 9B) shows episeptal deposits lining the concave part of the septum. Their development and fusion with structuraly changed septum is presumed to be a condition preceding truncation. This hypothesis is based primarily on the specimen of *S. disjunctum* (NM L 41032, Figs 12B–D, 13A, D, E). While the average thickness of the free parts of the septa (measured in the mid point between outer shell wall and siphonal opening) is 0.9 mm, thickness of the septum fused with cameral deposits in the ventral sector (measured in the mid point between the ventral side and siphonal opening) is 4.4 mm. The ventral part of this "septum" is formed by white-grey sparitic calcite; only the convex surface of the septum is coloured by darker pigment. Dorsally from the siphonal opening, the septum fused with cameral deposits is markedly thinner (near the axis of the shell its thickness is 2.7 mm). Further dorsally it narrows, and finally its thickness is almost the same as the thickness of neighbouring septa. In one quarter of the distance between the ventral side and the septal foramen, a honey-coloured lamella appears on the concave side of the septum, gradually thickening medially and near axis of the shell, becoming the total thickness of this compound septum/deposit structure.

Figure 4. *Sphooceras truncatum* (Barrande, 1860); specimen NM L 40919a; Ludlow, latest Gorstian or earlier Ludfordian, Praha-Braník, Školní vrch, Kopanina Formation. • A –incomplete adult growth stage cut in median plane. Two last phragmocone chambers and adjacent part of body chamber not illustrated. The first chamber almost completely filled with cameral deposits showing radial structure in their outer part with graptolites *Saetograptus fritschi* within the siphuncle segment of third chamber, × 1.6. • B – the same specimen; detail of the outer shell wall; arrows indicate the place of truncation and (?)traces of a connecting ring, × 3.8.

These deposits do not substantially reduce the volume of the septal foramen. If this compound structure later formed the apical callus, secretion of a plug closing the siphuncle and perhaps one another septum was the next step in preparation for truncation.

As cameral deposits inside the phragmocone have been found in two cases only, their secretion shortly before truncation is hypothesized. In one adult specimen (MCZ 160432; see Figs 3F, 9D, 14H) both episeptal and hyposeptal deposits are developed. They are present in the 5th phragmocone chamber, *i.e.* close to the animal's centre of gravity. The previous and following chambers are empty except for the apical callus. Their morphology indicates that they were not related to the truncation process. They probably appeared in fully-grown specimens reducing its positive buoyancy. It also means that occasionally, typical cameral deposits may appear inside the phragmocone chamber.

Thickening of the apical part of the shell in *S. disjunctum* corresponds to initial stages of the apical callus in *S. truncatum*. The phragmocone of *S. disjunctum* has no more than five chambers and the chambers are very short. To maintain neutral buoyancy, the shell is more delicate with a very thin apical callus.

Plug closing septal foramen

The plug closing the septal foramen shows a structure slightly differing from the surrounding cameral deposits. The convex surface of the callus corresponds to the convex part of the structurally reworked septum and the sealed septal foramen is clearly visible. In well-preserved specimens, concentric and fine radial structures can be seen on the outer surface of the plug. The outer margin bordering the plug usually forms a grove and the central part of the plug is frequently slightly submerged. In the very centre of the plug, a crater-like depression is usually present, with 1/5 to 1/6 of the diameter of the siphonal opening (Figs 9B, C, E, 12 A, 15B, M). The outermost smooth layer deposited around the plug either only borders the plug, or either partly or completely overlays the fingerprint-pattern layer. In former case, the boundary between the smooth layer and the fingerprint-pattern layer is sharp (Figs 15B, 16B). Different material and different outer morphology of the plug indicates that the plug was formed by tissue entering the siphonal opening from the inside of the first chamber. The sharp border between the plug and outer layers covering the callus excludes the possibility that this layer was formed by cameral mantle extended through the siphonal opening. Also, the necessity of sealing the siphonal opening before truncation would have prevented repairs to detachment zone by cameral mantle (comp. Gnoli & Kiselev 1994). Successive phases of closing of the septal foramen, from initial narrowing of the tube to a completed plug can be traced in various medially sectioned specimens. In one medially cut specimen of *S. disjunctum* (NM L 40938, Fig. 7A, G, H), the siphonal opening in the first septum appears plugged but there are no traces of any episeptal deposits, formation of which very probably preceeded formation of the plug. Therefore, it seems more probable that the siphonal opening in the first septum did not lie exactly in the medium plane, and the brownish colour of the "plug" is in fact the wall of the siphonal neck.

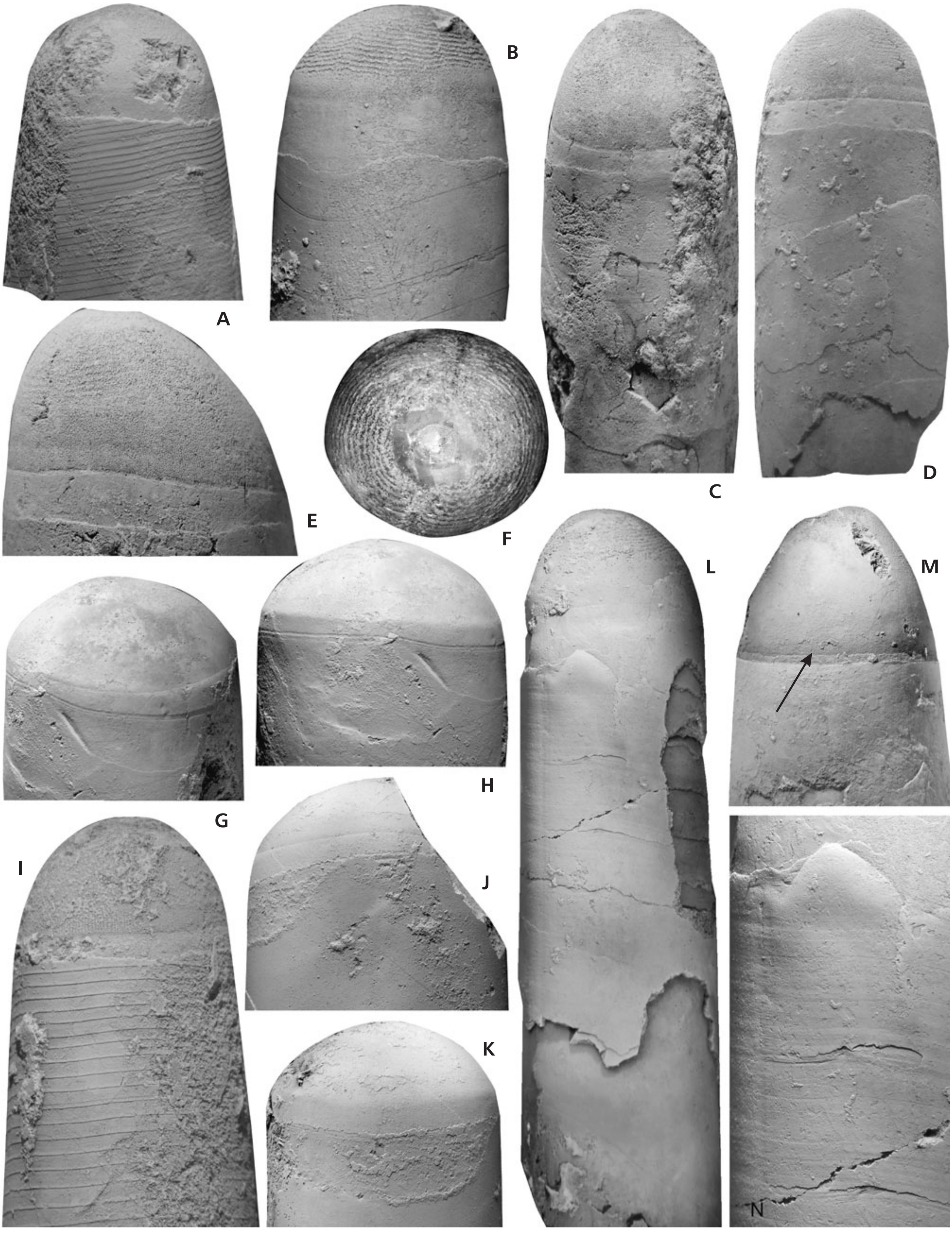
Deciduous part of phragmocone

One argument against periodic truncation in *Sphooceras* was the alleged absence of deciduous parts of the shell in the fossil record (Teichert 1964, Dzik 1984, Kröger 2008), but claims of this absence are based solely on Barrande's earliest writings (Barrande 1860). Later, in 1877, he mentioned that his collection contained such parts of cephalopod shells. During our fieldwork, we have found that specimens of *Sphooceras truncatum* having three to five chambers but lacking the body chamber are quite common (*e.g.* Barrande 1868, pl. 343, figs 4, 5; Figs 15D, I, L, 16I and 17E herein). The absence of body chambers was not due to separation from the phragmocone during collecting – they were already missing in the sediment. *S. disjunctum* is less abundant and only a few specimens have been obtained during recent field works. Isolated apical parts of phragmocones coming from old collections do not exclude the possibility that remaining part was lost during excavation. Therefore, existence of phragmocone parts in *S. truncatum* is further evidence confirming the truncation process in *Sphooceras.*

Colour pattern and its significance for the determination of the life orientation of the shell

The colour pattern in *Sphooceras* has been found so far in only one specimen (MCZ 160328, Fig. 2A–E) from the "Kosoř" locality (Ludfordian, Kopanina Formation), and it is especially important for tracing the process of

Figure 5. A – *Sphooceras* sp., specimen NM L 40976, Ludlow, Ludfordian, *Pristiograptus fragmentalis* Zone, Praha-Lochkov, Nad ubikacemi, Kopanina Formation; adapical part of the shell with densely spaced growth lines; lateral view, × 2.8. • B–N – *Sphooceras truncatum* (Barrande, 1860), Ludlow, Kopanina Formation. • B – specimen NM L 00008, Zadní Kopanina; adapical part of the shell with well seen finger-print pattern layer, detachment zone and abruptly finishing growth lines; ventrolateral view; × 3.2. • C, D, E – specimen NM L 42165, Zadní Kopanina; incomplete shell showing detachment zone – dorsal, ventral and lateral views, C, D × 1.4, E × 1.9. • F – specimen NM L 9194, illustrated by Barrande (1868, pl. 343, figs 4, 5), Zadní Kopanina; apical view with smooth layer around the plug indicating secretion of this layer from plugged siphonal opening abapically, × 1.9. • G, H, J, K – basal part of body chamber; internal mould showing single lobe of retractor muscles. • G, H – specimen NM L 40977, dorsal and dorsolateral views, × 1.6. • J, K – specimen NM L 40958, Řeporyje – Mušlovka Quarry, dorsolateral and dorsal views, × 1.3. • I – specimen NM L 21467 illustrated by Barrande (1870, pl. 448, figs 3–5), Slivenec, valley; "naked" apical part, detachment zone and well preserved surface sculpture, × 2.3. • L, N – specimen NM L 9193 illustrated by Barrande (1868, pl. 343, figs 1–3), Zadní Kopanina, anomalous shell growth (healed sublethal injury); notice also two small V-shaped damages adaperturally, L × 1.6, N × 3.2. • M – specimen NM L 40980, vicinity of Prague; part of the shell with strongly vaulted apical part and very narrow detachment zone, indicated by arrow, × 1.8.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truncation. The colour pattern is present in the apical region of the shell. The incomplete specimen has six phragmocone chambers and an adjoined part of the body chamber. The shell is exfoliated, except for the apical part; relicts of the adjacent phragmocone chamber shell are preserved. The body chamber is moderately deformed; its adapertural part is secondarily dislocated, damaged, and partly filled with grey matrix.

The colour pattern is characterised by stripes extending radially from the circumference of the plugged siphonal opening, but they are only present on the dorsal half of the shell. The stripes widen adaperturally and fuse dorsally into an undivided brownish-grey area. Following the expansion of the apical part of the shell, new stripes were inserted laterally. A bright-brown longitudinal stripe is developed in the middle of the right side. The light-grey area between this and the adjacent stripe is about twice as wide as the stripes. Moving dorsally, there are stripes that are progressively less discernible, owing to the darker colour of the shell. The ventral half of the shell is uncoloured. Shell relicts preserved in the adjacent part of the phragmocone show no colour pattern, and the border between the coloured and uncoloured part of the shell is sharply delimited by a darker brownish belt along the first suture. This pigmentation also continues on the ventral side, where it is of secondary origin.

The original colouration of the apical region was perhaps bright, because the preserved stripes are well developed and because in colour preservation, remains of the dark pigment are usually preserved. Explaining the sudden diminishing of longitudinal stripes on the dorsal side in the adapertural direction is more difficult. It can imply that the colour pattern here was weakly expressed and disappeared post-mortem. A camouflage effect serving for protection of the animal could be provided by pigmentation of the soft tissue covering the shell but why should there be a colour pattern when the mantle still covered the shell? In order for the colour pattern to serve as camouflage, this part of the mantle might have been (i) speculatively translucent, (ii) retracted at one point, thus exposing the colour pattern or (iii) moved back and forth across the shell, depositing additional shell layers as in cypraeid gastropods. Owing to the periodic truncation, a short phragmocone was maintained during the entire ontogeny. It possibly enabled repeated complete covering of the shell by mantle extension, after each truncation. A similar model of mantle extension has been described for some Palaeozic (Korn 2000) and some Mesozoic ammonoids (Drushchits *et al.* 1978). The evidence for such behaviour is derived from secondary external shell layers and sometimes from healed shell injuries (Kröger 2002).

It is interesting to compare the colour pattern on the first phragmocone chamber of *Sphooceras* with those in embryonic shells of nautiloids, although it is only rarely preserved in fossil nautiloids. Three nautiloid specimens displaying this feature are from the Silurian of Bohemia and Gotland. The first one is an oncocerid, namely "*Cyrtoceras*" *parvulum* Barrande, 1866 (Barrande 1877, pl. 504, figs 1, 2). The second one is an undetermined oncocerid deposited in the Shary collection. The third one is a *Pentameroceras mirum* (Barrande, 1865), from the Silurian of Gotland (see Turek & Manda 2011, fig. 6a). Although it is difficult to determine exactly the hatching phase in these shells, the adapical part of the embryonic shell of *Pentameroceras*, "*Cyrtoceras*" *parvulum* and the undetermined oncocerid is dark with transversal light coloured bands, and the colour pattern consists of undulating bands near the presumed aperture of the embryonic shell. The juvenile colour pattern observed in all these specimens differs markedly from those of the postembryonic growth stages. In the Recent *Nautilus,* the shell is initially ivory coloured and the typical white-brown colour pattern appears gradually, first on the flanks and later on the venter, about a quarter to half a whorl before the nepionic constriction (Stenzel 1964, Arnold *et al.* 1987b). The colour pattern in *S. truncatum* has a distinct beginning at the margin of the plugged siphonal opening – the stripes are straight, not interrupted, and clearly defined.

The development of colour stripes only on the dorsal half of the shell has been documented in a few Early Palaeozoic orthocerids and pseudoorthocerids (Ruedemann 1921, Teichert 1964, Turek 2009, Manda & Turek 2009) and one Ordovician endocerid (Balashov 1964). Some authors (Ruedemann 1921, Flower 1955 and others) have assumed that it is a characteristic of the majority of orthocerids, indicating horizontal life position of the shell. However, data are scarce concerning the colour pattern in this group of cephalopods. In the Silurian pseudoorthocerid "*Orthoceras*" *pelucidum* Barrande, 1868 with a slightly curved adapical part of the phragmocone and in the related species "*Orthoceras*" *columnare* Marklin from Gotland, longitudinal stripes are present around the entire circumference. A specimen of *Dawsonoceras annulatum* (Sowerby, 1816) shows the same characteristic. A recently discovered colour pattern in two earlier Devonian (Lochkovian) straight-shelled cephalopods from Central Bohemia (Turek 2009) also shows its development around the entire circumference of the shell. Both specimens, belonging perhaps to separate species, are fragments flattened in shale, so their internal morphology, which could indicate their living position, is unknown. Regardless of the scarcity of data concerning the colour pattern in cephalopods with straight or very slightly curved shell, it appears reasonable to assume that colouring of shells reflects aspects of their autecology. Cephalopods with colour pattern around the entire circumference of a straight shell

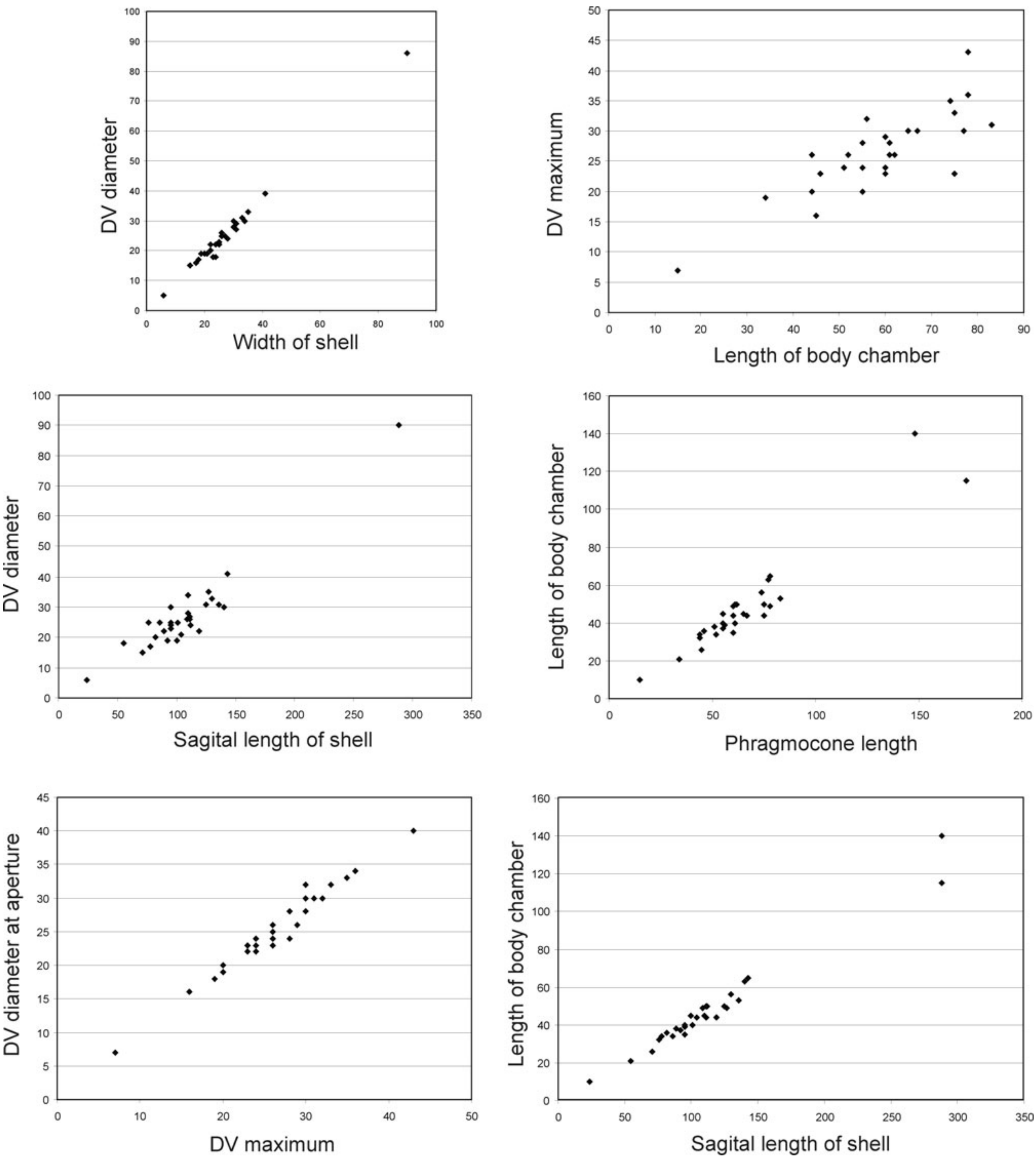


Figure 6. Relations between selected parameters of shell in *Sphooceras truncatum*; notice linear correlation between individual parameters. DV – dorsoventral. All measurements are in mm. For data see Table 1.

might indicate a vertical life position (Manda & Turek 2009) while cephalopods keeping their shell horizontal might have had the colour pattern only on the dorsal side of the shell (Flower 1955, Furnish & Glenister 1964); this is also case of *Sphooceras.*

Embryonic shell in *Sphooceras*

Sphooceras shells that are definitely embryonic have not been reported. In his discussion concerning this genus, Dzik (1984) wrote that "the apical part of the shell of

Sphooceras appears to be a protoconch, an interpretation supported by the lack of any broken-off orthoceratid shell fragments that might be referred to *Sphooceras*… If the entire ovate apical part of the shell is an embryonic shell, the egg must have been greater in size than the mature shell aperture! Since this could not be the case, the larva must have developed outside of its egg capsule…" (p. 135). He characterised the family Sphooceratidae as nautiloids with "very short, straight, compressed shell with very large-sized protoconch (?), and cameral deposits with radial microstructure" (p. 141). However, in a later discussion (1987, p. 225), he rejected this speculation concerning the identification of the apical part of *Sphooceras* as a protoconch. Teichert (1964), based on Barrande's observations, noted the lack of truncated parts of phragmocones, and stated that only the mature portion of the conch of *Sphooceras truncatum* is known with certainty. Furnish *et al.* (1962) noted several species of "*Orthoceras*" which could possibly represent deciduous portions of the conch in *S. truncatum*. Actually, as was already mentioned above, isolated apical parts of phragmocones belonging to this species and representing different ontogenetic stages (including nepionic ones) occur frequently in the Silurian cephalopod limestone of the Prague Basin, and probably do represent deciduous portions of shells.

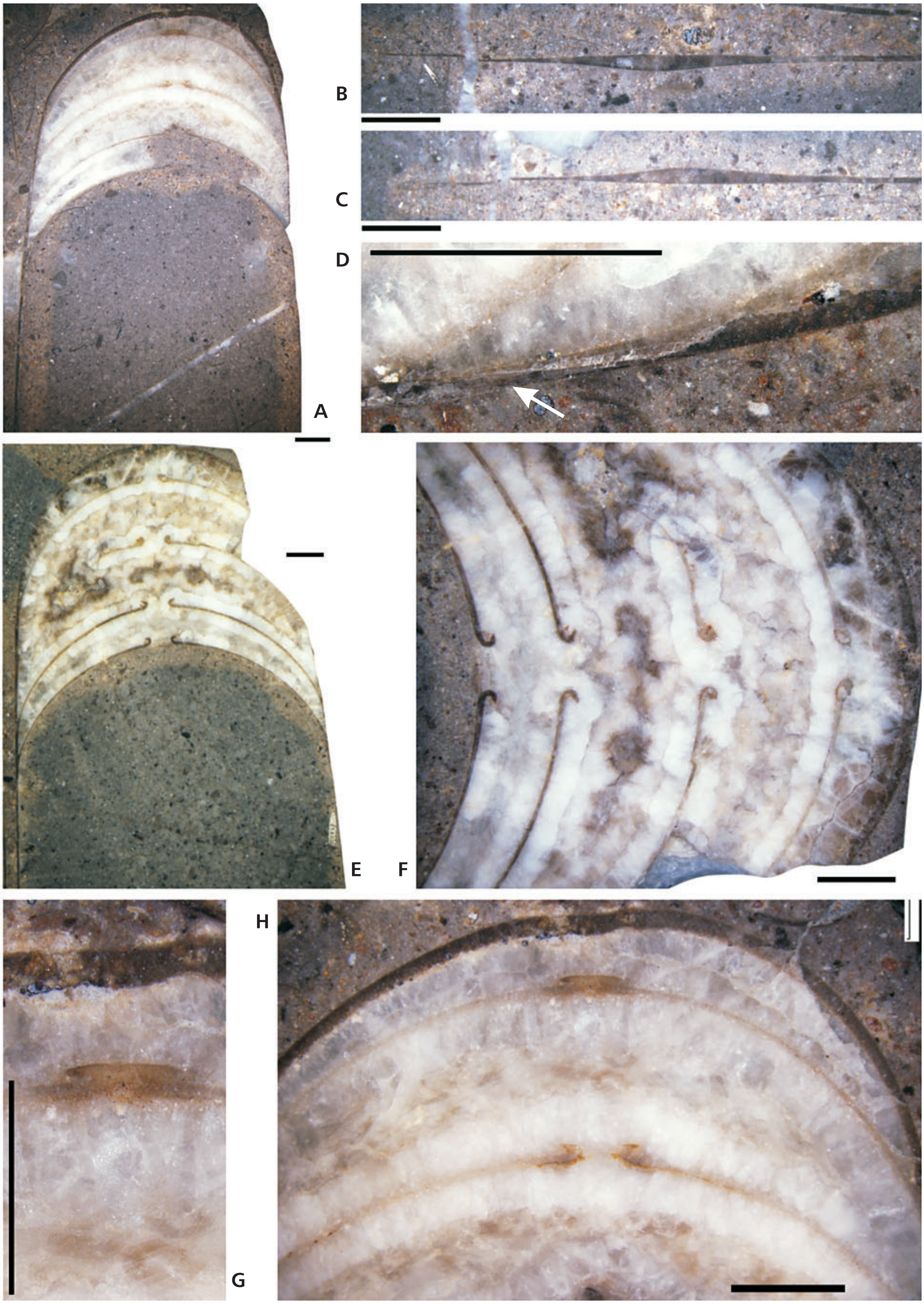
Barrande (1860, 1868) and Turek & Marek (1986) illustrated shells of different growth stages in *Sphooceras truncatum* (fig. 3, p. 251) from lower parts of the Kopanina Formation. The dorsoventral diameter in specimens unequivocally assigned to *S. truncatum* ranges from 2–80 mm, with a maximum reconstructed shell length of 260 mm. Such a size range of the apical part was presented as one piece of evidence for truncation.

The material preserved in yellowish, heavily weathered cephalopod limestone from the Draská Gorge locality near the village of Zadní Kopanina contains different growth stages of *S. truncatum*. Nautiloid shells, unsorted by size, are rather chaotically deposited (Fig. 18). In this cephalopod assemblage analysed by Manda (2003, p. 92), *S. truncatum* is the second most common species (20.4% of collected shells). Associated orthocones have longicone smooth shells, circular in cross section, usually with rather long phragmocone chambers. *Kopaninoceras* sp. prevails in the assemblage, with 30% of the collected shells. However, it is not clear whether one or several species of *Kopaninoceras* are present here. Less common is a longicone nautiloid with a markedly compressed shell, oblique straight sutures and densely spaced phragmocone chambers (*Plagiostomoceras* sp., 11% of collected shells). *Sphooceras* co-occurs here with very small embryonic shells of straight-shelled cephalopods representing growth stages shortly after hatching (Figs 17, 19). All these specimens of *S. truncatum* are of a similar size, their length is 4 to 5 mm and they markedly resemble adult specimens in shape. The spherical initial chamber is very small and is separated from the adjacent chamber by a conspicuous constriction. A faint constriction is recognizable roughly in the midpoint of the body chamber. The best-preserved specimen shows 7 to 8 phragmocone chambers and a relatively long body chamber. The shell is annulated; this annulation appears to be suppressed adaperturally and is not expressed on the internal mould.

Embryonic shells with a spherical initial chamber separated from the adjacent part of the shell by a marked constriction are characteristic for the subfamily Sphaerorthoceratinae Ristedt, 1968, and bactritoids as well as ammonoids (Ridstedt 1968). Embryonic shells of *Sphooceras* particularly resemble embryonic shells of *Parasphaerorthoceras* Ridstedt, 1968. However, no later growth stages of cephalopods, which could be assigned to *Parasphaerorthoceras* or related straight-shelled cephalopods have been collected from the locality mentioned above. Kolebaba (1973) illustrated similar types of embryonic shells from the early Homerian stage of the Prague Basin. These specimens, preserved as internal moulds, show no annulation, but were not systematically evaluated. Plagiostomocerids have similar embryonic shells with small spherical embryonic chambers less than 1 mm in diameter, separated from later growth stages by a constriction. They are probably related to the Sphooceratidae (Manda & Frýda 2010).

In the Draská Gorge locality near the village of Zadní Kopanina, both the preservation of different growth stages of *S. truncatum* (including juvenile specimens with a dorsoventral diameter of 2 to 3 mm and adults with a dorsoventral diameter 20 to 30 mm) and a comparison of some common morphological features of embryonic and adult shells present in the taphocenosis support the idea that the embryonic shells, so far not precisely identified, belong to *Sphooceras truncatum*. All other co-occurring

Figure 7. *Sphooceras disjunctum* (Barrande, 1868). Ludlow, *Neodiversograptus nilssoni* Zone, Praha-Butovice, Kopanina Formation. Specimens sectioned in median plane. • A – specimen NM L 40938a, phragmocone and adjacent part of body chamber; note great differences in in length of phragmocone chambers. • B, C – specimens NM L 40937a and NM L 40937b; detail of outer shell-wall in adapertural part of body chamber. Note extremely thin shell near aperture and thickening of peristome. • D, G – specimen NM L 40937; detail of shell-wall showing place of truncation (comp. also Fig. 13B), thickened cameral deposits forming apical callus and plugged or, what is more probable, eccentrically lying siphonal opening. • E, F – specimen NM L 40737; internal structures of shell; suborthochoanitic to cyrtochoanitic siphonal necks and very thin apical callus. • H – specimen NM L 40938a; detail of adapical part of the shell with apical callus. Scale bar: 2 mm.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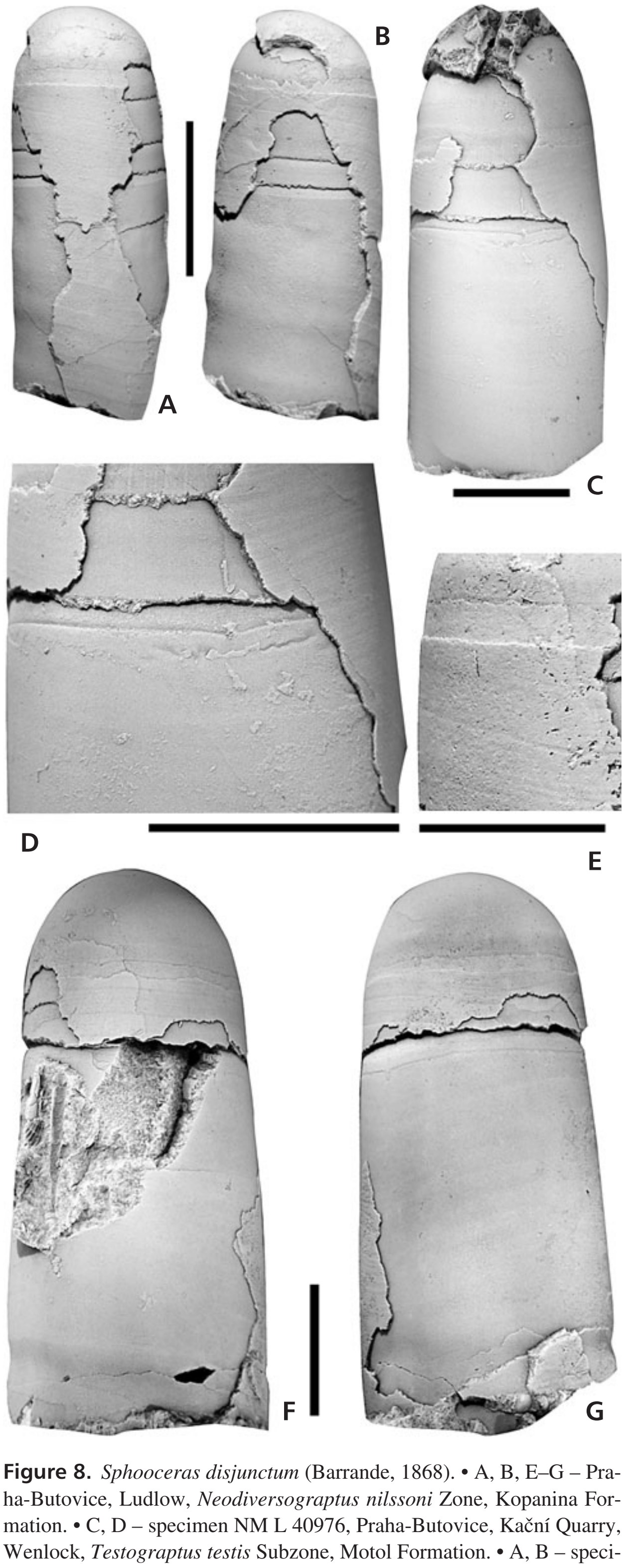


Figure 8. *Sphooceras disjunctum* (Barrande, 1868). • A, B, E–G – Praha-Butovice, Ludlow, *Neodiversograptus nilssoni* Zone, Kopanina Formation. • C, D – specimen NM L 40976, Praha-Butovice, Kační Quarry, Wenlock, *Testograptus testis* Subzone, Motol Formation. • A, B – specimen NM L 40975; almost complete young growth stage, partly exfoliated, with very low first chamber; dorsal and lateral views. • C, D – specimen NM L 40978, annular elevation; dorsal view. • E – the same specimen as in Fig. 8A; detail of detachment zone. • F, G – lectotype NM L 17549, illustrated by Barrande (1868, pl. 345, figs 11, 12); ventral and dorsal views. Scale bar: 10 mm.

cephalopod species at this locality have different types of embryonic shells. The presence of annulation in the embryonic shell, which has not been observed in later growth stages of *Sphooceras* does not exclude this possibility; in postembryonic growth stages, annulation frequently disappears (Ristedt 1968, Kröger 2008). Weakening of annulation in adapertural direction is another feature observed in these juvenile growth stages. As shown by Ristedt (1968), the taxonomic value of annulation is very limited in some orthocerids.

Anomalous growth

Repaired damages of the apertural margin occur very frequently in Recent *Nautilus* (*e.g.* Ward 1987) and were also very common among fossil cephalopods with an outer shell. However, due to the usually entirely smooth shell surface in *Sphooceras*, the chance to detect healed injuries or other anomalies of the shell is limited. In specimens with well discernible growth lines, typical V-shaped injuries, usually interpreted as a result of biting (*e.g.* Klug 2007), have not been found.

A strange anomaly can be seen in specimen NM L 40963 (Fig. 5L, N). A lobe-shaped thickening of the smooth shell on the flank crosses the border between the apical part and the adjacent part of phragmocone. Continued traces of this injury are evident further along the shell, in subsequent growth stages. There is a shallow longitudinal furrow nearby. It is presumed that the damage to the shell was repaired by apposition of shell material by the inner mantle surface. In another specimen (NM L 40964), an anomaly has been found in the internal mould of the phragmocone, more likely a result of anomalous growth than of taphonomic processes. This injury looks similar as sublethal damages of the shell observed on internal moulds of Devonian bactritoids (Klug 2007).

Marked anomalies in the course of growth lines were observed in the embryonal shell of specimen NM L 40965 (Fig. 17C). Just behind the protoconch, small ribs on the lateral side are not transversal but markedly obliquely oriented. A similar feature was documented by Ristedt (1968) in *Parasphaerorthoceras*. This anomaly of growth might have occurred inside the egg capsule, perhaps due to deformation on the bottom, an explanation corresponding to the shell anomalies observed in Cretaceous nautiloids (Chirat 2001).

Palaeobiology of *Sphooceras*

Origin of cameral deposits and their function

Cameral deposits in orthoceracone cephalopods belong to the most widely discussed structures (*e.g.* Flower 1955,

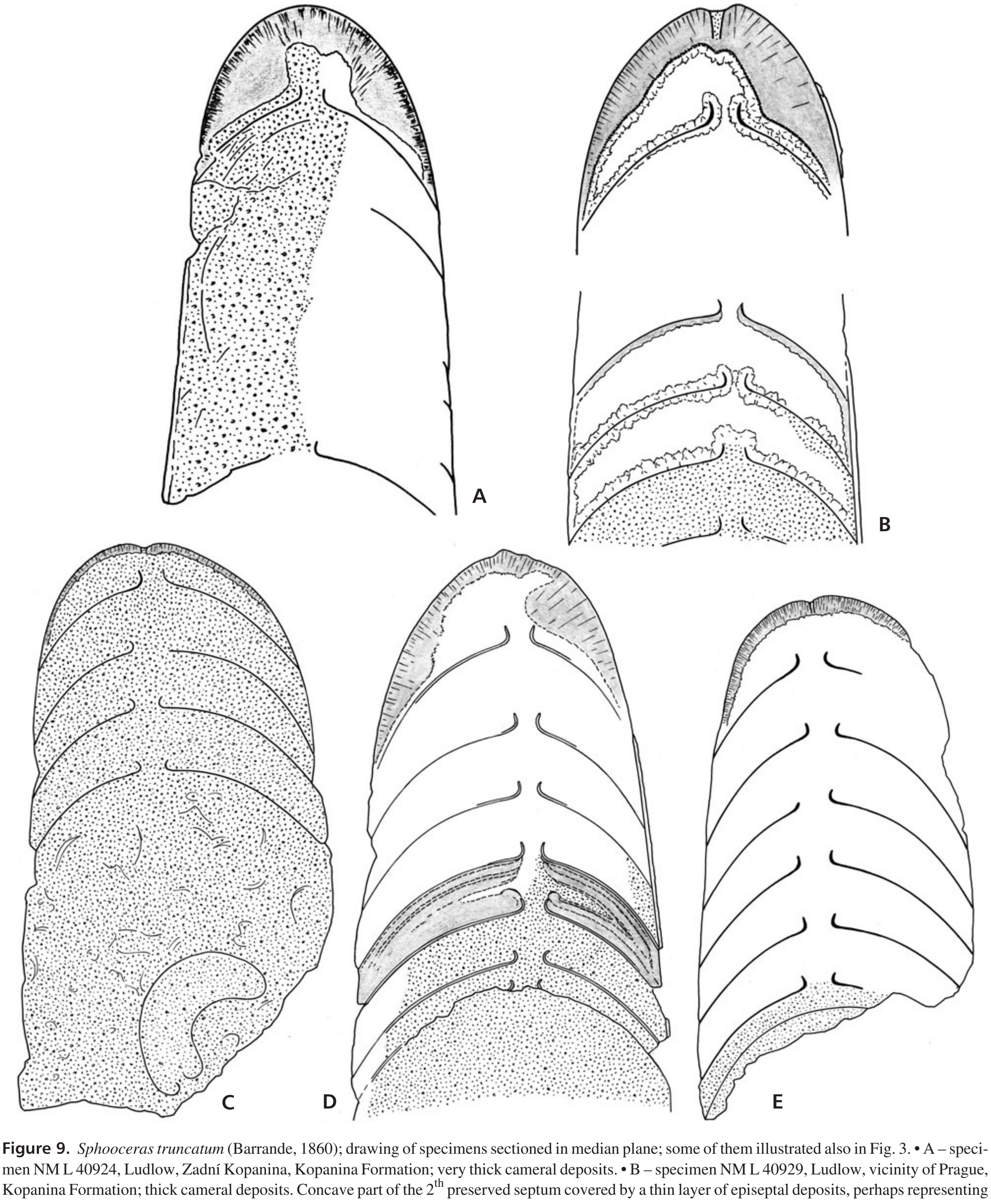


Figure 9. *Sphooceras truncatum* (Barrande, 1860); drawing of specimens sectioned in median plane; some of them illustrated also in Fig. 3. • A – specimen NM L 40924, Ludlow, Zadní Kopanina, Kopanina Formation; very thick cameral deposits. • B – specimen NM L 40929, Ludlow, vicinity of Prague, Kopanina Formation; thick cameral deposits. Concave part of the 2th preserved septum covered by a thin layer of episeptal deposits, perhaps representing initial stage of their growth preceding truncation. • C – specimen RM Mo 42513, Ludlow, Sandarve Kulle, Gotland, Hemse beds, upper part. Grow stage early after truncation; slightly developed cameral deposits form a thin layer. • D – specimen MCZ 160432, Kosoř, Ludlow, Kopanina Formation; besides strong deposits forming the apical callus, primary cameral deposits (both episeptal and hyposeptal) almost completely unfilled the 5th phragmocone chamber. • E – specimen RM Mo 42801, Wenlock, Othem, Gotland; progressive shortening of phragmocone chambers during growth of the shell. Despite the presence of 7th phragmocone chambers apical callus is unusually thin.

1964; Seuss *et al.* in press) and have been subject of controversial opinions. Several principal questions concerning these structures were discussed: Are they primary, *i.e.* precipitated by the animal itself, or are they of secondary nature originating from post-mortem processes? If both types of cameral deposits are present, which of them belong to the former and which to the later type? If they are primary, were they precipitated from extrapallial fluids, which penetrated the chambers through the siphuncle, or is their origin owed to soft tissue, which was in direct contact with them?

The theory of the primary origin of cameral deposits, first expressed by Woodward (1851) and substantially supported by Barrande (1866), has been widely but not quite unequivocally accepted, and was the subject of controversial opinions (see discussion in Mutvei 1956, 2002 and Crick 1982). The main arguments for their primary secretion were summarised by Flower (1964) and Teichert (1964); important supporting observations were added later (*e.g.* Fischer & Teichert 1969, Crick 1982, Bandel & Stanley 1989, Blind 1991, Histon 1993). Today, based on new supporting evidence, primary secretion of cameral deposits is considered beyond dispute (Seuss *et al.* 2011).

A somewhat controversial theory of the cameral mantle expressed by Flower (1939) was refused by some cephalopod workers (*e.g.* Mutvei 1957, Dzik 1984) and was substantially supported by further investigation of Flower (1941, 1955, 1964), Teichert (1964), Holland (1965), Histon (1993), Kolebaba (1999, 2002), as well as Zhuravleva & Doguzhayeva (2002). *Sphooceras* can contribute significant data for the discussion of these questions. Contrary to other straight-shelled cephalopods with a long phragmocone, cameral deposits are developed only in the “first” phragmocone chamber. Their primary origin in *Sphooceras* is confirmed by their development during ontogeny, internal structure, form and location inside the shell. As in other othoceratoids with long phragmocone, cameral deposits are more developed ventrally for stability and equilibrium, *i.e.* to help hold the animal horizontal (presuming they managed to achieve neutral buoyancy with the little amount of phragmocone chambers). Their growth due to this function had to be physiologically controlled. Their appearance in a phragmocone chamber other than in the adapical one is interpreted as a temporary condition, usually preceding truncation. A single specimen showing both episeptal and hyposeptal cameral deposits in one phragmocone chamber located near the centre of gravity (specimen MCZ 160432 L40929) is exceptional. Vascular imprints on the surface of cameral deposits and on the convex surface of the first septum support the hypothesis of the presence of a cameral mantle; soft tissue entered into the adapical chamber through an opening in the siphuncle in this chamber. It seems probable that cameral deposits evolved repeatedly and independently in unrelated evolutionary lines, and thus their morphology and mode of formation may vary profoundly.

Apical callus, vascular imprints

The first supposed step of formation of an apical callus was secretion of cameral deposits on the concave part of the septum (which later became septum of truncation) in the adapertural half of the phragmocone. Development of cameral deposits was accompanied with their fusion with septum, which became structurally altered. A content of organic material in septum of truncation increased owing to growth of organic radial lamellae inside the septum. During this process the border between septum and deposits disappeared. Then followed the formation of a calcareous plug closing the siphuncle in this part of the shell. The septal opening was sealed gradually along the whole internal circumference. It caused cutting of the adapically lying part of phragmocone from the physiological – processes preceded natural removal of the apical part of the phragmocone from the rest of the shell. This hypothesis is based especially on the specimen *Sphooceras disjunctum* NM L 41032 (Figs 12B–D, 13A, D, E) in which boundary between septum and growing cameral deposits disappeared. The mantle of molluscs has the ability to secrete shell as well as to remove what it has deposited (Carriker 1972), so removal of the apical part of the shell during truncation could have been done by chemical dissolution. The shell wall at the separation boundary could have been chemically weakened by the mantle edge. After this part was eroded, the apical part of shell would fall away. Another, in light of new observations less probable possibility considered is that the site of truncation was area between septum and episeptal deposits. The connection between the septum and the episeptal deposits, whose outer part is structurally different from their inner part, could be weakened prior to the actual separation of the adapical part of the phragmocone by the termination of metabolic processes in that part. It may have enabled separation of the structures during the truncation. In this case a new apex would be formed only by episeptal deposits. The septum became a detached part of phragmocone (further discussion see in part dealing with truncation).

Symmetrical traces showing a characteristic pattern on the concave surface of cameral deposits in *S. truncatum* are occasionally preserved (Barrande 1860, 1870, pl. 341, figs 18, 19; Kiselev *et al.* 1993, fig. 5; Figs 2H, 15A, C, D, G, H, K, L, 16C, E, F, I, 20). A deep furrow is present midventrally and middorsally. The traces are clearly visible in the infilling of originally empty space of the adapertural part of the first chamber, and exceptionally also on the convex surface of the first septum. They are interpreted as vascular imprints of the cameral tissue entering the first

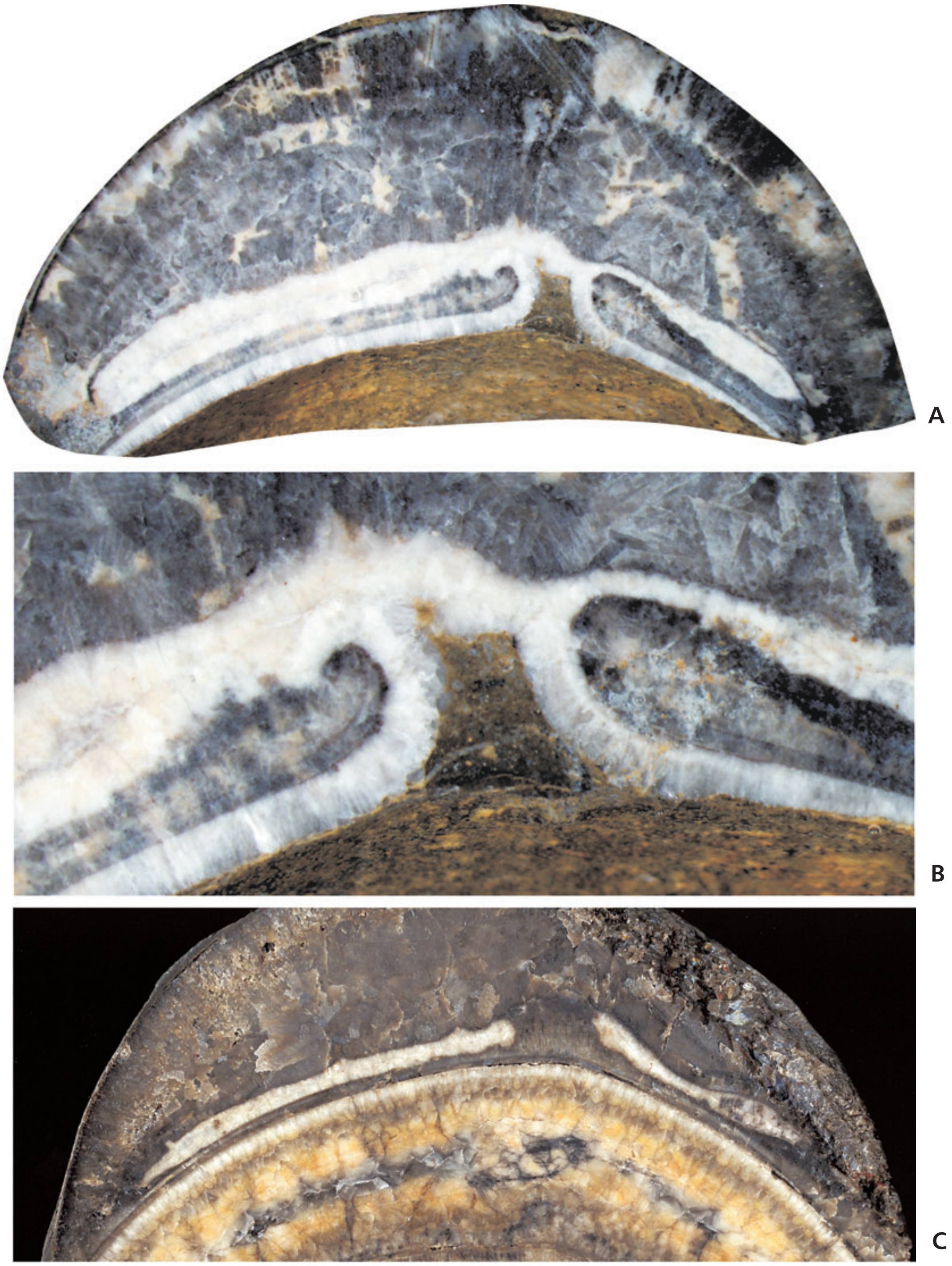


Figure 10. *Sphooceras truncatum* (Barrande, 1865). • A, B – specimen NM L 40921b, Ludlow, *Neodiversograptus nilssoni* Zone, Praha-Butovice; first chamber of adult specimen almost completely filled by cameral deposits and detail of siphonal opening; thin hyposeptal cameral deposits cover also free part of septum and septal neck being more heavily developed ventrally, A (× 2.1), B (× 6). • C – specimen NM L 40919b, Ludlow (see Fig. 4), Praha-Braník, Školní vrch, Kopanina Formation. Sagittal section, first chamber almost completely filled with cameral deposits, × 1.7.

phragmocone chamber through the siphuncle. Similarly, in Recent *Nautilus* "muscle fibres in the mantle as well as blood vessels located within the septal mantle and on its visceral side occasionally leave imprints on the inside of the wall of the body chamber and the apertural side of cephalopod septa" (Klug *et al*. 2008, p. 485). Their origin is attributed to soft tissue responsible for the secretion of these deposits.

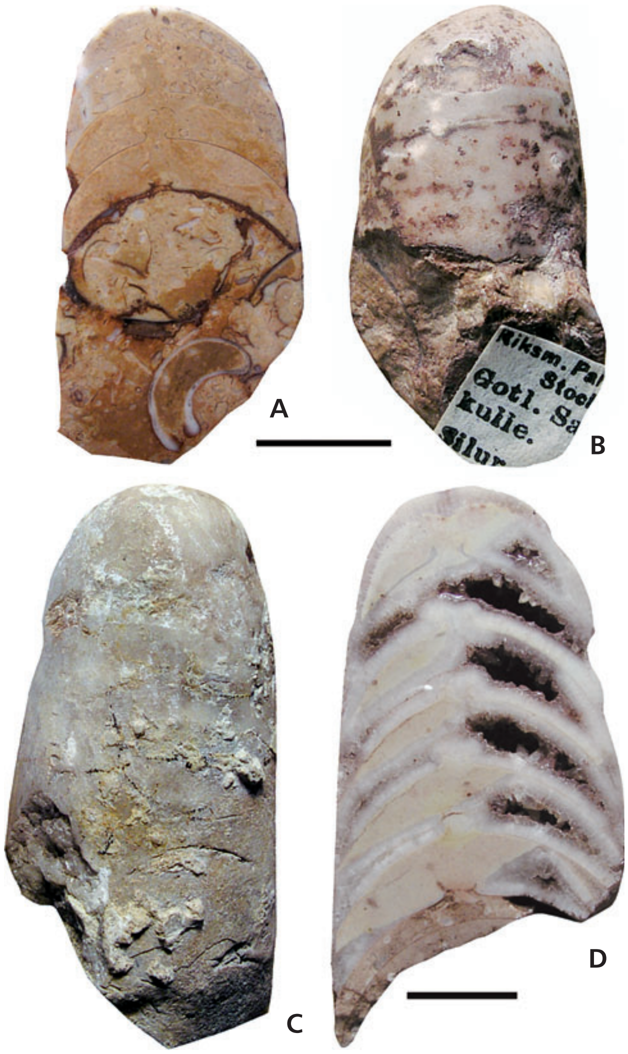


Figure 11. *Sphooceras truncatum* (Barrande, 1865). Incomplete specimens cut in median plane; see also Fig. 9C, E. • A, B – specimen RM Mo 42513, Ludlow, middle Ludfordian, *O. sagitta* Zone, Sandarve Kulle, Gotland, Hemse Beds, upper part. • C, D – RM Mo 42801, Wenlock, Sheinwoodian, Slite beds, Othem, Gotland. Different stages of development of cameral deposits. The convexity (high) of the first phragmocone chamber is highly variable. Scale bar: 10 mm.

Secretion of cameral deposits probably resulted from the opening of the thin uncalcified connecting ring into the first phragmocone chamber – a phenomenon discussed and documented in detail for some other straight-shelled cephalopods by Kolebaba (1999a, b, 2002). His observation supports Flower's idea (1941, 1955) about a direct connection between the siphonal tissue and the cameral mantle.

The presence of soft tissue in the first phragmocone chamber of *Sphooceras* is well documented by Barrande's illustrations (Barrande 1868, pl. 341). The space that was available for the soft tissue initially lining the first phragmocone chamber gradually became smaller, as the cameral deposits grew. The free space acquired an irregular, flattened lenticular shape.

Outer layers covering the callus and their origin

The following scheme of secretion of additional calcareous layers on the outer shell surface is proposed: as the mantle completely covered the shell, it initially deposited a layer with roughly concentric wrinkled striae, in a somewhat fingerprint-like pattern, on the exposed cameral deposits. The plugged siphonal opening shows finer striae, in a more geometrically precise concentric pattern; in some specimens, fine radial striae are also discernible. An interesting feature of the layer with the fingerprint pattern is a disruption in the course of the individual striae by V-shaped invaginations, situated on the ventral and dorsal sides of the conch, but not always in the plane of symmetry (Figs 2M, 5F, 15J, 16B). These may indicate places where two extended mantle lobes met. With regard to the position of this layer on the shell and supposed mode of secretion the layer is compared with the nacreous layer in other cephalopods. In agreement with published opinions concerning the wrinkle layer in ammonoids, bactritoids and nautiloids (Doguzhaeva & Mutvei 1986), wrinkles might have served for the attachment of the mantle and to control its movement in this region during secretion of layers on the "naked" convex surface of the cameral deposits. A very thin layer bearing a colour pattern in the dorsal half of the shell then overlaid the wrinkled layer. The mode of secretion of these two layers on the outer shell surface could have been similar to cypraeid gastropods (see Savazzi 1998) in which the shell has been temporarily completely covered by mantle and a new layer was deposited on the surface. Similarly some bellerophontoids had a part of the last whorl cowered by mantle extended from the aperture as it can be indicated from the morphology of their shell (Harper & Rollins 1985, Frýda & Gutiérrez-Marco 1996).

In some specimens of *S. truncatum*, the finger-pattern layer is missing (*e.g.* Barrande 1868, pl. 343, figs 11–13) and the surface of the apical part of the shell is radially striated (Figs 2O, 16H). In the case where no additional layers were deposited, such a shell can be interpreted as that left by the animal dying just after truncation, or as a result of secondary dissolution of both layers – the finger-pattern layer and smooth outer layer with the colour pattern. Similarly, in some specimens studied, the finger-pattern layer was the last one to form the outer surface of the apical region (Figs 5B, F, 15B, J). As the outer layer was very thin in the apical part of the shell, this state of preservation probably resulted from partial or complete dissolution of the outer layer during post-diagenetic processes or from weathering. The radially striated layer (specimen MCZ

Figure 12. *Sphooceras truncatum* (Barrande, 1868). Ludlow, Kopanina Formation. Specimens sectioned in median plane. Ludlow, *Neodiversograptus nilssoni* Zone, Praha-Butovice, Kopanina Formation. • A – specimen NM L 41313; notice thin apical callus and crater-like depression in place of plugged siphuncle. • B–D – specimen NM L 41032; B – incomplete phragmocone [apical chamber(s) missing], C, D – details of last two septa; notice thickened next-to-last septum, owing to fusion of septum with episeptal deposits (comp. also Fig. 13A, D, E). Scale bars in A and B equal 5 mm, C and D 2 mm.

160328) can be sometimes seen just under the translucent outer shell wall, especially in the abapical part of the first chamber. It seems probable that in this part of the shell, the secretion of the layer with roughly concentric wrinkles was suppressed. The finger-pattern layer has not yet been observed in any *S. disjunctum*.

Secretion of additional calcareous layers in the remaining part of the shell during mantle extension was very limited. It is possible that secretion of these layers probably proceeded from the apex down as the uppermost layer is reduced abapically (Barrande 1860). If this thin layer was deposited on the whole surface of the shell is not clear but this could explain why the shell surface in *Sphooceras* is usually entirely smooth, or with hardly discernible growth lines (*e.g.* Figs 2A–G, 5B–D, L–N), lacking typical healed damages of the shell so frequently occurring in nautiloids. It is supposed that the pigment-bearing layer in *Sphooceras* was confined to the outermost portion of the shell wall, as in present day *Nautilus* (Valenciennes 1841). Although only fragments of the shell are preserved in the second and third chambers of the specimen discussed, the absence of any traces of colour pattern in the adjoining part of the phragmocone is remarkable. It may indicate that secretion of the layer bearing the colour pattern did not exceed the

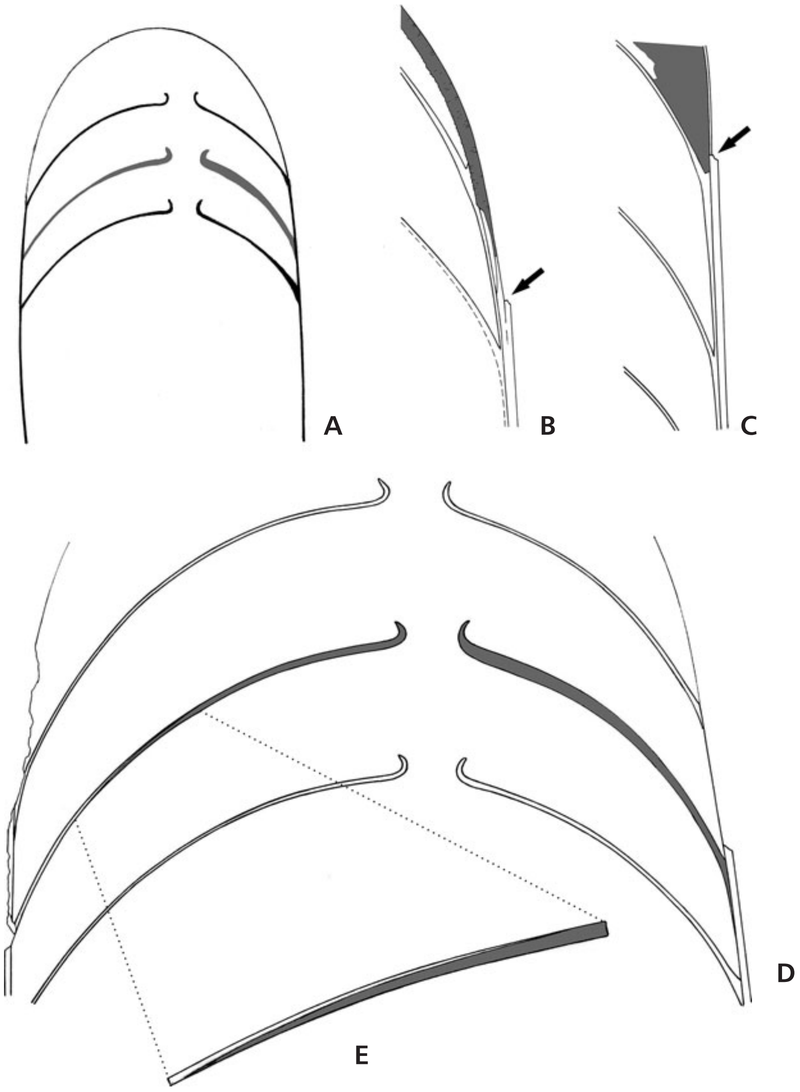


Figure 13. Drawing of specimens sectioned in median plane. • A, B, D, E – *Sphooceras disjunctum* (Barrande, 1868). Ludlow, *Neodiversograptus nilssoni* Zone, Praha-Butovice, Kopanina Formation. • A, D, E – specimen NM L 41032; A – incomplete phragmocone and adjacent part of body chamber; apical chamber(s) missing; D – detail of last two chambers; outer shell wall partly exfoliated during collection; E – part of septum fused with episeptal deposits. • B – specimen NM L 40938a (see also Fig. 7A, D), detail of ventral side. • C – *Sphooceras truncatum* (Barrande, 1860); specimen NM L 40919A; Ludlow, latest Gorstian or earlier Ludfordian, Praha-Braník, Školní vrch, Kopanina Formation; detail of dorsal side (see also Fig. 4). Arrows indicate site of truncation. Not in scale.

borderline separating the apical region of the shell from the rest of the phragmocone. It shows that the secretion of the outermost shell layer was not a uniform process; the layer covering calcareous deposits forming the callus was formed after truncation.

In *Sphooceras*, the internal structure and the possible covering of the shell by the mantle in some growth stages of the shell indicate an analogy with the rostrum of belemnites, an idea already expressed by Barrande (1860).

Truncation – an overlooked feature of cephalopod evolution

Contrary to soft-bodied coleoids, the maximum evolutionary size of externally shelled cephalopods might have been constrained by physiological limits. The shell size was one of the features, which also affected its physical properties, such as resistance to hydrostatic pressure, drag, and hydrodynamics. In straight-shelled possible planktonic cephalopods, some shells with low expansion rates occurring in Prague Basin reached huge diameters (200–250 mm) and it is hard to imagine that the creature inside could handle such a shell. The morphological features of the shells also strongly influenced swimming modes of the shells. Several cephalopod lineages evolved a common solution to this problem: rejection of the apical part of the phragmocone, namely truncation. This perhaps common mode of shortening of the phragmocone is not yet well understood. Development of an anomalous septum and closing of the siphonal tube usually preceded truncation.

Truncation in *Sphooceras*

Due to the discrepancy of opinions concerning the truncation in cephalopods, the question has been reopened (Turek

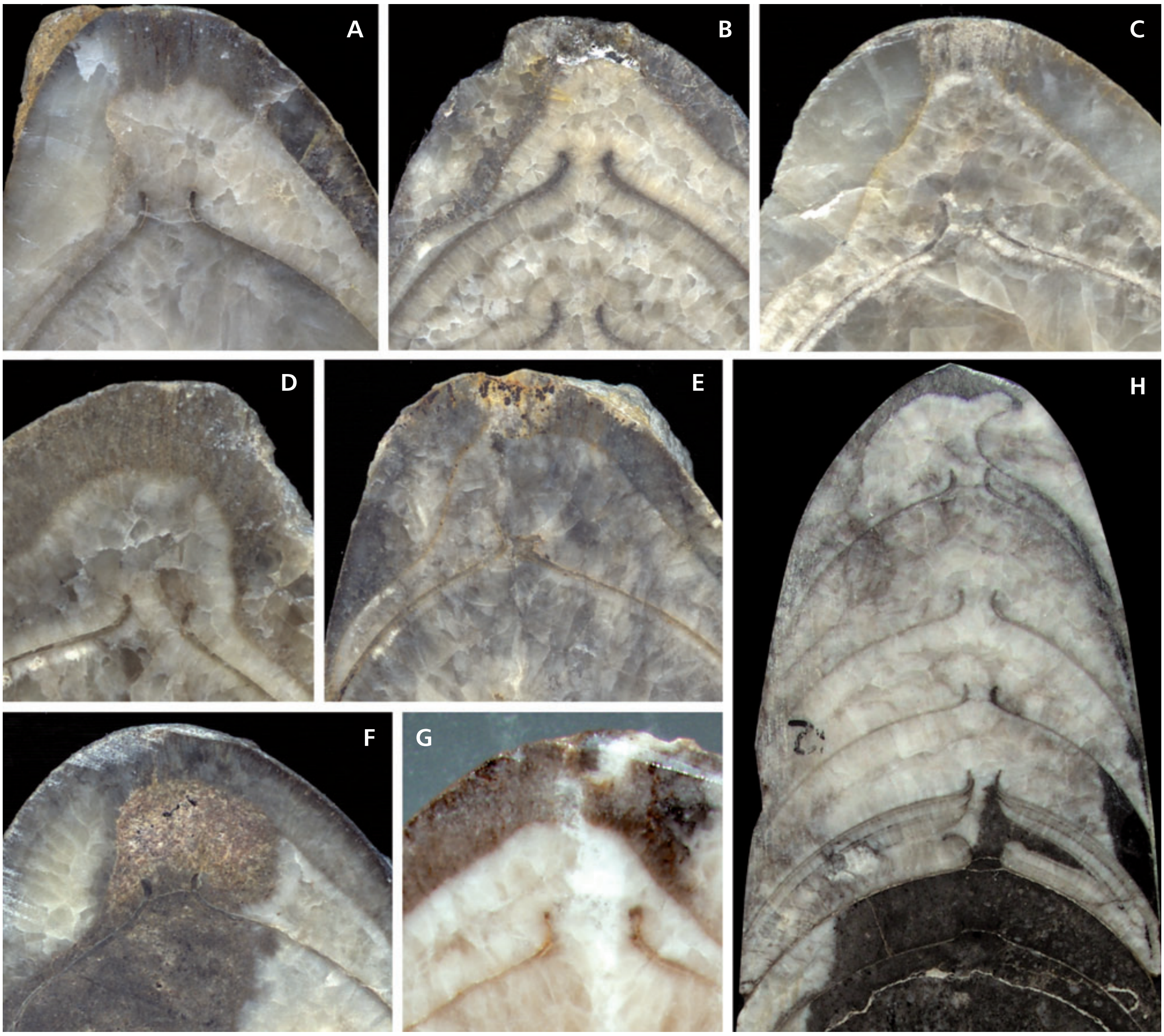


Figure 14. *Sphooceras truncatum* (Barrande, 1865), Ludlow, Kopanina Formation, Bohemia. Specimens sectioned in median plane, details of apical parts; A–F – notice strong asymmetry of cameral deposits, differences in their thickness, shape, their radial structure and orthochoanitic to suborthochoanitic septal necks. • A – specimen NM L 40932a, Zadní Kopanina, × 2.7; see also Fig. 3A. • B – specimen 40928a, vicinity of Prague, × 2.9. • C – specimen NML 40926a, Zadní Kopanina, × 3.4. • D – specimen NM L 40927a, Zadní Kopanina, × 3.7. • E – specimen NM L 40933a, Zadní Kopanina, × 2.6. • F – NM L 40925a, vicinity of Prague, × 3.6. • G – NM L 40979, Zadní Kopanina, × 3.8. • H – specimen MCZ 160432, Kosoř; besides apical callus both episeptal and hyposeptal deposits present in 5th phragmocone chamber, × 2 (comp. also Figs 3F and 9D).

2007). Existence of this process in *Sphooceras* is supported by the following observations:

a) The shell has a very short phragmocone with a limited number of phragmocone chambers – three to eight (documented in specimens of *S. truncatum* with measured dorsoventral diameter ranging from 2 to 85 mm (early juvenile growth stages possessing protoconcha and probably belonging to *Sphooceras* are not included) and three to five in *S. disjunctum* with dorsoventral diameter ranging from 12 to 31 mm;

b) A characteristic structure of the apical portion of the shell contains a strongly narrowed and then plugged siphonal perforation and thickened apical end of the shell in different ontogenetic stages. A different pattern on the surface of the apex is sometimes due to exfoliation of a layer or may be a result of a primary condition – death of the animal just after truncation or in different stages of secretion of outer layers;

c) Two shell layers cover the convex apical surface formed by naked cameral deposits – the inner one with the characteristic finger print pattern and the outer layer, which is smooth;

d) Discontinuity of growth can be traced in the boundary between the truncated part and the rest of the shell – annular groove and sometimes thickening of the shell along this boundary, disrupted course of growth lines and sudden disappearance of colour pattern,

e) Discontinuity in the structure of the shell wall has been observed in polished sections;

f) Presence of episeptal deposits in one another phragmocone chamber (besides the first chamber) was discovered in two specimens – a supposed symptom preceding later truncation;

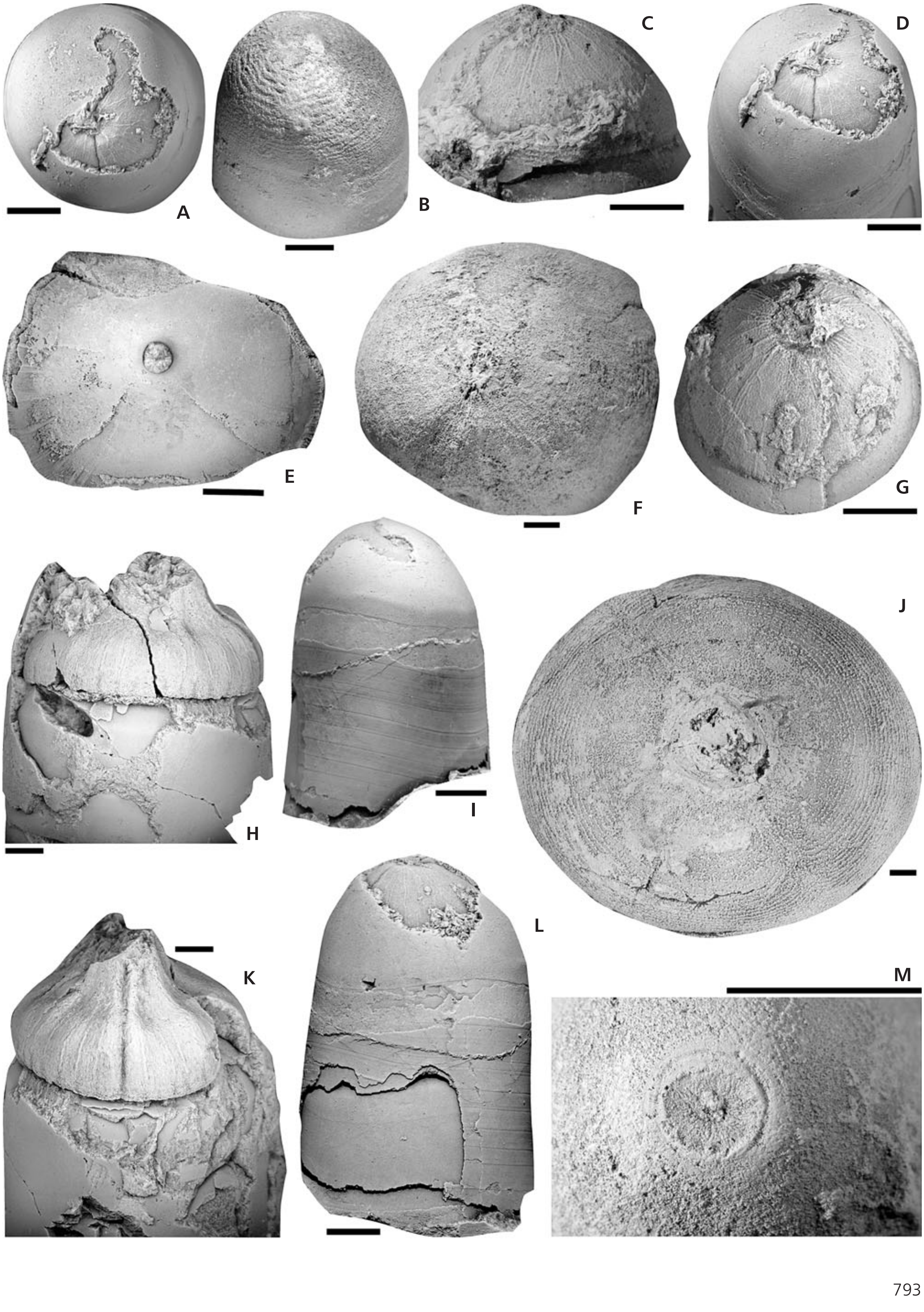
g) Complete shells of *Sphooceras* co-occur with isolated apical parts, which may represent truncated portions of the shells;

h) Findings of early juvenile shells having to 6 to 8 phragmocone chambers.

As it is indicated in one specimen *S. disjunctum* cut in medium plane (NM L 41032, Figs 12B–D, 13A, D, E) thin episeptal deposits gradually fused with adjoining septum so that the border betweem septum and deposits disappeared. The septum is markedly thickened, its colour is dark brown; its original structure was probably changed. Next steps of growth of cameral deposits are supposed: In subsequent stages the content of organic matter in cameral deposits markedly increases forming radial lamellae and the composite structure septum-episeptal deposits changes into new shell structure – apical callus. Formation of a calcareous plug closing the septal foramen follows. Secretion of these structures preceded the periodic natural removal of the apical part of the shell, comprising four to five phragmocone chambers in *S. truncatum* and two or perhaps even only one in *S. disjunctum*. In *S. truncatum*, the episeptal deposits were secreted in the 5th or 6th chamber and in *S. disjunctum* with wery short phragmocone in the last or penultimate chamber. Adapical part of the shell has to be uncovered by the mantle before truncation. Whether the mantle was completely or only partially retracted into the body chamber before truncation is not clear. The annular belt bordering the first chamber is interpreted here as the detachment zone. After truncation, the mantle might have completely surrounded the new apical region and secreted the two additional calcareous layers mentioned above. The ability of the animal to repeatedly entirely cover its shell with its mantle in these growth stages was facilitated by a very short phragmocone and a long body chamber (see also Kröger 2002). This process is substantiated by the discovery of a colour pattern in the apical region of the shell, which could not have been secreted by cameral mantle (comp. Gnoli & Kiselev 1994) as the siphonal opening from which siphocameral tissue could be theoretically expanded was already plugged. Also, it seems highly improbable that this internal tissue contained pigments cells having ability to secrete colour pattern. Dark brownish longitudinal stripes are present on the dorsal half of the shell only. This pattern, together with the general morphology of the shell supports the idea of a horizontal living position in this cephalopod, for which nectonic or nectobenthonic mode of life is presumed. Functionality of the colour pattern depends on its visibility, so the soft tissue covering the new apex may have been translucent, or the mantle was retracted from the new apex after secretion of the outer layer containing colour pigments. The camouflage effect would have been improved by pigmentation of the soft tissue.

Based on the number of phragmocone chambers in individual specimens and the size of the largest ones, Barrande (1860) estimated that truncation, during which *Sphooceras truncatum* losted three to five phragmocone chambers could have happened about 50 times during ontogeny of the largest specimens, which, without truncation would have attained a length of 160 cm. Barrande (1872) amended this opinion, calculating that having the dorsoventral diameter 80 mm and average apical angle 8° would result in a total shell length (without truncation) of about 530 mm. Truncation then could have been repeated 24 times. According to our investigation, based on a recently discovered specimen, the total length of this largest known specimen possessing 8 phragmocone chambers was only about 260–270 mm and total shell length without truncation would have been about 700 mm). We consider constant apical angle 8°, and body chambere representing one and half of the length of phragmocone (*i.e.* 8 phragmocone chambers).

Figure 15. *Sphooceras truncatum* Barrande, 1860; A, B, D–F, H–M – Ludlow, Kopanina Formation, C, G – Wenlock, Gorstian, Motol Formation, *Testograptus testis* Subzone. • A, D, I, L – specimen NM L 40943, Praha-Butovice, *Neodiversograptus nilssoni* Zone; incomplete phragmocone, apically partially exfoliated with preserved replica of cameral deposit surface, with impression of vascular tissue; apical (A), oblique apical (D), dorsolateral (I) and lateral (L) views; note detachment zone and abrupt ending of shell sculpture due to truncation. • B – specimen NM L 40962, Beroun, Kosov Quarry; apical part of shell covered by finger-print pattern layer bearing crinoid holdfast. • C, G – specimen NM L 40961, Praha-Řeporyje, Arethusinová Gorge; apical part of shell; replica of cameral tissue surface, frontally with relict of finger-print patterned-layer, lateral (C) and oblique apical (G) views. • E, F – unfigured paratype of "*O. sarcinatum*" Barrande, 1868, *Neodiversograptus nilssoni* Zone; apical part. First septum from internal (concave) side (E); note radial structures of cameral deposits close to margin; weathering of convex surface reveals spongious structure of cameral deposits, radial structures and fragment of layer with finger-print pattern close to the right margin (F). • H, K – specimen NM L 9180 illustrated by Barrande (1868, pl. 341, figs 1–5), see also Fig. 2H in this paper, Zadní Kopanina, Zmrzlík; apical part with replica of cameral tissue on concave surface of almost completely removed cameral deposits, preserved on sparitic infilling of first phragmocone chamber. • J – lectotype NM L 9184, Praha-Butovice, *Neodiversograptus nilsoni* Zone; finger-print pattern on apical part of shell; note asymmetrically located V-shaped invagination of wrinkles; see also Fig. 2M in this paper. • M – specimen NM L 9193, Zadní Kopanina; detail of apex showing infilling of septal perforation (plug). Scale bar: 5 mm.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Truncation in other cephalopods: comparison with *Sphooceras*

Truncation is thought to have evolved independently in some other cephalopods besides *Sphooceras*. Barrande (1860) mentioned some other straight-shelled cephalopods, one oncocerid (gomphocerid) and ascocerids in which he considered truncation a certainty, and subsequent researchers confirmed this conclusion. Flower (1964) was also convinced of the process in Ecdyceratida. Furnish *et al.* (1962) mentioned truncation in the Carboniferous orthocerid *Brachycycloceras*, but in this case, Niko & Mapes (2010) raised doubts. Stridsberg (1985) documented truncation in three brevicone oncocerid species from Gotland.

Truncation in ascocerids was supported by Lindström (1890) on the basis of well-preserved specimens from Gotland. He supposed that the ascocerid phragmocone was broken off several times during ontogeny, a theory later widely accepted (Flower 1941, 1963a; Furnish & Glenister 1964; Holland 1999). Frye (1982, p. 1275), studying Ordovician ascocerids, stated that it was not certain "whether truncation occurred ontogenetically or post-mortally" in these nautiloids and Dzik (1984, p. 111, 135) briefly discussing this problem in context with *Sphooceras* as well as the Ascoceratidae and *Brachycycloceras* concluded: "One cannot suggest any reasonable mechanism of shell truncation." The fact that, with a few exceptions, the "ascoceras stage" occurs separately from the "cyrtoconic stage" of the shell (*sensu* Lindström) he explained as secondary, caused by sampling. In *Brachycycloceras* he supposed that truncation is insufficiently supported.

Although ascocerids are generally very rare fossils, surprisingly rich material containing 71 specimens was gathered during recent fieldwork by Ladislav Zedník, Štěpán Manda and Ladislav Čížek in the Prague Basin. None of the specimens has the juvenile part of the shell, and careful fieldwork excludes the possibility that the juvenile part was lost during excavation. Holland (1999) concurs with earlier researchers regarding truncation in *Ascoceras*. In discarding the adapical cyrtoconic part of the shell, the animal acquired a more streamlined shell shape with greater resistance to mechanical damage by shallow sea dynamics (see also Holland 1999, Gnoli & Kiselev 1994). Solid evidence for the truncation in the Ordovician ascocerids was recently given by Kröger (2007).

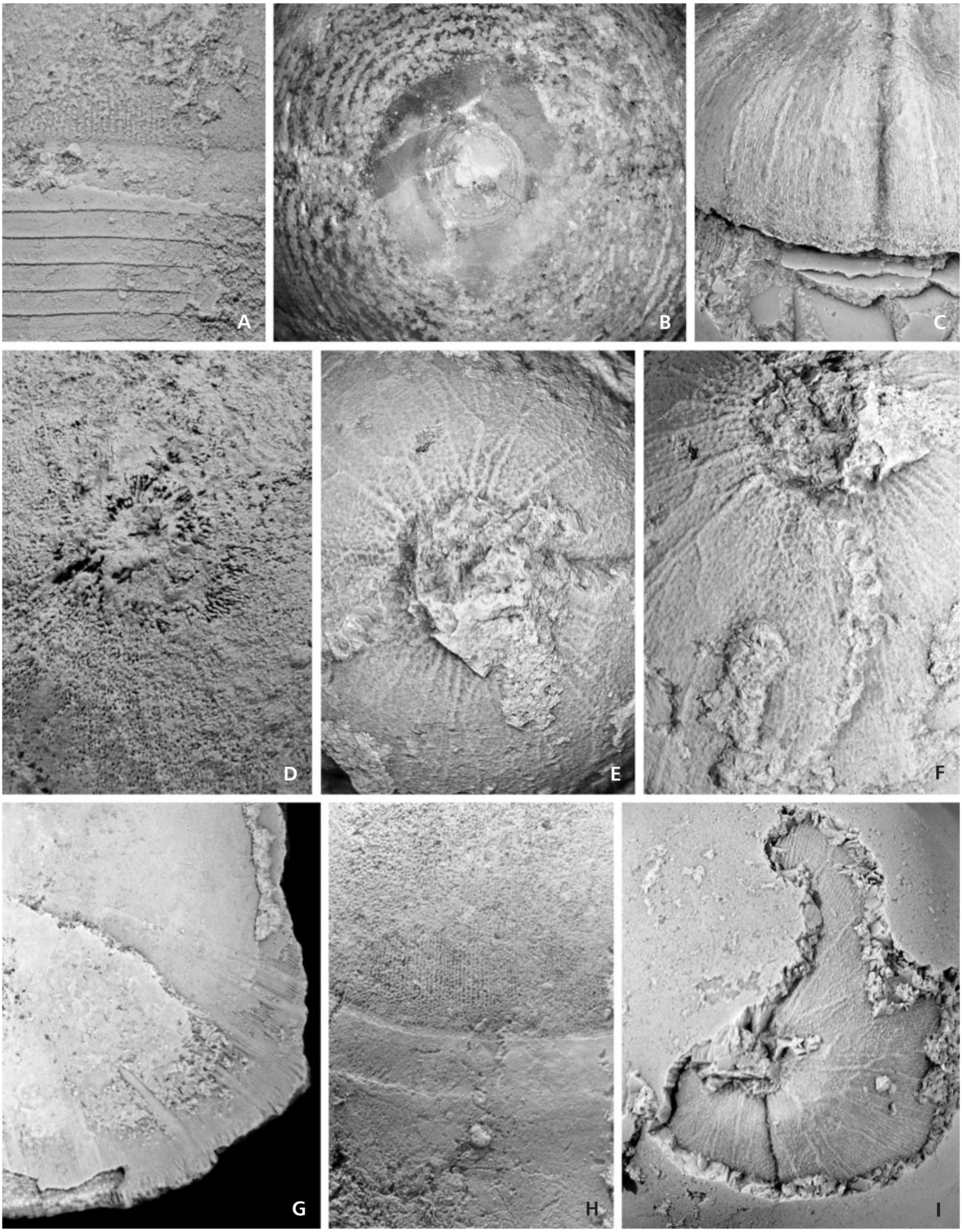
Although truncation in *Sphooceras* achieved similar results to the supposed truncation in the above-mentioned nautiloids, the actual processes differ substantially:

As the real apex of *Sphooceras* is never formed by typical septum, Turek (2007) supposed that the septum of truncation remained with the discarded portion of the shell. However, separation of septum from adjacent episeptal deposits during truncation has not been explained in a satisfactory manner. On the other hand the structure of cameral deposits forming apical callus and structure of septa differs substantially and therefore natural detachment of both layers could be possible. Owing to discovery of an exceptionally well-preserved specimen of *S. disjunctum* a more realistic alternative discussed above is proposed. In the remaining portion of the shell, the apical end was formed by a composite shell part – septum fused with episeptal deposits. During continued growth of the animal, secretion of two additional layers followed, overlying the callus from the outside. The inner fingerprint pattern layer (thought to be the nacreous layer) and smooth outer layer (with colour pattern, thought to be the outer prismatic layer) were secreted by the mantle, extended from the body chamber.

In ascocerids, a thickened septum of truncation formed after decollation of the apical end of the mature shell, and probably no additional layer was deposited on its outer surface. A long body chamber as well as the position of the phragmocone above the body chamber in the late growth stage theoretically enabled extension of the mantle to protect the thin-walled shell. However, if some fragments of the deciduous shell remained attached to the part occupied by the living animal, they would have prevented covering of the septum of truncation by soft tissue (Furnish & Glenister 1964). In any case, no proof has been found for extension of the mantle in ascocerids.

Stridsberg (1985, pp. 16–18) discussed in detail the truncation in the two oncocerid genera – *Trimeroceras* and *Pentameroceras*. The septum of truncation in these "gomphocerids" is thicker and more strongly curved than other septa. He mentioned and illustrated the specimen just before truncation; the septum of truncation is not the last preserved, but next to last. Interestingly, the shell wall in the

Figure 16. *Sphooceras truncatum*, Ludlow, Kopanina Formation, Bohemia; details. • A – specimen NM L 21467 illustrated by Barrande (1870, pl. 448, figs 3–5), Fig. 5I herein, Slivenec, valley; detail of surface in adapical part of shell with growth lines, detachment zone and radial structure of cameral deposits emerging here to the surface, × 5. • B – specimen NM L 9194, illustrated by Barrande (1868, pl. 343, figs 4, 5); apex showing plugged siphonal opening and surrounding deposits (smooth layer), sharply delimited from finger-pattern layer, × 5.7. • C, E, F, I – natural cast of vascular imprints on the concave surface of cameral deposits; lateral, top and oblique views; C – specimen NM L 9180 illustrated also in Figs 2H, 15H, K, Zmrzlík, × 8.9. • D, G – specimen NM L 40922, Praha-Butovice, *Neodiversograptus nilssoni* Zone; D – spongious structure of cameral deposits in "*O. sarcinatum*", seen on their weathered surface; apical view, see also Fig. 15F, × 6; G – the same specimen, radial structure on the concave surface of cameral deposits, see also Fig. 15E, × 3.3. • E, F – specimen NM L 40961, Praha-Řeporyje, Arethusinová Gorge, × 8. • H – specimen illustrated here also in Fig. 5C; detail of surface of cameral deposits and detachment zone, × 4.8. • I – specimen NM L 40943, apical part with partly exfoliated shell with replica of soft tissue surface; see also Fig. 15A, D, × 5.4.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oldest preserved chamber is much thinner than the shell wall in the adjacent part of phragmocone. He states: "The reason for this decreasing thickness might either be internal resorption, or absence of the internal reinforcement occurring in later chambers."

Natural removal of the apical part of the shell by other means than mechanical breakage is not limited to nautiloids and straight-shelled cephalopods. Doguzhaeva & Mutvei (1989) documented removal of the initial part of the shell in heteromorphic lytoceratid *Ptychoceras.* Based on investigation of the shell structure in this ammonoid, they concluded that its shell might have been at least partially covered by mantle during its lifetime. An interesting case of truncation was described in *Hematites*, one of the oldest-known (Early Carboniferous) coleoids (Doguzhaeva *et al*. 2002). The initial portion of the phragmocone was plugged by a central rod structure of the rostrum and contained an additional septum. Some analogy with *Sphooceras* can be found in this process, which was concluded by the rostrum formation in *Hematites*.

It appears highly probable that the truncation of the apical portion of the shell was much more widespread in Early Palaeozoic cephalopods than was previously assumed. Temporary encasement of the entire shell in *Sphooceras* is here assumed as certain. Bandel & Stanley (1989) suggested that the conch of the Devonian genus *Atrhrophyllum* with characteristic deposits developed in posterior chambers of the phragmocone might have been external as well as internal.

Ecology of *Sphooceras*

Conclusions concerning its ecology are based especially on the study of *Sphooceras truncatum* and *S. disjunctum*, the best-known species of this genus. Early juvenile specimens of *Sphooceras* may have lived as pelagic forms (Manda & Frýda 2010). In discussions on buoyancy and swimming activity of later growth stages, the following aspects have been considered: a) general morphology; b) correlation between shell growth, development of the apical callus offering a counterweight to prolonged phragmocone and length of the body chamber; c) a very short phragmocone, which periodically changed its length and the ratio between the length of the phragmocone and the length of the body chamber; d) the formation of cameral deposits before truncation; e) the colour pattern limited to the dorsal half of the shell only, suddenly diminishing behind the area of truncation.

It is speculated that *Sphooceras* was a nektonic or nektobenthonic animal with neutral buoyancy, maintaining its shell in a horizontal position (Fig. 21). This is supported by the following features: a) hydrodynamic shape of the shell with smooth surface; b) very thin shell walls, so that the shell was very light; c) oblique course of the aperture to shell axis; the dorsal side is thus longer, protecting the head while the shorter ventral side gives more space for protrusion of the powerful hyponome; d) phragmocone possessing cameral deposits and is always shorter than the body chamber, so encasing of the whole shell by soft tissue was possible; e) siphuncle is shifted slightly ventrally from the centre, so that septa are vaulted more ventrally then dorsally; f) shapes of cameral deposits forming an apical callus are in correlation with the prolongation of the phragmocone; their thickness is greater in the ventral part of the shell than the dorsal, giving the shell a preferred floating orientation; g) longitudinal colour stripes are developed only on the dorsal part of the shell, creating a camouflage effect from above.

The proposed nektonic or nektobenthonic mode of life corresponds with the opinion of Gnoli & Kiselev (1994), who viewed truncation in *Sphooceras* as a "step towards modern cephalopod evolution, obtaining a very streamlined body, such as modern coleoids, which supports its manoeuvrability and more efficient swimming".

Periodic shortening of the phragmocone may seem as a traumatic event strongly disturbing supposed maintaided horizontal position of the shell. However, it probably did not significantly influence buoyancy. Although the animal lost three or four phragmocone chambers at a time, positive buoyancy of this part of the shell was gradually reduced by progressively growing cameral deposits. The apical callus, which was still only slightly developed at the time of truncation, was perhaps sufficient for maintaining neutral buoyancy and a horizontal life position of the shell after truncation, *i.e.* centre of buoyancy was speculatively located just above the centre of mass. Regarding the role of cameral liquid in maintaining floatation equilibrium during truncation, we can only speculate.

Cephalopods with straight shells have been considered to have been active swimmers (Flower 1957, Furnish & Glenister 1964, Teichert 1964), but according to some recent views (Mutvei 2002) the dorsal position of their muscle scars shows that their swimming ability was weak, possibly even indicating a planktonic lifestyle (Mutvei 2002, Kröger *et al.* 2005, Klug *et al.* 2010). The possibility of negative buoyancy and a benthic mode of life of orthocerids was proposed by Ebel (1999), but has not been widely accepted. Some straight-shelled cephalopods, however, possess some very progressive features, similar to coleoids (for summary see Mehl 1984, Engeser 1996, Gabbot 1999). The question remains, whether the mechanism of swimming in these cephalopods was the same as in the Recent *Nautilus.* Rapid swimming in the Recent *Nautilus* is produced by contraction of powerful retractor muscles attached to the lateral sides of the shell wall in front of the last septum, which pull the body into the shell. This is accompanied by simultaneous contraction of the

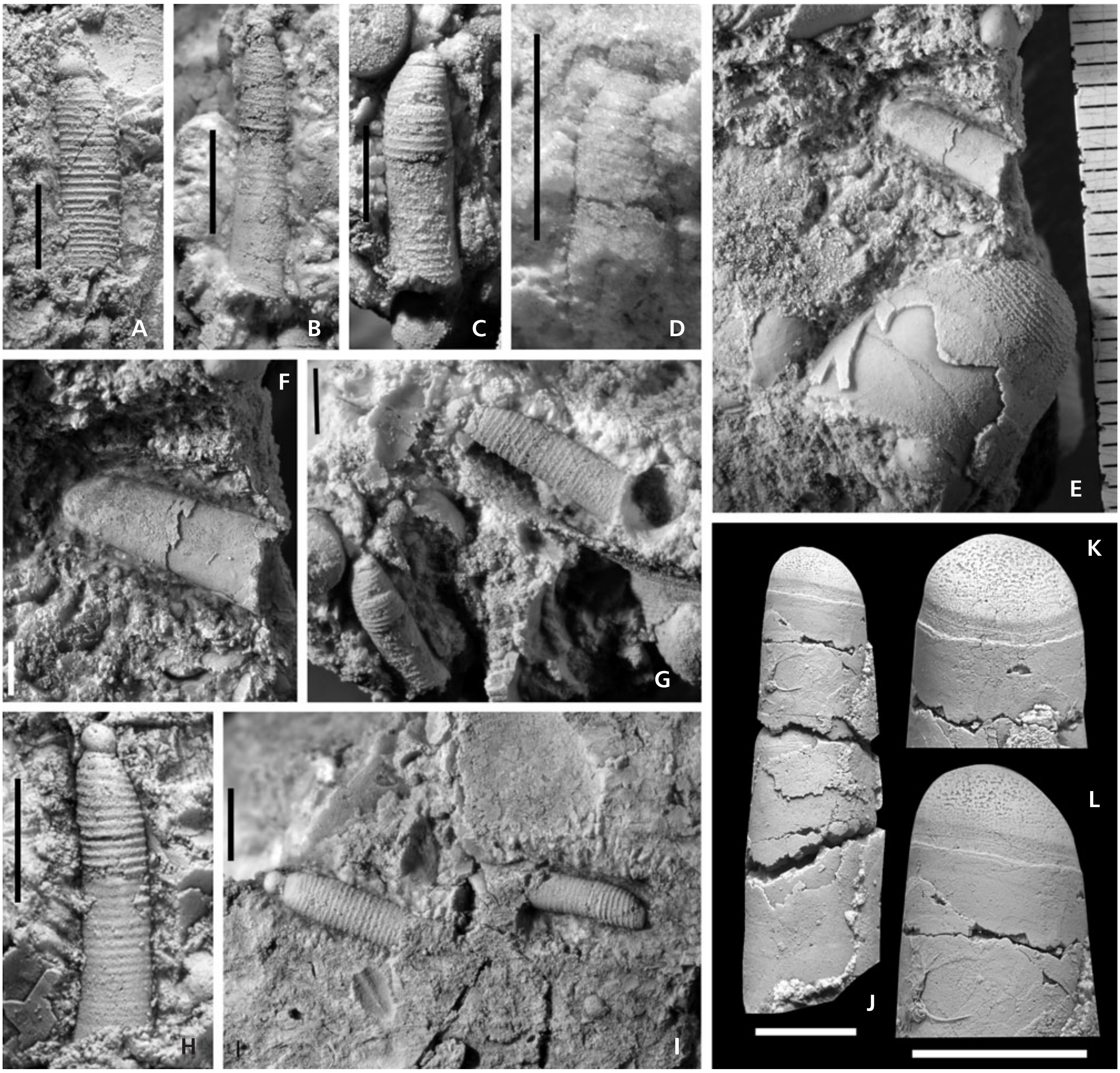

Figure 17. A–D, G, H, I – possible early stage of S*phooceras truncatum* (Barrande, 1860). Ludlow, *Saetograptus linearis* Zone, Zadní Kopanina, Draská Gorge, Kopanina Formation; early growth stages of shell with preserved protoconchs; note marked constriction of protoconcha, slight constriction of shell in lateral view, annuli fading adaperturally and unusual course of transversal sculpture (Fig. 17C). • A – specimen NM L 40966. • B – specimen NM L 40967. • C – specimen NM L 40968. • D – specimen NM L 40969. • G –specimen NM L 40970. • H – specimen NM L 40971. • I – specimen NM L 40972, two juveniles – ventral and dorsolateral views. • E, F, J – *Sphooceras truncatum* (Barrande, 1860). Ludlow, *Saetograptus linearis* Zone, Zadní Kopanina, Draská Gorge, Kopanina Formation. • E – specimen NM L 40973, damaged juvenile specimen associated with three phragmocone chambers (?detached portion of shell) of larger specimen. • F – enlarged younger specimen illustrated in Fig. 17E. • J – specimen NM L 40 974, young damaged specimen from lateral and dorsal views. Scale bar: 2 mm (A–I) and 5 mm (J–L).

hyponome (Mutvei 2002b). He stated that the contraction of the retractor muscles in orthocerids attached to the dorsal side of the shell close to the last septum "could not be used to expel water from the mantle cavity for swimming by jet propulsion, as in *Nautilus*" (p. 391). Considering the superficial similarity of *Sphooceras* and some other straight-shelled cephalopods to some coleoids, it seems possible that the mantle was also liberated to become a muscular pumping organ that led to much more powerful jet propulsion, enabling rapid swimming (see also Barskov *et al.* 2008).

Sphooceras was widely distributed during the Wenlock and Ludlow in the tropical and subtropical shallow seas of Baltica, Kazachstania, Avalonia and Perunica, even reaching the somewhat colder waters of the peri-Gondwanan

Figure 18. A limestone sample with *Sphooceras*. Ludlow, early Ludfordian, *Saetograptus linearis* Zone; Zadní Kopanina, Draská Gorge; Kopanina Formation, × 0.9. The sample contains five different growth stages of *Sphooceras truncatum* (Barrande, 1860).

basins (Fig. 22). *Sphooceras* ranges from early Wenlock up to the Přídolí, with the most reliable fossil record appearing in the Tian-Shan Mountains and Bohemia. In others basins, *Sphooceras* occurs only in short intervals. Its abundance varies strongly, depending on facies (Figs 23, 24). It occurs very rarely in tropical carbonate platforms of Baltica and Avalonia. The distribution pattern of *Sphooceras* is best known from the Prague Basin. *Sphooceras truncatum* appeared there in the early Homerian and continued to the early Přídolí, with two Lazarus gaps after mass extinctions (Lundgreni/ Mulde and Kozlowskii/ Lau events). Its abundance fluctuated strongly through time and facies. Its fossils occur most commonly in cephalopod limestone facies, but also in other principal facies, such as shallow water brachiopod limestones or deeper water shales, which shows that populations of *Sphooceras* also inhabited oxygenated environments below wave base. Its presence in anoxic deeper water facies (*e.g.* graptolite shale) is strongly limited (Turek 1983, Manda 1996). In some places, *Sphooceras* became one of the most numerous species in cephalopod assemblages. Nevertheless, assemblages with very common *Sphooceras* occur in various environmental settings. The species is common (17% of collected cephalopods) in the early Homerian (Wenlock) sediments, in a thin cephalopod limestone bed, embedded in anoxic shales in Praha-Řeporyje, Arethusina Gorge. In this case, the population of invertebrates inhabited deeper water, during a short time span, when currents oxygenated the sea floor. In the early Ludfordian (early *S. linearis* Zone, Ludlow), *Sphooceras* occurs commonly (25% of collected cephalopods) in thin cephalopod limestone beds above shales/ mudstones and below thick grainstone banks (Mušlovka and Požáry quarries). In this case, the cephalopod limestones were deposited by currents active during earlier Ludfordian shallowing. The late *S. linearis* biozone (Zadní Kopanina, Draská Gorge locality) contains a slightly younger cephalopod limestone assemblage with abundant *Sphooceras* (20% of collected cephalopods, but with local accumulations in some thin beds). In this locality, the cephalopod limestone is rich in brachiopods, trilobites and gastropods; even tabulate corals are occasionally present. Although the rock is strongly dolomitized, the abundant benthic fauna indicates a deposition directly below the fair weather wave base, in very shallow water (to the SW, the cephalopod limestone passes into shallow water crinoidal grainstone).

Explaining this distribution pattern is difficult, especially since cephalopod shells are easily transported, sometimes over large distances. Usually, certain cephalopod species were fixed to an environmental setting and depth zone. Pelagic cephalopods are an exception, although their abundace increases toward open-sea facies (Fig. 23). The mosaic character of *Sphooceras* populations indicates strongly varying abundance – a distribution pattern somewhat resembling that of certain modern nektonic coleoids. The distribution pattern supports the recent conclusion that *Sphooceras* was an opportunistic active swimmer. Empty cephalopod shells served as suitable substrate for the attachment of epibenthic organisms, although epizoans rarely settled on shells of *Sphooceras*. Post-mortem colonisation with discoidal bryozoan colonies has been found in only two specimens. The finding of a complete exoskeleton of a Ludfordian trilobite *Encrinuraspis beaumonti* in a *Sphooceras* body chamber was used to support the moulting-refuge hypothesis, *i.e.*, the use of empty cephalopod shells as a hiding place during trilobite moulting (Davis *et al.* 2001).

Systematic part

Class Cephalopoda Cuvier, 1797
Angusteradulata Lehmann, 1967

Discussion. – Despite the fact that many new data concerning morphology, ecology, evolution, stratigraphic range and geographic distribution of Palaeozoic cephalopods have been accumulated since 1950, the classification of Palaeozoic cephalopods still rests strictly on morphological features. As the disparity and taxonomic value of these features have been understood differently by different authors, their approaches to classification of cephalopods have been quite varied. No consensus has been reached concerning the number of orders and subclasses, and their classification is therefore unsettled. Achieving a relatively stable state of classification in this macrosystem will depend not only on morphology, but also on evaluation of the disparity of morphological features and interpretation of the functional significance of this disparity (Barskov *et al.* 2008). However, to recognize the major evolutionary patterns in non-ammonoid cephalopods, more intensive studies of their early ontogeny is necessary.

Systematic position and classification of straight-shelled cephalopods with lamellar and pouch-like cameral deposits has long been a matter of discussion, and many discrepancies have appeared. Three main concepts have been published, although none have been widely accepted: Starobogatov (1974) proposed the suborder Lituitida, which Dzik (1984) accepted and he added the suborder Lituitina; Marek (1998) introduced the order Palliocerida and Zhuravleva & Doguzhaeva (2004) created the superorder Astrovioidea.

All these high-rank taxa are based on a similar presumption – the homology of cameral deposits, so we will address only one of them, the Palliocerida. Marek (1998) proposed the new order Palliocerida for cephalopods with indication of the primary presence of soft tissue in their phragmocone chambers. He distinguished two groups in this new order, according to the morphology of the cameral mantle derived from the morphology of cameral deposits: one with a pouch-like cameral mantle and one, in which the mantle consisted of radially arranged lamellae. He assigned the family Leurocycloceratidae Sweet, 1964 to the former and Lamellorthoceratidae Teichert, 1961 to the latter. One of the most important diagnostic features for Marek's new Palliocerida order is the presence of connecting rings with wide openings, so that internal space of the siphuncle is joined with the cameral space. However, Kolebaba (1999, 2002) documented a gradual opening of the siphuncle during ontogeny and the existence of connecting rings with both dorsal openings and no openings (tubular rings) within one specimen. Although he amended Marek's diagnosis of Palliocerida (Kolebaba 2002, p. 184), he noted that re-evaluation of this order would probably be necessary.

As opposed to the above-mentioned groups, *Sphooceras* is assigned here to cephalopods, in which the interconnection of the siphuncle and a single phragmocone chamber prior to truncation has been well documented. Interconection of only one segment of siphuncle with the first phragmocone chamber is the unique feature occurring in no other group of cephalopods. Discovery of episeptal and hyposeptal deposits in the centre of the phragmocone in one specimen only might be important (presuming it represents no anomally) and indicates that the taxonomic value of cameral deposits should be assessed carefully.

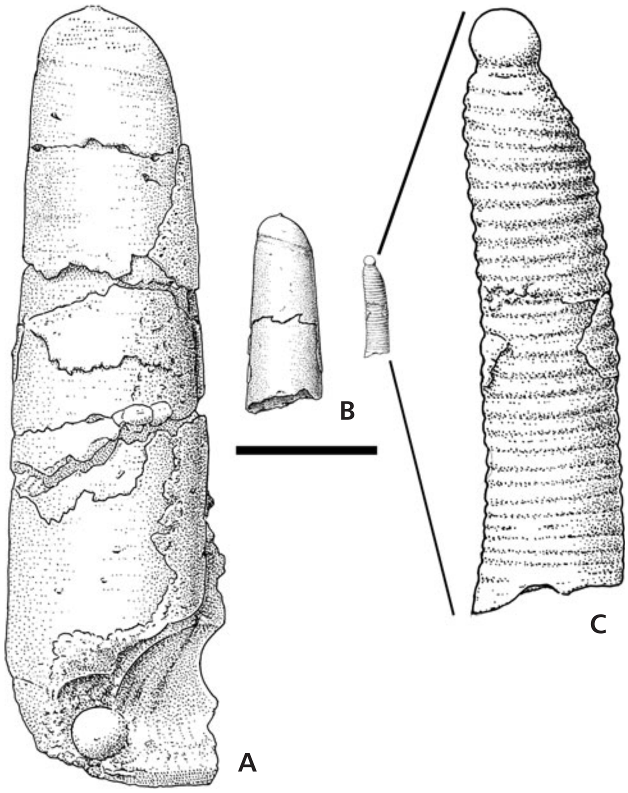

Figure 19. Early ontogeny of *Sphooceras.* Due repeated process of truncation the earliest growth stage cannot be assigned to this genus unequivocally. Based on specimens illustrated in Fig. 15F, J. Scale bar is 5 mm.

Based on the study of internal structures of some Palaeozoic orthocone cephalopods with so-called cameral mantle, Zhuravleva & Doguzhaeva (2002) established the new superorder Astrovioidea. Contrary to other cephalopod workers (*e.g.* Teichert 1961, Bandel & Stanley 1989, Dzik 1984, Kolebaba 1999a, b), Zhuravleva & Doguzhaeva (2002) made a big account of minor differences in morphology and structure of cameral deposits (see, *e.g.*, the discussion of *Lamellorthoceras* or *Plagiostomoceras*). Their interpretation of some structures is questionable and they place undue emphasis on the taxonomic value of those. Structure and character of cameral deposits is an important anatomical feature, but we do not share the opinion that its taxonomical importance is sufficient to warrant establishing a new taxonomic unit at the level of orders (see also Barskov *et al.* 2008). The crucial problem of all the above-mentioned concepts is their fixation on the structure of cameral deposits. Cambrian cephalopods have empty phragmocone chambers. Consequently, there is no evidence of homology of lamellar deposits in different groups of cephalopods, and cameral deposits were developed convergently. In any case, the construction and function of endocameral as well as endosiphuncular deposits must be better understood prior to its application to higher rank systematics.

A useful indicator of higher-level cephalopod classification is the morphology of embryonic shells. In straight-shelled cephalopods, there are substantial differences in the morphology of their embryonic shells, and these differences are much more distinct than in nautiloids. Embryonic shells thus provide a good basis for classification of straight-shelled cephalopods, and it may even be possible to split them into more orders. However, this depends on the correlation of juvenile shells with adult shells, so basically the entire ontogeny has to be known. *Orthoceras* and *Michelinoceras*, both typical orthocerids, have a subspherical protoconch lacking a cicatrix with either a very gentle constriction at the base (*Orthoceras*, see Balashov 1957), or no constriction at all (*Michelinoceras*, Serpagli & Gnoli 1977). The oldest known orthocerid *Bactroceras* has an embryonic shell similar to *Michelinoceras* (Evans 2005).

A small spherical protoconch without cicatrix, distinct constriction and later rapidly expanding embryonic shell may be an indicator for classifying cephalopods at a systematic level higher than family. Similarities between embryonic shells in the discussed straight-shelled cephalopods and in bactritoids, ammonoids and belemnites are evident. *Sphooceras* most probably had such a spherical apex and consequently, its position in the Orthocerida is questionable, but more data is needed in order to solve higher-level classification of cephalopods with straight shells and lamellar deposits. To express our interpretation about the closer relationship of *Sphooceras* with coleoids than to nautiloids, we assign this genus to Angusteradulata, group including bactritoids, ammonoids and coleoids also some orthocerids (Engesser 1996).

Cameral deposits limited to a single chamber and the periodic truncation process are unique and derived features of *Sphooceras*. Its early growth stage morphology and lamellar cameral deposits strongly resemble those of the Silurian *Plagiostomoceras* Teichert & Glenister, 1952 and *Murchisoniceras* Babin, 1966. Both these cephalopods have longicone shells and well developed cameral deposits. The process of truncation is not yet well documented in these genera, but Barrande assumed it in *Plagiostomoceras* as early as 1860. Truncation appears probable in *Plagiostomoceras endymion* (Barrande, 1867) from the late Wenlock and earlier Ludlow of Bohemia. Shells of *Plagiostomoceras* and *Murchisoniceras* are very slowly expending (Barrande 1868, 1870) and their length would likely have caused difficulties in maneuvering. Reduction of shell length through periodic truncation would have considerably reduced such problems. Vascular imprints on the surface of cameral deposits strongly resemble similar mantle imprints described in Silurian *Leurocycloceras* (Flower 1941, Holland 1964).

Family Sphooceratidae Flower, 1962

Discussion. – Gnoli & Kiselev (1994) divided the family into two subfamilies, Sphooceratinae and Disjunctoceratinae. The former contains only *Sphooceras* and the latter contains *Disjunctoceras* and *Andigenoceras*, both lacking a callus in the posterior portion of the shell. We consider *Disjunctoceras* and *Andigenoceras* to be synonymous with *Sphooceras* and thus the division of Sphooceratidae into subfamilies superfluous (see following discussion).

Genera included. – *Sphooceras* Flower, 1962.

Genus *Sphooceras* Flower, 1962

[Synonymy: *Andigenoceras* Gnoli *in* Kiselev, 1992, *Disjunctoceras* Gnoli *in* Kiselev, 1992]

Type species. – *Orthoceras truncatum* Barrande, 1860; Kopanina Formation; Silurian, Ludlow, Gorstian, *Neodiversograptus nilssoni* Zone; Praha-Butovice ("Butowitz").

Amended diagnosis (cf. Kröger 2005). – Shell is straight, short, very slowly expanding; in fully-grown specimens, apical angle at midpoint of body chamber is frequently slightly decreasing. Body chamber is 1.5–3 times longer than phragmocone, which has at most seven or eight short or moderately long chambers. Sutures are transversal or slightly oblique to shell axis. Apex with plugged siphonal opening is bluntly rounded; viewed laterally, ventral side is more convex than dorsal. In median section, apex is markedly thickened owing to episeptal deposits forming a callus; one or two additional layers form an outer cover – an inner one with roughly concentric wrinkles (fingerprint pattern) and an outer layer, which is smooth and very thin. Siphuncle moderately wide, shifted slightly ventrally from the centre. Siphonal necks are orthochoanitic to cyrtotochoanitic. Surface of shell is usually entirely smooth or with slightly expressed growth lines laterally oblique to shell axis, delimiting a wide hyponomic sinus. Dorsally situated retractor muscle scars fused into single lobe. Colour pattern forms longitudinal stripes on dorsal side. Protoconch small, probably subglobular.

Discussion. – Kröger (2008, p. 55), following up on the generic diagnosis of the *Sphooceras* by Sweet (1964), published an amended diagnosis, partially based on new specimens from Morocco. However, these specimens are not well preserved, as he himself mentioned, so their assignment to *Sphooceras* is questionable. The most problematic

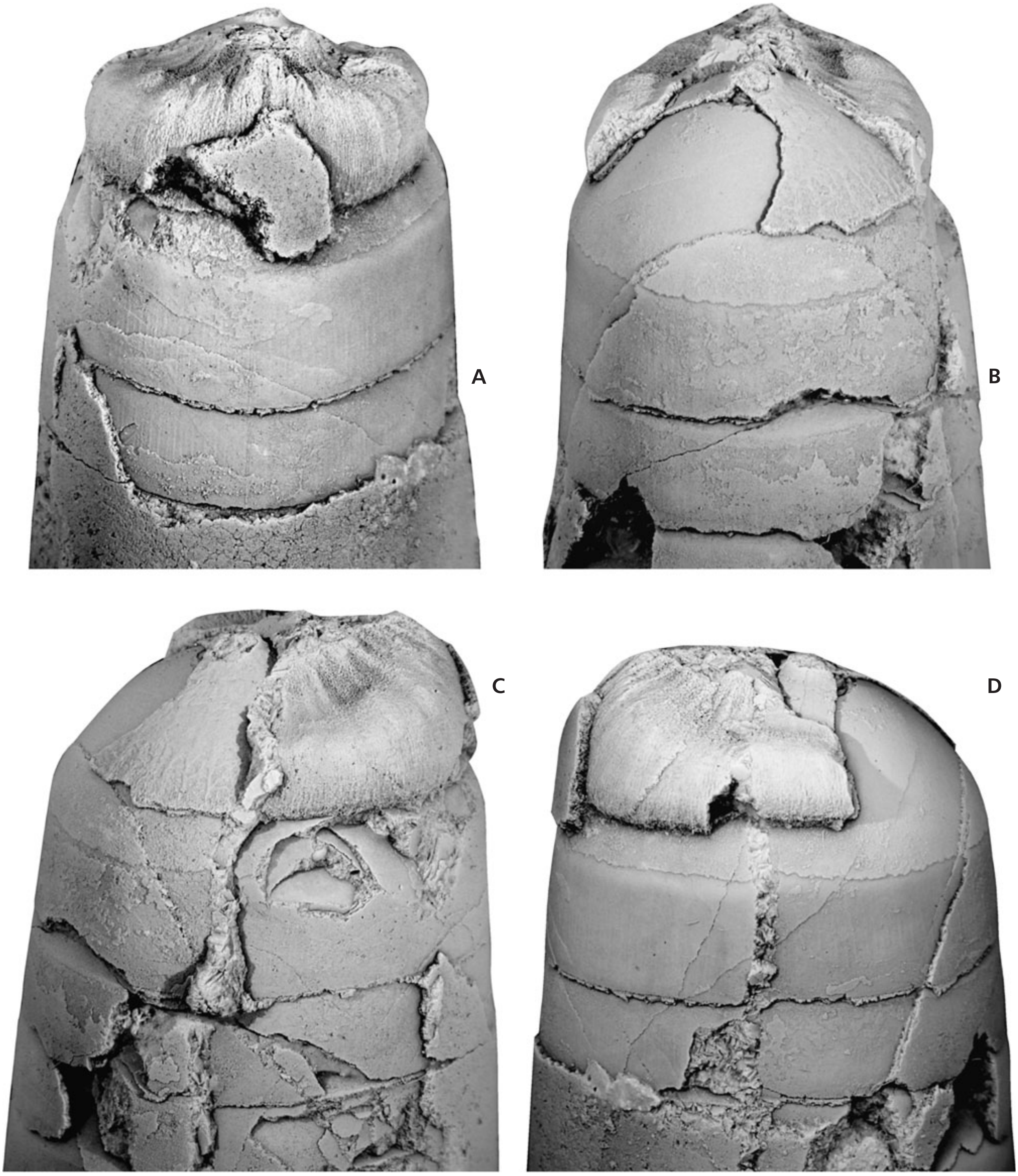

Figure 20. *Sphooceras truncatum* Barrande, 1860; Ludlow, Kopanina Formation, Zadní Kopanina, Bohemia. Internal structures in the first phragmocone chamber showing replica of cameral tissue. • A–D – specimen NM L 9181 illustrated by Barrande (1868, pl. 341, figs 6–10); for explanation of individual shell structures compare Fig. 1B in this paper. Ventral, dorsal and lateral views; × 4.

structures are cameral and epichoanitic deposits, precipitation of which, as mentioned by Kröger (2008), could be post-mortem. No similar deposits have been found in any of the numerous well-preserved specimens of *Sphooceras* from Bohemia or Gotland. Therefore, these features cannot be accepted as diagnostic. Kröger's superposition of layers forming the apex of the shell is reversed, and phragmocone chambers with highly variable convexity are generally short. Deciduous portions of the conch, so far reported as unknown, actually occur together with complete ones rather frequently.

Erection of the two new genera *Disjunctoceras* Gnoli *in* Kiselev, 1992 as well as *Andigenoceras* Gnoli *in* Kiselev, 1992 and classifying them within Sphooceratidae has significantly changed the content of this originally monogeneric family. During our study of *Sphooceras truncatum*, the specimens assigned to *Disjunctoceras disjunctum* were also examined. According to Gnoli & Kiselev (1994), *Disjunctoceras disjunctum* "differs substantially from *S. truncatum* in the presence of recumbent septal necks and the absence of a terminal callus". However, the single longitudinally cut specimen (NM L 17550), showing internal structures and studied by Gnoli is in fact incomplete. It has three phragmocone chambers adjacent to the body chamber. The apical part, preserved as an internal mould is not cut exactly in the median plane and the specimen is completely exfoliated, so it would have been impossible for Gnoli to have seen any traces of the siphuncle and callus. Several other specimens of "*O.*" *disjunctum* have been recently cut in the medium plane, and three of them have very well preserved internal structures, showing a terminal callus. The lectotype (NM L 17549) shows the outer surface of the shell in the apical region. It has three phragmocone chambers, *i.e.* the minimum number supposed. The short and fine longitudinal striae, commonly observed in *Sphooceras*, are recognizable around the entire circumference of the base of the first chamber. This feature characterises the surface of the apical callus in *Sphooceras*, confirming the existence of slightly developed cameral deposits. Except for the plugged siphuncle, the convex adapical region of the shell is smooth.

The other feature separating *Disjunctoceras* and *Sphooceras* is the more flared (suborthochoanitic to cyrtochoanitic) septal necks (Gnoli & Kiselev 1994). However, the variety of septal necks in *Sphooceras* is remarkable, often even within one specimen. For instance, in the specimen NM L 9199 (Barrande 1868, pl. 343, fig. 15), the septal necks are orthochoanitic in the first chamber but suborthochoanitic in the others. In "*O.*" *disjunctum*, they are subortochoanitic to cyrtochoanitic. *Sphooceras* exhibits a fairly strong inverse correlation between the length of phragmocone chambers and flaring of the septal necks. Variation in septal neck shapes in the Sphooceratidae is not important enough to warrant classification into separate genera. We therefore assign both species "*D.*" *disjunctum* and *S. truncatum* to the single genus *Sphooceras*.

Manda & Kříž (2007, p. 40, fig. 5) tentatively attributed the poorly known species *Orthoceras sacculus* Barrande, 1860 from the Gorstian (*L. scanicus* Biozone) to *Sphooceras*. However, this assignment has not been confirmed.

Sphooceras amplum Kiselev, 1968 in Balashov & Kiselev (1968, pl. 1, fig. 5) from the late Silurian of Podolia exhibits a slowly expanding longicone shell with widely spaced septa and a relatively thick subcentral siphuncle, with moderately vaulted connecting rings. These features clearly illustrate that this species does not belong to *Sphooceras*.

Orthoceras sarcinatum Barrande, 1868 was described based on two specimens, but only one, from Butovitz e1 locality bas been illustrated (Barrande 1868, pl. 341, figs 19, 20, holotype by monotypy NM L 17531). This species is reassigned here to *Sphooceras truncatum*.

Disjunctoceras shurabense Kiselev, 1992 from the late Wenlock and early Ludlow of Tian-Shan also actually belongs to *Sphooceras*, but this species is poorly known. It differs from *Sphooceras truncatum* in having a greater angle of shell expansion (Kiselev *et al.* 1993).

Sphooceras furmanense Kiselev, 1992 from the early Wenlock, Podoli in Ukraine, was insufficiently illustrated and thus the position of this species remains questionable, and it may be considered a *nomen dubium*.

Dzik (1984, p. 135) suggested that Hirnantian species "*Ecdyceras*" *foerstei* Flower, 1946 from Kentucky could be assigned to *Sphooceras*, but this species does not exhibit any diagnostic feature of *Sphooceras*.

Species included. – *Sphooceras truncatum* (Barrande, 1860); *Sphooceras disjunctum* (Barrande, 1860); stratigraphic range and geographic distribution – see below; *Sphooceras shurabense* (Kiselev, 1992), late Wenlock and early Ludlow of Tian-Shan; *Sphooceras andigense* (Kiselev, 1992), Přídolí, Tian-Sha; *Sphooceras furmanense* Kiselev, 1992, early Wenlock, Podoli in Ukraine.

Sphooceras truncatum (Barrande, 1860)

Figures 2–5, 9–11, 13C, 14–20

1855 *Orthoceras truncatum* (nom. nud.). Barrande, p. 280.

1860 *Orthoceras truncatum* (n. sp.); Barrande, pp. 573–600, pl. 9, figs 1–20.

1868 *Orthoceras truncatum* Barrande. – Barrande; pl. 342, figs 1–20, pl. 344, figs 1–6.

1868 *Orthoceras sarcinatum* Barrande; Barrande, pl. 341, figs 19, 20.

1868 *Orthoceras apperiens* Barrande. – Barrande, pl. 344, figs 19–21.

1870 *Orthoceras truncatum* Barrande. – Barrande, pl. 448, figs 3–5.

1874 *Orthoceras truncatum* Barrande. – Barrande, pp. 556–559.

1882 *Orthoceras truncatum* Barrande, 1860. – Blake, p. 151, pl. 14, fig. 8.

1888 *Orthoceras truncatum* Barrande. – Foord, pp. 23–26.

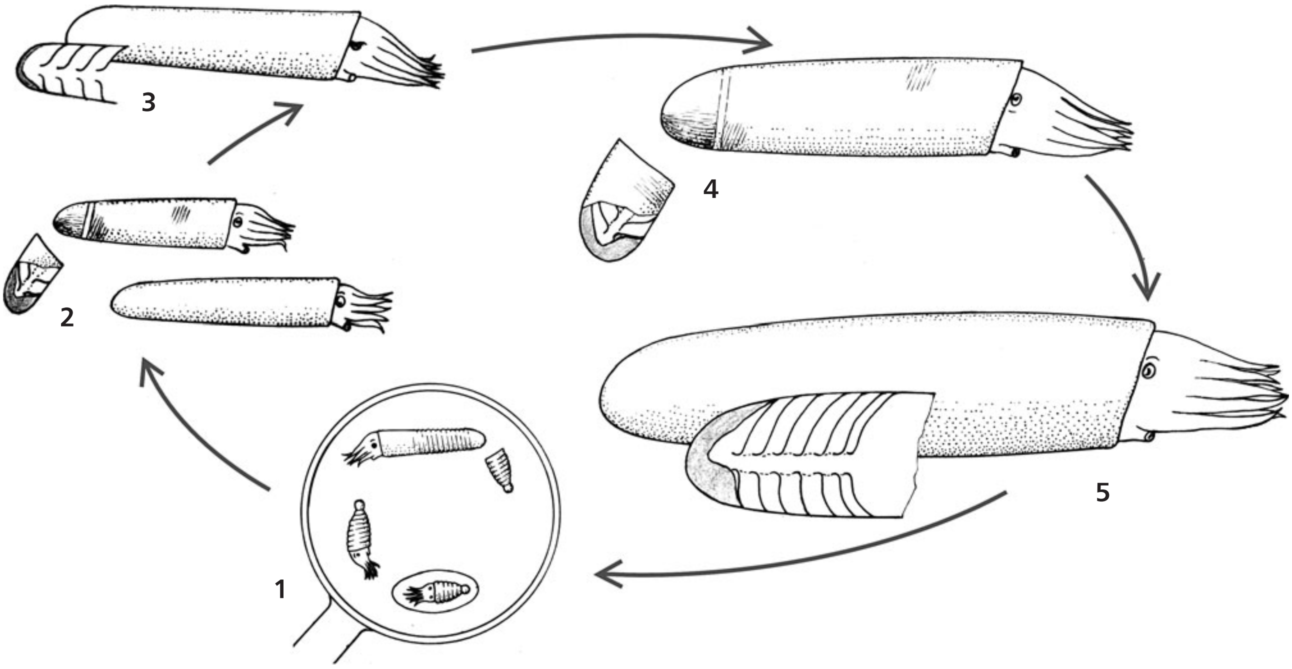

Figure 21. Schematic drawing of *Sphooceras* ontogeny, showing selected phases of growth. 1 – egg containing embryo, freshly hatched embryo and juvenile executing first truncation; 2 – young growth stage with relatively long phragmocone, just before and during truncation process; 3 – specimen after truncation with only four phragmocone chambers and thin apical callus; 4 – immature specimen during truncation showing "naked" cameral deposits forming new apex; mantle is withdrawn into body chamber; truncated part of phragmocone (four chambers) with partially removed outer shell-wall shows thick cameral deposits; 5 – adult specimen covered by mantle extended from aperture. Shell slightly narrowing to aperture, cameral deposits thick, last septa narrowly spaced.

1888 *Orthoceras truncatum* Barrande. – Schröder, p. 220.
1925 *Orthoceras truncatum* Barr. – Heller, p. 245, pl. 3, fig. 19.
1929 *Orthoceras truncatum* Barrande, 1860. – Heritsch, p. 67, pl. 7, figs 684, 685.
1941 *Orthoceras truncatum* Barrande. – Flower, pp. 473, 474.
1955 *Orthoceras truncatum* Barrande. – Flower, p. 100.
1955 *"Orthoceras" truncatum* Barrande. – Flower, p. 860.
1962 *Orthoceras truncatum* Barrande. – Furnish *et al.*, p. 1344.
1963 *Sphooceras truncatum* (Barrande). – Flower, p. 95.
1964 *Sphooceras truncatum* (Barrande). – Sweet, pp. K231/2, fig. 156A5.
1975 *Sphooceras truncatum* (Barrande). – Balashov, pp. 81–85, pl. 3, fig. 5.
1978 *Sphooceras truncatum* (Barrande). – Zhuravleva, p. 19.
1984 *Sphooceras truncatum* (Barrande, 1860). – Dzik, pp. 112, 135, 138, pl. 31, figs 5–7, text-figs 42.19, 55.35.
1986 *Sphooceras truncatum* (Barrande). – Turek & Marek, pp. 240, 252, fig. 3.1–9.
1987 *Sphooceras truncatum* (Barrande). – Kiselev *et al.*, p. 50, pl. 13, fig. 4.
1990 *Sphooceras truncatum* (Barrande). – Gnoli, pp. 302, 304, pl. 4, fig. 2a–5.
1991 *Sphooceras truncatum* (Barrande). – Gnoli & Serpagli, pp. 188, 194, pl. 1, fig. 7.
1992 *Sphooceras truncatum* (Barrande). – Kříž, p. 104, pl. 1, fig. 24.
1992 *Sphooceras truncatum* (Barrande). – Kiselev, p. 16.
1993 *Sphooceras truncatum* (Barrande, 1860). – Kiselev *et al.*, p. 55, pl. 11, fig. 5.
cf. 1994 *Sphooceras truncatum* (Barr.). – Kiselev & Modzalevskaya, p. 84.
1994 *Sphooceras truncatum* (Barrande). – Gnoli & Kiselev, pp. 416/7, text-figs 1a–c.
non 2008 *Sphooceras truncatum* (Barrande, 1860). – Kröger, p. 56, pl. 6, fig. 2, pl. 11, fig. 2 (= ?*Plagiostomoceras* sp.).

Diagnosis. – Type species of *Sphooceras* Barrande (1860), whose shell, with 7 or 8 phragmocone chambers, could attain lengths up to 30 cm, with dorsoventral diameter up to 90 mm. Apical angle in the midpoint of the body chamber in fully-grown specimens is usually slightly decreasing. Cameral deposits forming the apical callus are relatively thick in mature specimens and almost fill the first phragmocone chamber, subsequently covered by two outer layers. The inner one has roughly concentric wrinkles (fingerprint pattern) and the outer layer is smooth. The siphuncle has orthochoanitic to suborthochoanitic siphonal necks.

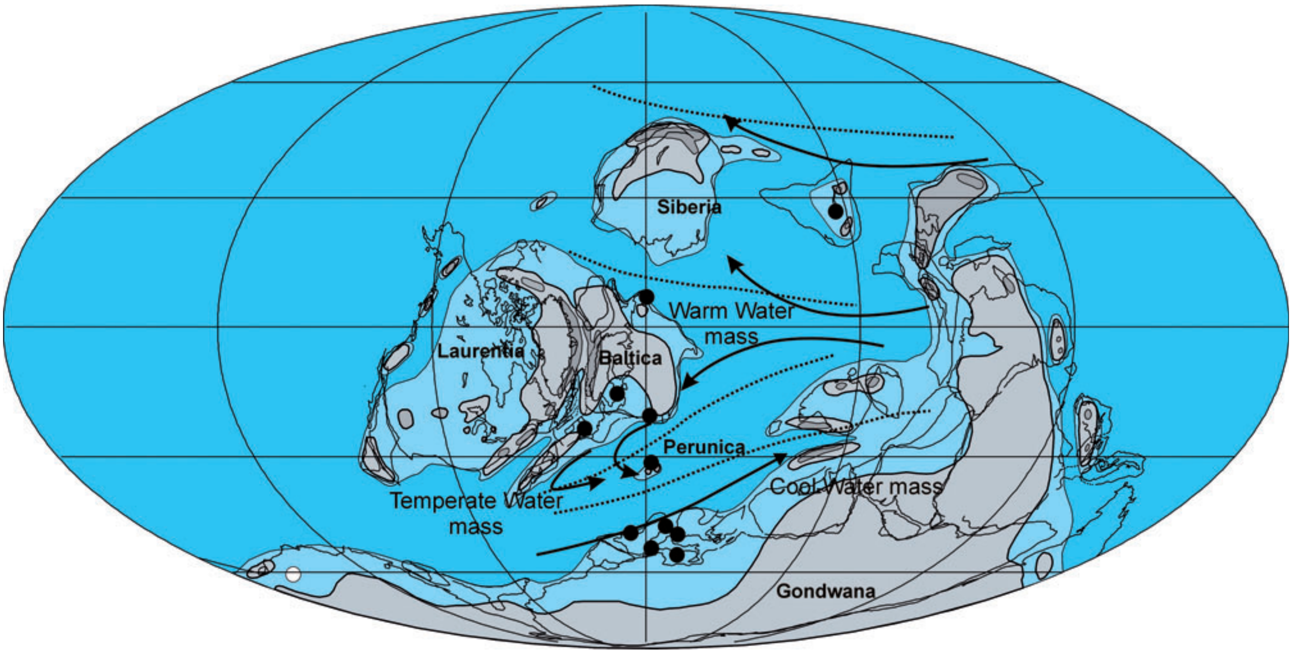

Figure 22. Distribution of *Sphooceras* and reconstruction of oceanic currents (Wilde *et al.* 1991) and distribution of warm, temperate and cool water masses. For data see the text. Palaeogeographic reconstruction of the Wenlock based on the Paleomap Project of C.R. Scotese, Perunica microplate position after Cocks & Torsvik (2002).

Remarks. – Barrande (1860, 1868) gave special attention to the species "*Orthoceras*" *truncatum.* Type and additional specimens were carefully selected and precisely illustrated on several plates. He recognized the high variability within this species. Barrande expressed the detection of differences in the morphology of these specimens by distinguishing two varieties: *O. truncatum* var. *index* and *O. truncatum* var. *perornata.* We suppose these forms to be only morphs within the populations falling into intraspecific variability. Barrande's concept of the species *O. truncatum* corresponds with our view.

All newly described features (colour pattern, muscle scars, occasional cameral deposits in addition to the apical callus, embryonic shell presumably of *S. truncatum*) have been discussed above in the section concerning morphology.

Occurrence. – Central Bohemia (Barrandian, Prague Basin).

Motol Formation, Wenlock, Homerian; *C. lundgreni* Zone, *T. testis* Subzone: Butovice, Kační Quarry; Lištice Herinky, Barrande's pits; Lištice U cestičky section No. 759, bed No. 3; Praha-Velká Ohrada, Arethusinová Gorge section No. 687; Kosov Quarry near Beroun, new quarry, 6th level, section No. 767; Tachlovice, Prostřední Mill. *M. ludensis* Zone: Praha-Bráník, Školní vrch, section No. 764, bed No. 8.

Kopanina Formation, Ludlow, Gorstian. *N. nilssoni* Zone: Praha-Butovice, Na břekvici section 584, bed Nos. 10 and 11; Praha-Butovice, road cut to Hemrovy Rocks; Praha-Lochkov, field E of the village (nodules from field); Tachlovice, Prostřední Mill.

L. scanicus Zone: Kosov near Beroun, new quarry, top of western wall above pool and section No. 780; Praha-Braník, Školní vrch; Praha-Reporyje, roadcut to W of village; Praha-Malá Chuchle, Vyskočilka Hillside, bed No. 6; Praha-Velká Ohrada, Cromus Hillside; Sedlec, Barrande's pits, bed No. 3.

Early *S. linearis* Zone: Kosov near Beroun, section No. 780; Praha-Velká Ohrada, Mušlovka Quarry; Praha-Řeporyje, Požáry Quarry.

Late *S. linearis* Zone: Dlouhá hora near Beroun, U lanovky section; Kosov Quarry near Beroun, section 780; Praha-Lochkov, Barrande's pits; Praha-Lochkov, Nad ubikacemi; Praha-Řeporyje, Požáry Quarry, bed No. 1; Praha-Řeporyje, Marble Quarry, beds No. 1 and 2; Praha-Velká Ohrada, Mušlovka Quarry, bed Nos 1 and 2; Praha-Zadní Kopanina, Nad Jirasovým lomem section 887, bed No. 3 (lower part); Praha-Zadní Kopanina, Draská Gorge; Velký vrch near Koněprusy.

B. bohemicus and *N. inexpectatus* zones: Praha-Lochkov, Marble Quarry and Barrande's pits; Praha-Velká Ohrada, Mušlovka Quarry; Praha-Zadní Kopanina, Nad Jirasovým lomem section; Kosov Quarry near Beroun, section Nos. 418, 772.

N. kozlowskii Zone: Praha-Lochkov, Marble Quarry and Barrande's pits, Nad ubikacemi section; Praha-Slivenec, old quarry; Praha-Velká Ohrada, Mušlovka

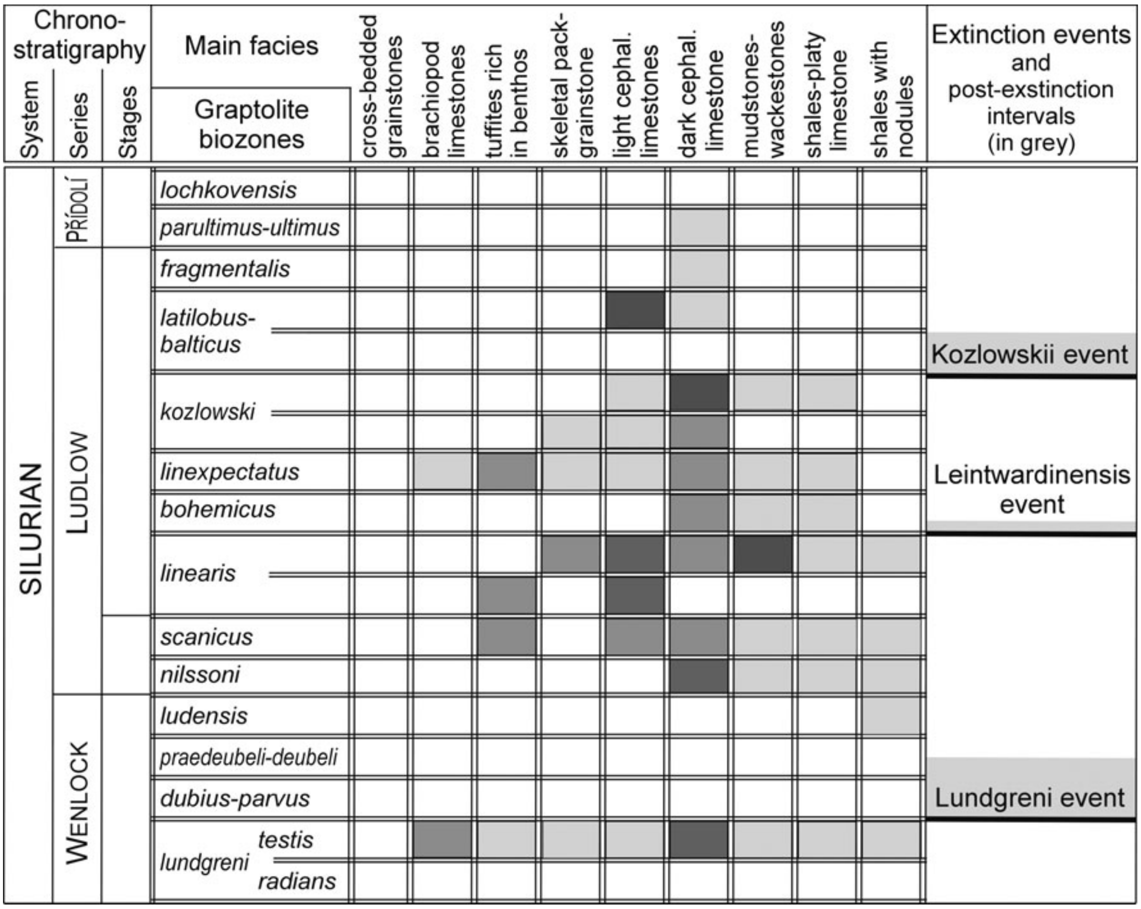

Figure 23. Distribution of *Sphooceras* in dependence on facies in the Silurian of the Prague Basin. Light gray infill indicates rare occurrence, medium gray infill common occurrence, dark-gray infill indicate very common or mass occurence.

Quarry; Praha-Nová Ves, Pod Hradištěm I, II, III; Praha-Řeporyje, Požáry Quarry; Praha-Zadní Kopanina, Nad Jirasovým lomem section.

Latest *N. kozlowskii* Zone: Koněprusy, Velký vrch, section 913, bed No. 5; Kosov near Beroun, section No. 782 (bed No. 22/23) and section No. 924 (bed No. 13); Praha-Lochkov, Marble Quarry; Praha-Nová Ves, Pod Hradištěm II, bed No. 13; Praha-Zadní Kopanina, Nad Jirasovým lomem section, bed No. 5.

Ps. latilobus-S. balticus Zone: Praha-Lochkov, Barrande's pits; Praha-Kosoř, old quarry; Praha-Lochkov, Marble Quarry; Praha-Lochkov, Nad ubikacemi section; Praha-Malá Chuchle, Vyskočilka; Praha-Pankrác, Sdružení.

M. fragmentalis Zone: Praha-Lochkov, Barrande's pits; Praha-Lochkov, Nad ubikacemi section; Praha-Dvorce, Podolí.

P. parultimus Zone: Praha-Lochkov, Nad ubikacemi section.

In addition to the Prague Basin, *Sphooceras truncatum* occurs in Elbersreuth, Germany (Heller 1925), Gotland, Sweden (Dzik 1984), Carnic Alps, Austria (Histon 1999), Montagne Noire and Calvados, France, south-west Sardinia, Italia (Histon & Gnoli 1999, Gnoli 2003), Poland (Dzik 1984), Podoli, Ukraine (Kiselev *et al.* 1987, Kiselev 1995), England (Blake 1882), ?Bardymsk Formation, early–middle Ludfordian, Ufimskij Amfiteatr (Kiselev & Modzalevskaya 1994), and Tian-Shian, Kazachstan (Kiselev & Starshinin 1987).

Sphooceras disjunctum (Barrande, 1868)
Figures 7, 8, 12, 13A, B, D, E

1860 *Orthoceras disjunctum* Barr. (nomen nudum). – Barrande, p. 588.
1868 *Orthoceras disjunctum* Barr.; Barrande, pl. 345, figs 8–12.
1874 *Orthoceras disjunctum*; Barrande, p. 631.
1888 *Orthoceras disjunctum* Barrande. – Foord, p. 27.
1888 *Orthoceras disjunctum* Barrande. – Schröder, p. 228.
1992 *Disjunctoceras disjunctum* (Barrande). – Kiselev, p. 17.
1994 *Disjunctoceras disjunctum* (Barrande). – Gnoli & Kiselev, pp. 417, 418, text-figs 2a–c.

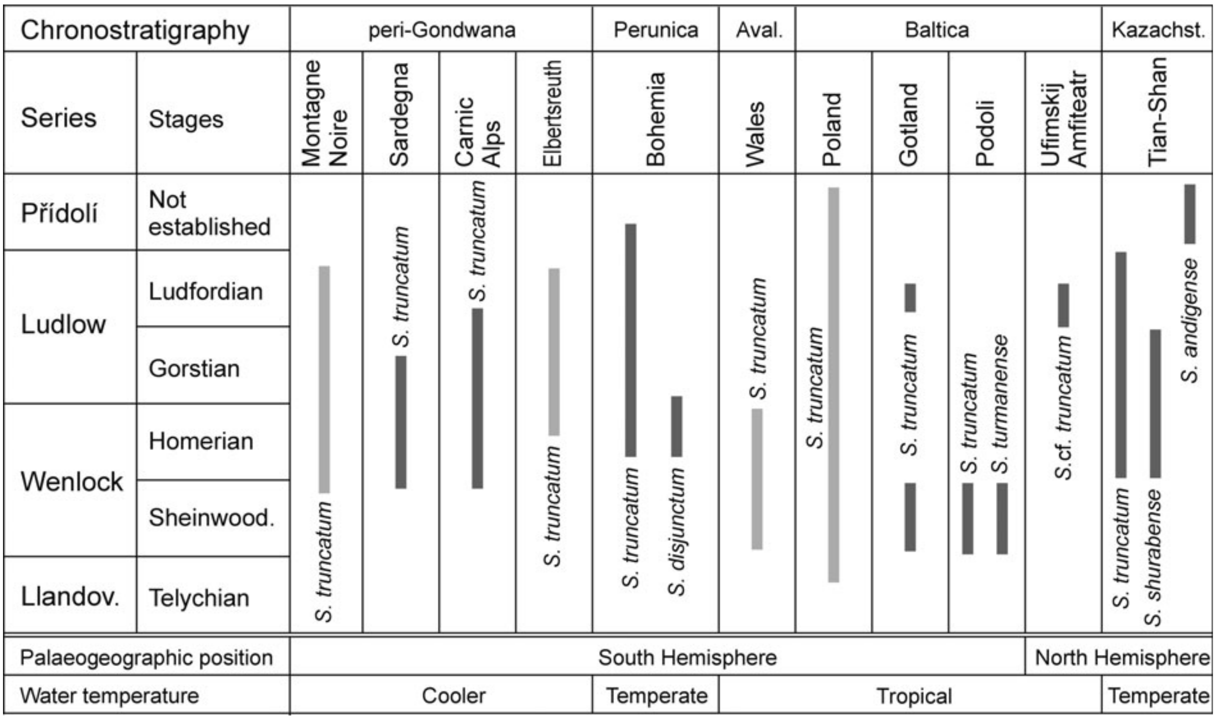

Figure 24. Stratigraphic range and latitudinal distribution of *Sphooceras* species. Light gray colored lines indicate uncertain stratigraphic ranges. For data see systematic part. Aval. Means Avalonia.

Diagnosis. – *Sphooceras* with very short shell, three to five short phragmocone chambers. Body chamber may be almost three times longer than phragmocone. Shell thin walled, with markedly thickened peristome (constriction visible on internal mould). Apex thickened owing to presence of thin apical callus, massive deposits inside the first chamber not developed. Sutures almost perpendicular to the shell axes, siphonal necks suborthochoanitic or even cyrthochoanitic.

Occurrence. – Central Bohemia (Barrandian, Prague Basin). Motol Formation, Wenlock, Homerian; *C. lundgreni* Zone, *T. testis* Subzone: Butovice, Kační Quarry. Kopanina Formation, Ludlow, Gorstian; *N. nilssoni* Zone: Praha-Butovice, Na břekvici section; Řeporyje. *L. scanicus* Zone: Praha-Malá Chuchle, Vyskočilka Hillside, bed No. 6.

Conclusions

Sphooceras is still the only known Early Palaeozoic cephalopod in which temporary complete encasing of the shell by mantle extended from the body chamber has been suggested. It was linked with the periodic natural truncation of the apical part of the phragmocone (3 to 5 chambers), a process that has been unequivocally documented. Therefore, throughout ontogeny, the shell was short and the length of the body chamber was one and half or even three times the length of the phragmocone. Temporary complete encasing of the shell by mantle is here suggested because of the presence of two calcareous layers secreted on the surface of the apical callus – exposed episeptal deposits including structurally reworked septum – which formed the apical part of the shell subsequent to truncation. The inner layer bears a characteristic fingerprint pattern (in *S. truncatum*) and the very thin, smooth outer layer shows a colour pattern. Longitudinal stripes running radially from the circumference of the plugged siphuncle are present only dorsally; the ventral side was unpigmented. The presence of colour stripes in this region serves as additional indication that the shell of this nautiloid was periodically completely covered by the mantle, an organ containing pigment cells secreting colour patterns in molluscs.

The colour pattern documents that these layers could not have been secreted by long arms (*cf.* Barrande 1860), nor a hood (Hyatt 1883–1884) nor a siphon-cameral tissue (*cf.* Gnoli & Kiselev 1994). A new idea is given here for the processes preceding truncation and subsequent completion of the new apex. A remarkable feature, documented especially in *Sphooceras disjunctum*, is an extremely thin shell wall in the apertural region. It would not have been able to withstand wave action in the shallow water environment inhabited by the animal without being protected by the soft tissue – another indication of covering of the shell by the mantle.

Affinity of some Early Palaeozoic straight-shelled cephalopods to coleoids has been already indicated, especially by finds in orthocerids of coleoid type of radula (Mehl 1984, Gabbot 1999); reported traces of ten tentacles (Flower 1955b, Stürmer 1985) has been, however, doubted. A "semi-internal" shell of *Sphooceras* temporarily completely encased by soft tissue, reduction of the length of the phragmocone, shortening of the shell accompanied by relative prolongation of body chamber possessing oblique aperture, dorsally situated retractor muscle imprints, probably very small subglobular protoconch lacking cicatrix, noncalcified connecting rings and hydrodynamic shape of the shell are all features, which evolved in the genus *Sphooceras* in convergence to the Angusteradulata. *Sphooceras*, however, lacks some important coleoid features such as a rostrum-like shell deposited on a significant portion of the outside, a ventral siphuncle with more or less straight connecting rings as well as the characteristic sinuses and projections of the aperture (proostracum *etc.*). On the other hand there is extreme disparity of septal neck shapes in Carboniferous coleoids. In some oldest coleoids connecting rings expanded within phragmocone chambers. In *Rhiphaeoteutethis* there are suborthochoanitic septal necks and the siphuncle could not be simply tubular, also in *Hematites* connecting rings were very probably inflated, similarly as in *Sphooceras* (see Doguzhayeva *et al.* 2010). Also proostracum-like structures are missing in some of these coleoids, *e.g.* in Donovaniconida and Hematitida.

The character of truncation in *Sphooceras* may be viewed as a case of autapomorphy, a progressive evolutionary experiment appearing as early as in Silurian cephalopods, indicating some parallels with coleoids. The mode of shell repair in *Sphooceras* differs significantly from that in other nautiloids in which truncation has been reported, as well as from some gastropods in which it occurs more frequently.

The shell of *Sphooceras* was highly variable both in outer morphology (shape, surface sculpture) and internal structures (convexity of septa, their orientation to the shell axis, shape of siphonal necks), and the occasional presence of massive cameral deposits in an additional phragmocone chamber besides the first one. A qualitative analysis of shell variability in *Sphooceras* supports that it is the only known genus of the Sphooceratidae family; we consider the genera *Disjunctoceras* Gnoli & Kiselev and *Andigenoceras* Kiselev synonyms of *Sphooceras*.

Sphooceras, probably closely related to *Plagiostomoceras*, *Murchisoniceras* and *Parasphaerorthoceras*, derives from other straight-shelled cephalopods with fully developed cameral deposits. Due to the reduction of the phragmocone, cameral deposits were limited to the apical callus.

The morphology of the shell and its wide distribution in tropical and subtropical seas of Europa and Asia indicate that *Sphooceras* was an active nektonic or nectobenthonic animal with neutral buoyancy, keeping its body horizontal. Musculature of the mantle and hyponome probably enabled effective swimming.

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References

ARNOLD, J.M. 1987. Reproduction and embryology of *Nautilus*, 353–372. *In* SAUNDERS, W.B. & LANDMAN, N.H. (eds) *Nautilus. The Biology and Paleobiology of a Living Fossil*. Plenum Press, New York.

ARNOLD, J.M., LANDMAN, N.H. & MUTVEI, H. 1987. Development of the embryonic shell of *Nautilus*, 373–400. *In* SAUNDERS, W.B. & LANDMAN, N.H. (eds) *Nautilus. The Biology and Paleobiology of a Living Fossil*. Plenum Press, New York.

BABIN, C. 1966. *Mollusques bivalves et céphalopodes du Paléozoïque armoricain. Étude systématique. Essai sur la phylogénie des Bivalves. Esquisse paléoécologique*. 438 pp. Imprimérie commerciale et administrative, Brest.

BALASHOV, Z.G. 1957. Protoconchs of older Paleozoic forms of the genus *Orthoceras*. *Doklady Akademii Nauk SSSR 116*, 855–857.

BALASHOV, Z.G. 1964. On wall structure and coloration of shells of Ordovician Endoceratida from the Pre-Baltic region. *Voprosy Paleontologii 4*, 106–110.

BALASHOV, Z.G. 1975. Cephalopods of the Molodov and Kitaigorod horizon of Podolia. *Voprosy Paleontologii 7*, 63–101.

BALASHOV, Z.G. & KISELEV, G.N. 1968. Some cephalopod molluscs of the Malinoveceky, Skalsky, Borchovsky, and Chortkovsky Formations of Podolia, 7–29. *In* BALASHOV, Z.G. (ed.) *Silurian-Devonian fauna of Podolia*. Izdatelstvo Leningradskogo Universiteta, Leningrad.

BANDEL, K. & STANLEY, G.D. 1989. Reconstruction and biostratinomy of Devonian cephalopods (Lamellorthoceratidae) with unique cameral deposits. *Senckenbergiana lethaea 69*, 391–437.

BARRANDE, J. 1855. *Ascoceras* der Prototyp von *Nautilus. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefacten-Kunde*, 257–285.

Barrande, J. 1860. Troncature normale ou périodique de la coquille dans certains céphalopodes paléozoïques. *Bulletin de la Societé géologique de France, séries 2 17*, 573–601.

Barrande, J. 1865–1877. *Systême silurien du Centre de la Bohême, I ère partie: Recherches Paléontologiques, vol. II, Classe de Mollusques, Ordre des Céphalopodes.* 1865. ser. 6, pl. 1–107; 1866. ser. 7, pl. 108–244; 1867. ser. 1, 712 pp.; 1868. ser. 8, pl. 245–350; 1870. ser. 2, 266 pp., ser. 9, pl. 351–460; 1874. ser. 3, 804 pp.; 1877. ser. 4, 742 pp., ser. 5, 743 pp., supplement 1, 297 pp., supplement 2, pl. 461–544. Privately published, Prague & Paris.

Barskov, I.S., Boiko, M.S., Konovalova, V.A., Leonova, T.B. & Nikolaeva, S.V. 2008. Cephalopods in the marine ecosystems of the Paleozoic. *Paleontological Journal 42*, 1167–1284. DOI 10.1134/S0031030108110014

Blake, J.F.A. 1882. *A monograph of the British fossil Cephalopoda. Part 1, Introduction and Silurian species.* 248 pp. Palaeontographical Society, London.

Blind, W. 1991. Über Anlage und Funktion von Kammerablagerungen in Orthoceren-Gehäusen. *Palaeontographica, Abteilung A 218*, 35–47.

Calner, M. 2008. Silurian global events – at the tipping point of climate change, 21–58. *In* Ashraf, M.T. (ed.) *Mass extinctions*. Springer-Verlag, Berlin & Heidelberg.

Carriker, M.R. 1972. Observations on removal of spines by muricid gastropods during shell growth. *Veliger 15*, 2.

Chirat, R. 2001. Anomalies of embryonic shell growth in post-Triassic Nautilida. *Paleobiology 27*, 485–499. DOI 10.1666/0094-8373(2001)027<0485:AOESGI>2.0.CO;2

Cocks, L.R.M. & Torsvik, T.H. 2002. Earth geography form 500 to 400 million years ago: A faunal and palaeomagnetic review. *Journal of the Geological Society, London 159*, 631–644. DOI 10.1144/0016-764901-118

Crick, R.E. 1982. The mode and tempo of cameral deposit formation: evidence of orthoconic nautiloid physiology and ecology, 113–118. *In* Mamet, B. & Copeland, M.J. (eds) *Proceedings of the Third Northamerican Paleontological Convention 1*. Montreal.

Cuvier, G. 1797. *Tableau élémentaire de l'histoire naturelle des animaux*. 710 pp. Baudoin, Paris.

Davis, R.A., Fraaye, R.H.B. & Holland, C.H. 2001. Trilobites within nautiloid cephalopods. *Lethaia 34*, 37–45. DOI 10.1080/00241160130006825l

Doguzhaeva, L. & Mutvei, H. 1986. Functional interpretation of inner shell layers in Triassic ceratid ammonites. *Lethaia 19*, 195–209. DOI 10.1111/j.1502-3931.1986.tb00732.x

Doguzhaeva, L. & Mutvei, H. 1989. *Ptychoceras* – A heteromorphic Lytoceratid with truncated shell and modified Ultrastructure (Mollusca: Ammonoidea. *Palaeontographica, Abteilung A 208*, 91–121.

Doguzhaeva, L. & Mutvei, H. 1993. Shell ultrastructure, muscle-scars, and buccal apparatus in ammonoids. *Geobios M.S. 15*, 111–119. DOI 10.1016/S0016-6995(06)80366-9

Doguzhaeva, L., Mapes, R.H. & Mutvei, H. 2010. Evolutionary patterns of Carboniferous coleoid cephalopods based on their diversity and morphological plasticity, 171–180. *In* Tanabe, K., Shigeta, Y., Sasaki, T. & Hirano, H. (eds) *Cephalopods – Present and Past*. Tokai University Press, Tokyo.

Drushchits, V.V., Doguzhayeva, L.A. & Mikhaylova, I.A. 1978. Neobychnyye oblekayushchiye sloi ammonitov. *Paleontologicheskiy Zhurnal 2*, 36–44.

Dzik, J. 1984. Phylogeny of the Nautiloidea. *Palaeontologia Polonica 45*, 1–255.

Ebel, K. 1999. Hydrostatics of fossil ectocochleate cephalopods and its significance for the reconstruction of their lifestyle. *Paläontologische Zeitschrift 73*, 277–288.

Engeser, T. 1996. The position of the Ammonoidea within the Cephalopoda, 3–23. *In* Landman, N.H., Tanabe, K. & Davis, R.A. (eds) *Ammonoid Paleobiology*. Plenum Press, New York.

Evans, D.H. 2005. The Lower and Middle Ordovician cephalopod faunas of England and Wales. *Monograph of the Palaeontographical Society, London 158*, 1–81.

Fischer, A.G. & Teichert, C. 1969. Cameral deposits in cephalopod shells. *The University of Kansas Paleontological Contributions Paper 37*, 1–30.

Flower, R.H. 1939. Study of the Pseudorthoceratidae. *Paleontologica Americana 2*, 1–214.

Flower, R.H. 1941. Revision and internal structures of *Leurocycloceras*. *American Journal of Science 239*, 469–488. DOI 10.2475/ajs.239.7.469

Flower, R.H. 1955a. Cameral deposits in orthoconic nautiloids. *Geological Magazine 92*, 89–103. DOI 10.1017/S0016756800063408

Flower, R.H. 1955b. Trails and tentacular impressions of orthoconic cephalopods. *Journal of Paleontology 29*, 857–867.

Flower, R.H. 1957. Nautiloids of the Paleozoic. *Memoirs of the Geological Society of America 67*, 829–852.

Flower, R.H. 1963a. New Ordovician Ascoceratida. *Journal of Paleontology 37*, 69–85.

Flower, R.H. 1963b. Notes on the Michelinoceratida. *New Mexico Institute of Mining and Technology, State Bureau of Mines and Mineral Resources, Memoir 10*, 21–40.

Flower, R.H. 1964. Nautiloid shell morphology. *New Mexico Institute of Mining and Technology, State Bureau of Mines and Mineral Resources, Memoir 13*, 1–77.

Flower, R.H. & Gordon, M. 1959. More Mississippian belemnites. *Journal of Paleontology 33*, 809–842.

Foord, A.H. 1888. *Catalogue of the fossil Cephalopoda in the British Museum (Natural History). Part 1*. British Museum, London.

Frýda, J. & Gutiérrez-Marco, J.C. 1996. An unusual new sinuitid mollusc (Bellerophontoidea, Gastropoda) from the Ordovician of Spain. *Journal of Paleontology 70(4)*, 598–605.

Frye, M.W. 1982. Upper Ordovician (Harjuan) nautiloid cephalopods from the Boda limestone of Sweden. *Journal of Paleontology 56*, 1274–1292.

Fuchs, D. 2006. Fossil erhaltungsfähige Merkmalskomplexe der Coleoidea (Cephalopoda) und ihre phylogenetische Bedeutung. *Berliner Paläobiologische Abhandlungen 8*, 1–122.

Furnish, W.M. & Glenister, B.F. 1964. Nautiloidea-Ascocerida, K261–K277. *In* Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology, Part K, Mollusca 3, Cephalopoda*. Geological Society of America & The University of Kansas Press, Boulder, Colorado.

Furnish, W.M., Glenister, B.F. & Hansman, R.H. 1962. Brachycycloceratidae, novum, deciduous Pennsylvanian nautiloids. *Journal of Paleontology 36*, 1341–1356.

Furnish, W.M. & Glenister, B.F. 1964. Nautiloidea – Ascocerida, 261–277. *In* Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology, Part K, Mollusca 3, Cephalopoda – General Features, Endoceratoidea – Actinoceratoidea – Nautiloidea – Bactritoidea*. Geological Society of America & The University of Kansas Press, Boulder, Colorado.

Gabbot, S.E. 1999. Orthoconic cephalopods and associated fauna from the Late Ordovician Soom Shale Lagerstaette, South Africa. *Palaeontology 42*, 123–148. DOI 10.1111/1475-4983.00065

Gnoli, M. 1990. New evidence for faunal links between Sardinia and Bohemia in Silurian time on the basis of nautiloids. *Bollettino della Società Paleontologica Italiana 29*, 289–307.

Gnoli, M. 2003. Northern Gondwanan Siluro-Devonian palaeogeography assessed by cephalopods. *Palaeontologia Electronica 5(2)*, 1–19.

Gnoli, M. & Kiselev, G. 1994. Revision of the family Sphooceratidae Flower, 1962 (Orthocerida). *Bollettino della Società Paleontologica Italiana 33*, 415–420.

Gnoli, M. & Serpagli, E. 1991. Nautiloid assemblages from middle-late Silurian of Southwestern Sardinia: a proposal. *Bollettino della Società Paleontologica Italiana 30*, 187–195.

Gordon, M. 1964. California carboniferous cephalopods. *Geologica Survey Profesional Papers 483A*, 1–23.

Harries, P.J. & Knor, P.O. 2010. What does the 'Lilliput Effect' mean? *Palaeogeography, Palaeoclimatology, Palaeoecology 284*, 4–10. DOI 10.1016/j.palaeo.2009.08.021

Heller, T. 1925. Die Fauna des Obersilurischen Orthocerenkalks von Elbersreuth. *Geognostische Jahreshefte 38*, 1–197.

Heritsch, F. 1929. Faunen aus dem Silur der Ostalpen. *Abhandlungen der geologischen Bundesanstalt 23*, 1–179.

Hewitt, R.A. & Westerman, G.E.G. 2003. Recurrences of hypotheses about ammonites and *Argonauta*. *Journal of Paleontology 77*, 762–795. DOI 10.1666/0022-3360(2003)077<0792:ROHAAA>2.0.CO;2

Histon, K. 1993. Primary deposits in nautiloid cephalopods. *Lethaia 26*, 179–181. DOI 10.1111/j.1502-3931.1993.tb01811.x

Histon, K. 1999. Revision of Silurian nautiloid cephalopods from the Carnic Alps (Austria) – The Heritsch (1929) Collection in the Geological Survey of Austria. *Abadlungen der Geologischen Bundesanstalt 56*, 229–258.

Holland, C.H. 1964. On the nautiloid *Leurocycloceras* from the Ludlovian of Wales and the Welsh Borderland. *Palaeontology 7*, 527–540.

Holland, C.H. 1999. The Nautiloid Cephalopod Order Ascocerida in the British Silurian. *Palaeontology 42*, 683–689. DOI 10.1111/1475-4983.00092

Hyatt, A. 1883–1884. Genera of fossil cephalopods. *Boston Society Natural History Proceedings 22*, 273–338.

Kiselev, G.N. 1992. New data about the family Sphooceratidae Flower, 1962 (Cephalopoda). *Vestnik St. Petersburgskogo Universiteta, Seriya 7, Geologiya, Geografiya (1992)14*, 15–18.

Kiselev, G.N. 1993. Upper Silurian and Lower Devonian nonammonoid cephalopods of the western part of South Tianshan. *Vestnik Sankt Peterburgkogo Universiteta, Seriya 7, Geologiya, Geografiya (1993)2*, 22–28.

Kiselev, G.N. 1995. Siluryskie tsefalopody na rubekhe rannego i pozdego Silura v podoľskom Paleobasseine, 27–30. *In Iskopaemye organizmy Fanerozoya Ukrainy*. Natsionaľnaya Akademiya Nauk Ukrainy, Kiev.

Kiselev, G.N., Mironova, M.G. & Sinitsina, I.N. 1987. *Atlas Silurskich mollyuskov Podolii*. 180 pp. Izdateľstvo Leningradskogo Universiteta, Leningrad.

Kiselev, G.N. & Modzalevskaya, T.L. 1994. Silurian and Early Devonian brachiopods and cephalopods of the Ufimian amphitheater. *Vestnik Sankt Peterburgkogo Universiteta, Seriya 7, Geologiya, Geografiya 1994(1)*, 84–86.

Kiselev, G.N., Savickyj, J.V., Sinitsina, I.N. & Mirnova, M.G. 1993. *Atlas mollyuskov i brachiopod silura i devona yuzhnogo Tyan-Shanya*. 115 pp. Izdateľstvo St. Peterburskogo Universiteta, St. Petersburg.

Kiselev, G.N. & Starshinin, D.A. 1987. Golovonogie mollyuski srednego Paleozoya yuzhnogo Tyan-Shanya (Isucennost, taksonomicheskiy sostav, stratigraficheskoe rasprostranenie). *Vestnik Sankt Petersburgskogo Universiteta, Seriya 7, Geologiya, Geografiya 1987(3)*, 84–88.

Klug, C. 2007. Sublethal injuries in Early Devonian cephalopod shells from Morocco. *Acta Palaeontologica Polonica 52(4)*, 749–759.

Klug, C., Kröger, B., Kiessling, W., Mullins, G.L., Servais, T., Frýda, J., Korn, D. & Turner, S. 2010. The Devonian nekton revolution. *Lethaia 43*, 465–477. DOI 10.1111/j.1502-3931.2009.00206.x

Klug, C., Meyer, E.P., Richter, U. & Korn, D. 2008. Soft-tissue imprints in fossil and Recent cephalopod septa and septum formation. *Lethaia 41*, 477–492. DOI 10.1111/j.1502-3931.2008.00100.x

Kolebaba, I. 1973. Embryonální stádia hlavonožců ze svrchních poloh Liteňského souvrství (silur, spodní wenlock). *Časopis Národního muzea, Oddíl přírodovědný 142*, 28–40.

Kolebaba, I. 1999a. Sipho-cameral structures in some Silurian cephalopods from the Barrandian area. *Sborník Národního muzea v Praze, Řada B – přírodní vědy 55*, 1–15.

Kolebaba, I. 1999b. Gradual opening of the siphonal tube in an orthoconic cephalopod from the Silurian of Central Bohemia (Czech Republic). *Journal of the Czech Geological Society 44*, 131–136.

Kolebaba, I. 2002. A contribution to the theory of the cameral mantle in some Silurian Nautiloidea (Mollusca, Cephalopoda). *Bulletin of the Czech Geological Survey 77*, 183–186.

Korn, D. 2000. Mantle expansion upon the conch in the Late Devonian ammonoid *Erfoudites*. *Acta Geologica Polonica 50(1)*, 21–27.

Kříž, J. 1992. Silurian field excursions: Prague Basin (Barrandian), Bohemia. *National Museum of Wales, Geologica Series 13*, 1–111.

Kříž, J., Dufka, P., Jaeger, H. & Schönlaub, H.P. 1993. The Wenlock/Ludlow boundary in the Prague Basin (Bohemia). *Jahrbuch der Geologischen Bundesanstalt 136*, 809–839.

Kröger, B. 2002. Antipredatory traits of the ammonoid shell. Indications from Jurassic ammonoids with sublethal injuries. *Paläontologische Zeitschrift 76*, 223–234.

Kröger, B. 2007. Concentrations of juvenile and small adult cephalopods in the Hirnantian cherts (Late Ordovician) of Porkuni, Estonia. *Acta Palaeontologica Polonica 52*, 591–608.

Kröger, B. 2008. Nautiloids before and during the origin of ammonoids in a Siluro-Devonian section in the Tafilalt, Anti-Atlas, Morocco. *Special Papers in Paleontology 79*, 1–112.

Kröger, B., Klug, C. & Mapes, R.H. 2005. Soft-tissue attachment in orthocerid and bactritid cephalopods from the Early and Middle Devonian of Germany and Morocco. *Acta Palaeontologica Polonica 50*, 329–342.

Kröger, B., Vinther, J. & Fuchs, D. 2011. Cephalopod origin and evolution: A congruent picture emerging from fossils, development and molecules. *Bioessays 33(8)*, 602–613. DOI 10.1002/bies.201100001

Kuhn, O. 1940. *Paläozoologie in Tabellen*. 50 pp. Fischer Verlag, Jena.

Lindström, G. 1890. The Ascoceratidae and the Lituitidae of the Upper Silurian formation of Gotland. *Kungliga Svenska Vetenskaps-Akademiens Handlingar 23*, 1–54.

Manda, Š. 1996. *Cyrtograptus lundgreni* Biozone in the southwestern part of the Svatý Jan Volcanic Centre (Wenlock, Prague Basin). *Věstník Českého geologického ústavu 71*, 369–374.

Manda, Š. 2003. *Vývoj a společenstva silurských a ranně devonských hlavonožcových vápenců (pražská pánev, Čechy).* 114 pp. Unpublished diploma thesis, MS Přírodovědecká fakulta, Univerzita Karlova, Praha.

Manda, Š. 2008. Palaeoecology and palaeogeographic relations of the Silurian phragmoceratids (Nautiloidea, Cephalopoda) of the Prague Basin (Bohemia). *Bulletin of Geosciences 83*, 39–62. DOI 10.3140/bull.geosci.2008.01.039

Manda, Š. & Frýda, J. 2010. Silurian–Devonian boundary events and their influence on cephalopod evolution: a comparison of faunal and carbon isotopic records from GSSP area (Barrandian). *Bulletin of Geosciences 85*, 513–540. DOI 10.3140/bull.geosci.1174

Manda, Š. & Kříž, J. 2006. Environmental and biotic changes of the subtropical isolated carbonate platforms during Kozlowskii and Lau events (Prague Basin, Silurian, Ludlow). *GFF 128*, 161–168. DOI 10.1080/11035890601282161

Manda, Š. & Kříž, J. 2007. New cephalopod limestone horizon in the Ludlow (Gorstian, early *L. scanicus* Zone) of the Prague Basin (Bohemia, Perunica). *Bollettino della Società Paleontologica Italiana 46*, 33–45.

Manda, Š. & Turek, V. 2009. Minute Silurian oncocerid nautiloids with unusual colour patterns. *Acta Palaeontologica Polonica 54*, 503–512. DOI 10.4202/app.2008.0062

Manda, Š. & Turek, V. 2011. Late Emsian Rutoceratoidea (Nautiloidea) from the Prague Basin, Czech Republic: morphology, diversity and palaeoecology. *Palaeontology 54*, 999–1024. DOI 10.1111/j.1475-4983.2011.01089.x

Manda, Š., Štorch, P., Slavík, L., Frýda, J., Kříž, J. & Tasáryová, Z. 2012. The graptolite, conodont and sedimentary record through the late Ludlow Kozlowskii Event (Silurian) in the shale-dominated succession of Bohemia. *Geological Magazine* 149, 507–531. DOI 10.1017/S0016756811000847

Mapes, R.H., Doguzhaeva, L. Mutvei, H. & Landman, N. 2010. The oldest known (Lower Carboniferous-Namurian) protoconch of a rostrumbearing coleoid (Cephalopoda) from Arkansas, USA: phylogenetic and paleobiologic implications, 114–125. *In* Fuchs, D. (ed.) *Coleoid Cephalopods Through Time.* Musée National d'Histoire Naturelle, Luxembourg.

Marek, J. 1998. Pallioceratida ordo n. – a new order of the Palaeozoic cephalopods (Mollusca, Cephalopoda). *Bulletin of the Czech Geological Survey 73*, 181–182.

Mazurek, D. & Zatoń, M. 2011. Is *Nectocaris pteryx* a cephalopod*? Lethaia 44,* 2–4. DOI 10.1111/j.1502-3931.2010.00253.x

Mehl, J. 1984. Radula und Fangarme bei *Michelinoceras* sp.aus dem Silur von Bolivien. *Paläontologische Zeitschrift 58*, 211–229.

Mutvei, H. 1956. A preliminary report on the structure of the siphonal tube and on the precipitation of lime in the shells of fossil nautiloids. *Arkiv för Mineralogi och Geologi 2*, 179–190.

Mutvei, H. 1957. On the relations of the principal muscles to the shell in *Nautilus* and some fossil nautiloids. *Arkiv för Mineralogi och Geologi 2*, 219–254.

Mutvei, H. 2002a. Connecting ring structure and its significance for classification of the orthoceratid cephalopods. *Acta Palaeontologica Polonica 47*, 57–168.

Mutvei, H. 2002b. Nautiloid systematics based on siphuncular structures and position of muscle scars. *Abhandlungen der geologischen Bundesanstalt 57*, 379–392.

Naef, A. 1921–1928. *Die Cephalopoden. Fauna and Flora des Golfes von Neapel, Volume 1 and 2*. 864 pp. Friedländer Press, Berlin.

Niko, S. & Mapes, R. 2010. Redescription and new information on the Carboniferous cephalopod *Brachycycloceras normale* Miller, Dunbar and Condra, 1933. *Palaeontological Research 13*, 337–343. DOI 10.2517/1342-8144-13.4.337

Ristedt, H. 1968. Zur Revision der Orthoceratidae. *Abhandlungen der mathematisch-naturwissenschaftlichen Klasse 4*, 1–77.

Ruedemann, R. 1921. On color bands in *Orthoceras*. *Bulletin New York State Museum 227*, 63–130.

Savazzi, E. 1998. The colour pattern in cypraeid gastropods. *Lethaia 31*, 15–27. DOI 10.1111/j.1502-3931.1998.tb00484.x

Serpagli, E. & Gnoli, M. 1977. Upper Silurian cephalopods from Southwestern Sardinia. *Bollettino della Società Paleontologica Italiana 16*, 153–196.

Seuss, B., Mapes, R.H., Klug, C. & Nützel, A. in press. Exceptional cameral deposits in a sublethally injured Carboniferous orthoconic nautiloid from the Buckhorn Asphalt lagerstätte in Oklahoma, USA. *Acta Palaeontologica Polonica*.

Shevyrev, A.A. 2005. The cephalopod macrosystem: A historical review, the present state of knowledge, and unsolved problems: 1. Major features and overall classification of cephalopod mollusks. *Paleontologitscheskiy Zhurnal 39*, 33–42.

Schröder, H. 1888. Pseudoseptale Bildungen in den Kammern fossiler Cephalopoden. *Jahrbuch der königlichen preussischen geologischen Landesanstalt für 1887*, 164–229.

Smith, M.R. & Caron, J.B. 2010. Primitive soft-bodied cephalopods from the Cambrian. *Nature 465, 469–472*. DOI 10.1038/nature09068

Sowerby, J.C. 1816. *The mineral conchology of Great Britain. Volume 2.* 251 pp. Privately published, London.

Starobogatov, Y.I. 1974. Xenoconchias and their bearing on the phylogeny and systematics of some molluscan classes. *Paleontological Journal 8*, 1–13.

STENZEL, H.B. 1964. Living *Nautilus*, 59–93. *In* MOORE, R.C. (ed.) *Treatise on Invertebrate Paleontology, Part K, Mollusca* 3. The University of Kansas Press, Lawrence.

STRIDSBERG, S. 1985. Silurian oncocerid cephalopods from Gotland. *Fossils and Strata 18*, 1–65.

STÜRMER, W. 1985. A small coleoid cephalopods with soft parts from the lower Devonian discovered using radiography. *Nature 318*, 53–55. DOI 10.1038/318053a0

SWEET, W.C. 1957. Muscle attachment impressions of some Paleozoic nautiloid cephalopods. *Journal of Paleontology 33*, 293–305.

SWEET, W. 1964. Nautiloidea-Orthocerida, 216–261. *In* MOORE, R.C. (ed.) *Treatise on Invertebrate Paleontology, Part K, Mollusca*. Geological Society of America, Lawrence.

TASNÁDY-KUBACSKA, A. 1962. *Pathologie der Forzaitlichen Tiere: Palaeopathologie, v. 1*. 269 pp. Gustav Fischer, Jena.

TEICHERT, C. 1961. Les Nautiloides des genres *Arthrophyllum* Beyrich et *Lamellorthoceras* Term. & Term. *Annales de Paléontologie 47*, 91–113.

TEICHERT, C. 1964. Morphology of hard parts, 13–53. *In* MOORE, R.C. (ed.) *Treatise on Invertebrate Paleontology, Part K, Mollusca 3*. The Geological Society of America, Lawrence.

TEICHERT, C. & GLENISTER, B.F. 1952. Fossil nautiloid faunas from Australia. *Journal of Paleontology 26*, 730–752.

TUREK, V. 1983. Hydrodynamic conditions and the benthic community of upper Wenlockian calcareous shales in the western part of the Barrandian (Kosov Quarry). *Časopis pro mineralogii a geologii 28*, 246–260.

TUREK, V. 2007. *Sphooceras* – ortoceratoid s vnější i vnitřní schránkou (Cephalopoda, silur), 98–99. *8. paleontologická konferencia – Zborník abstraktov*. Bratislava.

TUREK, V. 2009. Colour patterns in Early Devonian cephalopods from the Barrandian Area: Taphonomy and taxonomy. *Acta Palaeontologica Polonica 54*, 491–502. DOI 10.4202/app.2007.0064

TUREK, V. & MANDA, Š. 2011. Colour pattern polymorphism in Silurian nautiloid *Phragmoceras* Broderip, 1839. *Bulletin of Geosciences 86*, 91–105. DOI 10.3140/bull.geosci.1240

TUREK, V. & MAREK, J. 1986. Notes on the phylogeny of the Nautiloidea. *Paläontologische Zeitschrift 60*, 245–253.

URBANEK, A. 1993. Biotic crises in the history of Upper Silurian graptoloids: A palaeobiological model. *Historical Biology 7*, 29–50. DOI 10.1080/10292389309380442

VALENCIENNES, M.A. 1841. Nouvelles recherches sur le Nautile flambé (*Nautilus pompilius* Lam.). *Archives du Muséum d'histoire naturelle 2*, 257–314.

WARD, P.D. 1987. *Natural history of Nautilus*. 263 pp. Allen & Unwin, Boston.

WILDE, P., BERRY, W.B.N. & QUINBY, H.M.S. 1991. Silurian oceanic and atmospheric circulation and chemistry, 123–143. *In* BASSETT, M.G., LANE, P.D. & EDWARDS, D. (eds) *The Murchison symposium; proceedings of an international conference on the Silurian System. Special Papers in Palaeontology 44*.

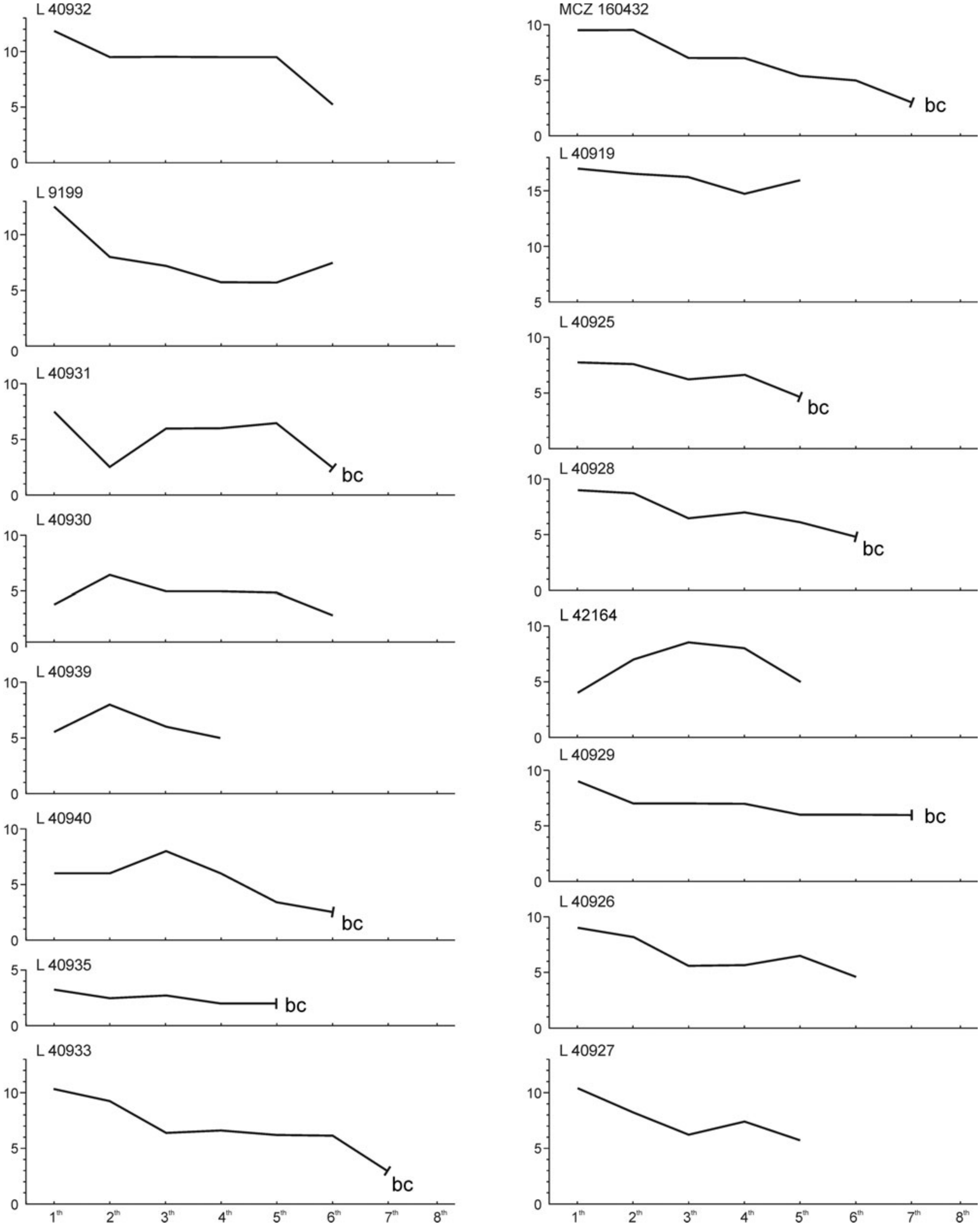
WOODWARD, S.P. 1851. *Manual of the Mollusca*. 542 pp. Virtue Bothers & Co., London.

ZHURAVLEVA, F.A. 1978. Devonskie nautiloidei Nadotrjad Orthoceratoidea. *Trudy Paleontologitscheskogo Instituta Akademie Nauk SSSR 178*, 1–224.

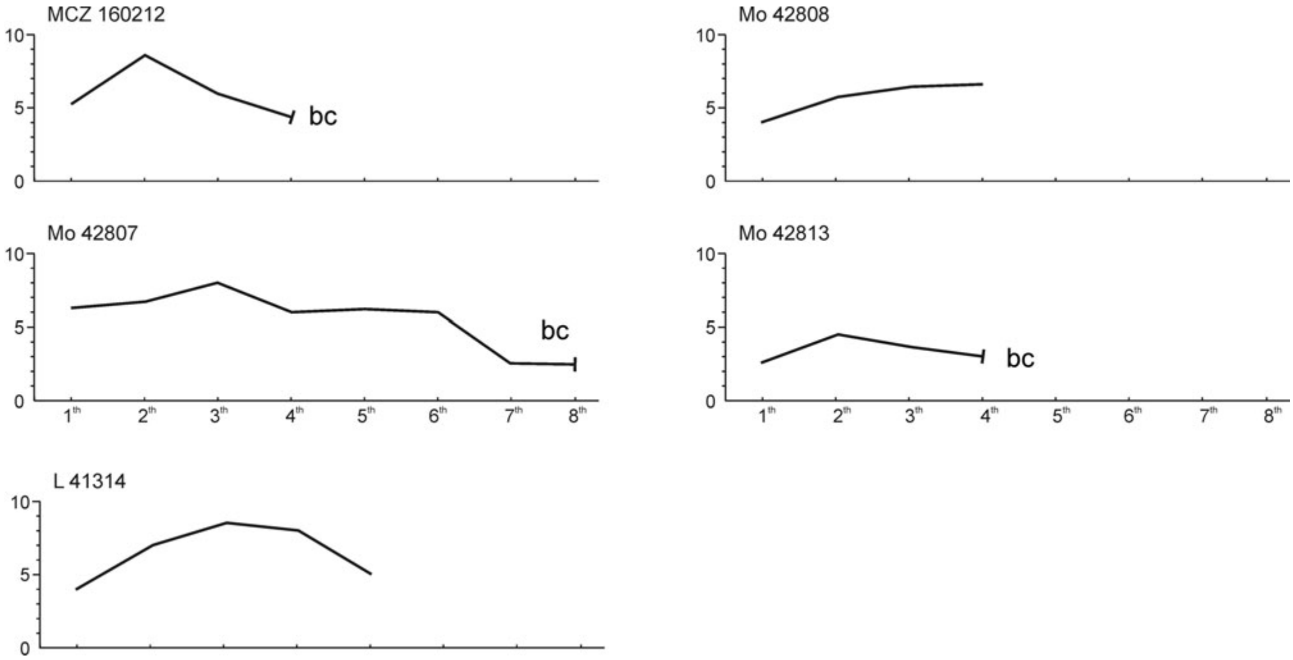
ZHURAVLEVA, F.A. & DOGUZHAEVA, L.A. 2002. Astrovioidea: A new superorder of Paleozoic cephalopods. *Paleontological Journal 38*, 1–73.

Appendix 1

Graphs showing changes in phragmocone chamber lengths during ontogeny in *Sphooceras truncatum*. All measurements based on



specimens cut in median plane; bc means that body chamber is preserved. Phragmocone chambers numbered along x-axis, from septum truncation (oldest still-attached chamber) toward aperture, y-axis shows length of each chamber in mm. For data see Table 1.



Appendix 2

Graphs showing changes in phragmocone chamber length during ontogeny in *Sphooceras disjunctum*. All measurements based on specimens cut in median plane; bc means that body chamber is preserved. Phragmocone chambers numbered along x-axis, from septum truncation (oldest still-attached chamber) toward aperture, y-axis shows length of each chamber in mm. For data see Table 2.