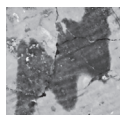


Discontinuous, asymmetric and irregular colour patterns in Silurian oncocerids (Nautiloidea) with cyrtoconic shells

VOJTĚCH TUREK & ŠTĚPÁN MANDA



The colour pattern is a conspicuous character of nautiloid shells. Better understanding to its evolution and possible function is limited by the rarity of preservation. The majority of colour patterns are preserved in demersal late Silurian breviconic oncocerids, while in other cephalopod orders and shell forms, it is limited or unknown. The colour pattern of late Silurian oncocerids (Oonoceratidae Flower, 1942 and Oocerinidae Teichert, 1939) possessing cyrtoconic and slightly curved shells is documented in nine species from Bohemia belonging to five genera. The cyrtocones *Richardsonoceras* Foerste, 1933 and *Oonoceras* Hyatt, 1884 exhibit slightly irregular oblique zig-zag patterns, which may be disrupted and may pass into irregular patches of dark pigment. By contrast, the colour pattern in *Oocerina* Foerste, 1926, possessing similar shell shape to *Oonoceras*, consists of narrow, transversal, slightly undulated bands. The short and very slightly curved shell of *Chromatoceras* gen. nov. displays bilaterally asymmetrical irregular bands or, as in the type species, irregular, asymmetrical, strongly discontinuous colouration. Distinct changes of patterning throughout ontogeny are documented herein in oncocerids, including narrowing of bands, irregular juvenile colouration passing into zig-zag bands and ventrally disappearing colouration in adult shell. Bilaterally asymmetric and irregular pattern, for the first time documented in nautiloids, appeared in probably more demersal cephalopods. The asymmetrical pattern exhibits high intraspecific variation unknown in other nautiloids. All studied oncocerids likely inhabited euphotic zone and the primary function of the colour patterns is camouflage. • Key words: Multiceratia, Oncocerida, Bohemia, asymmetric colouration, ontogeny, protective function.

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Shell colour patterns belong to the more prominent phenotypic characters in ectocochleate cephalopods. The origin and biological function of colour patterns is a matter of ongoing discussions and well-founded data concerning its evolution are still very limited (Williams 2017). However, the poor knowledge on colour patterns in fossil ectocochleate cephalopods significantly increased in the last decades (Mapes & Davis 1996, Turek & Manda 2011, Mapes & Larson 2016). Colour patterning of the nautiloid shell was studied in relation to animal phenotype, autecology, habitat and taphonomy; the applicability for nautiloid taxonomy was discussed (Ruedemann 1921, Foerste 1930a, Kobluk & Mapes 1989, Mapes & Davis 1996, Manda & Turek 2009a).

Up to now, colour patterns are documented in 47 early Palaeozoic nautiloid species (for a list with references, see Tab. 1). We have not regarded those species, in which colour patterns were mentioned (Foerste 1930a, Strids-

berg 1985) but neither illustrated nor described in detail (see Turek 2009).

Colour patterns in Early Palaeozoic nautiloids have been recorded in representatives of the orders Oncocerida, Discosorida, (both subclass Multiceratia), Tarphycerida and Nautilida, while colour patterning in evolutionary older Cambrian and Early Ordovician nautiloids is still unknown. The vast majority of species displaying colour patterns belong to the order Oncocerida possessing straight or slightly curved breviconic shells (Barrande 1865–1870, Foerste 1930a). Colour patterns in oncocerids with coiled or almost straight shell were documented in only a few cases (Manda & Turek 2009a, Turek 2009). Oncocerids display a high disparity of their shell form, ranging from straight, slowly expanding to coiled, trochoceraconic forms (Sweet 1964, Dzik 1984, Manda & Turek 2009b), which is linked to the disparity in colour patterns. The colour patterning in Multiceratia includes longitudinal and

transversal bands and their combination, densely spaced wave bands, zig-zag bands, chevron patterns and bands combined with irregularly dislocated patches of darker pigment that is in some cases associated with some other pattern (Foerste 1930a, Teichert 1964, Manda & Turek 2009b). All these observed types are interpreted as true colour patterns. Regardless of variations, the patterns are not random; they are characteristic for individual taxa and the bands are not parallel to growth lines or other sculpture elements. False colour patterns on cephalopod shells, most common where thickening of the shell is present, have been discussed in more detail by Mapes & Davis (1996), Klug *et al.* (2007), Mapes & Larson (2016). A great deal of attention to pigmentation and formation of colour pattern in molluscs shells paid Meinhard (2009), Gunji *et al.* (1999) and Hammer & Bucher (1999). In agreement with their conclusions dominating discontinuous zig-zag bands with other associate aspects of the colour patterns in cephalopods are characteristic for patterns self-organized by diffusion-reaction processes.

Until now, limited data has been published about colour patterns in nautiloids with exogastric, slowly and moderately expanding curved shell, *i.e.* forms that occur frequently in Early Palaeozoic cephalopod faunas. Here, we add descriptions of colour patterns in seven Silurian oncocerids of the family Oonoceratidae Flower, 1942 and Oocerinidae Teichert, 1939 including two species that were insufficiently illustrated or inadequately schematised by Barrande (1866, 1877). The new genus *Chromatoceras* gen. nov. is introduced and its distinct asymmetric colour pattern is considered as one of its diagnostic features. A summary of all Early Palaeozoic nautiloids displaying colour pattern is presented. We also focused on the variation in colour pattern, its species-specific characteristics, evolution and palaeobiological function.

Material and methods

Twenty-one specimens with preserved colour pattern are included in the present study. Seven specimens come from the historical Barrande's collection, other specimens were collected during field research over the past forty years. The specimens come from the Silurian rocks of an erosional remnant of a marine sedimentary succession of the Prague Basin (Lower Ordovician–Middle Devonian), which formed a part of a peri-Gondwanan terrain during the Early Palaeozoic. Most of the material was found in the cephalopod limestone, a time specific Silurian biofacies (Ferretti & Kříž 1995). The specimens come from the upper part of the Kopanina Formation, which corresponds to the upper Ludlow to lowermost Přídolí Series (Kříž 1992, 1998). Only one specimen was discovered in the carbonate facies of the Požáry Formation of the uppermost Přídolí Series (Kříž 1992, 1998).

Herein, we use the graptolite biozonation of the upper Ludlow Series according to Štorch *et al.* (2014) and Slavík *et al.* (2014); graptolite biozones of the Přídolí Series are adopted from Kříž *et al.* (1986); *ultimus* and *parultimus* biozones are combined according to the global graptolite zonal chart (Koren *et al.* 1996).

The morphological terminology is mostly adopted from Teichert (1964). The shells of the specimens discussed herein are slightly to moderately curved. The shell shape and angle of expansion changed during ontogeny in most oncocerid species to varying degrees. For measurement of the angle of shell expansion (ae), a shorter segment of the shell with constant shell expansion was taken into account using the following parameters: sh₁, sh₂ (= dorsoventral shell height) and shell segment length sl (= the chord line distance between centres of sh₁, sh₂). The parameters used to calculate the sh/sw (shell height/shell width) ratios were measured as close to the aperture as possible, where these values were not affected by damage or weathering. The term “longicone” is used for very slowly expanding shells and “brevicone” for rapidly expanding shells; these are not precisely defined (see Teichert 1964). Here, we use the term longicone or longiconic (very slowly expanding shell – up to 5°), slowly expanding (up to 10°), moderately expanding (up to 20°), and rapidly expanding conchs (up to 30°) while the term brevicone or breviconic includes conch forms with an angle of shell expansion exceeding 30°. Breviconic shells are also characterized by the proportion between height and length; a brevicone is typically short with shell length less than three times of the shell height.

As the colour bands are much better visible when the shell is wet, all specimens were immersed in alcohol or water before photographing to enhance the contrast. Some specimens were whitened with ammonium chloride before photographing. For this purpose, the equipment illustrated in text-fig. 4 by Parsley *et al.* (2018) was used.

All specimens studied are deposited in the collection of the National Museum, Prague (prefix NM).

Description of colour pattern

For the systematic description of the new genus *Chromatoceras* see the Taxonomic appendix below. Abbreviations: sl – maximum shell length; sh – maximum shell height; sw – shell width; bcl – body chamber length; ae – angle of shell expansion.

Family Oonoceratidae Flower, 1942

Richardsonoceras forbesi (Barrande, 1866)

Figures 1, 2

Material. – Four specimens NM-L 46534 (leg. V. Turek),

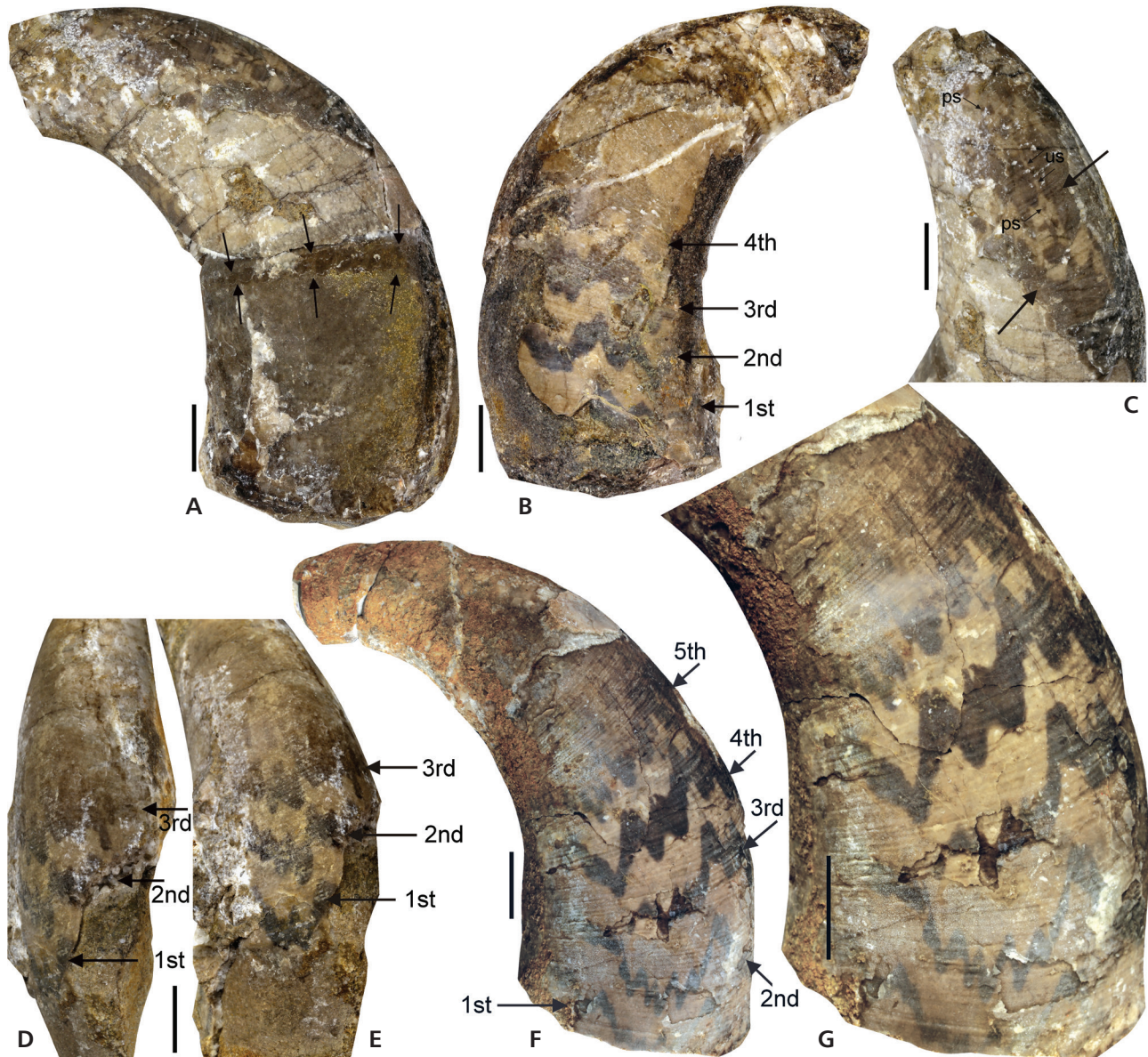


Figure 1. *Richardsonoceras forbesi* (Barrande, 1866); Ludlow Series, uppermost Ludfordian Stage, *fragmentalis* Zone; Beroun, Kosov Quarry, section 783; uppermost part of the Kopanina Formation, a bed just below the base of the Přidolí Series; A, C – NM-L 46535, lateral view (A) and a part of phragmocone, ventrolateral view (C), colour pattern in the form of distinct dark-grey area (arrow) and irregular patches preserved ventrolaterally (small arrow; ps – pigmented spot, us – unpigmented spot), notice also distinct muscle scars (buttress) on the base of the body chamber, margins of annular elevation indicated by arrows; B – NM-L 59873, lateral view, colour pattern in the form of rather irregular zig-zag bands preserved dextrally on the body chamber and adjacent part of the phragmocone; D, E – NM-L 46536, ventral (D) and ventrolateral (E) views, zig-zag bands running obliquely to growth lines (arrows) on adapertural part of phragmocone and adjacent part of body chamber; F, G – NM-L 46534, lateral view (F) and detail of colour pattern (G), the most distinct zig-zag band seen laterally and ventrally near the base of the body chamber; in the adapertural direction the bends are narrower and less distinct (arrows). Colour bands (1st–5th) are numbered in the adapical direction starting close to the shell aperture. Scale bars equal 10 mm.

NM-L 46535, 46536 (both leg. Š. Manda), NM-L 59873 (leg. L. Zedník); Ludlow Series, uppermost Ludfordian Stage, *fragmentalis* Zone; Beroun, Kosov Quarry, section 783 (Kříž 1992), bed no. 39 (Vokáč 1999); uppermost part of the Kopanina Formation, form an about 10 cm thick bed of rusty cephalopod pack-grainstone just below the base of the Přidolí Series; the cephalopod limestone overlays

a light-grey brachiopod-trilobite-cephalopod grainstone yielding the *Prionopeltis archiaci*-*Atrypoides modesta* Community (Havlíček & Štorch 1990).

Description. – All specimens of *R. forbesi*, which bear colour patterns, are relatively large (max. reconstructed shell length about 90 mm), moderately curved, moderately

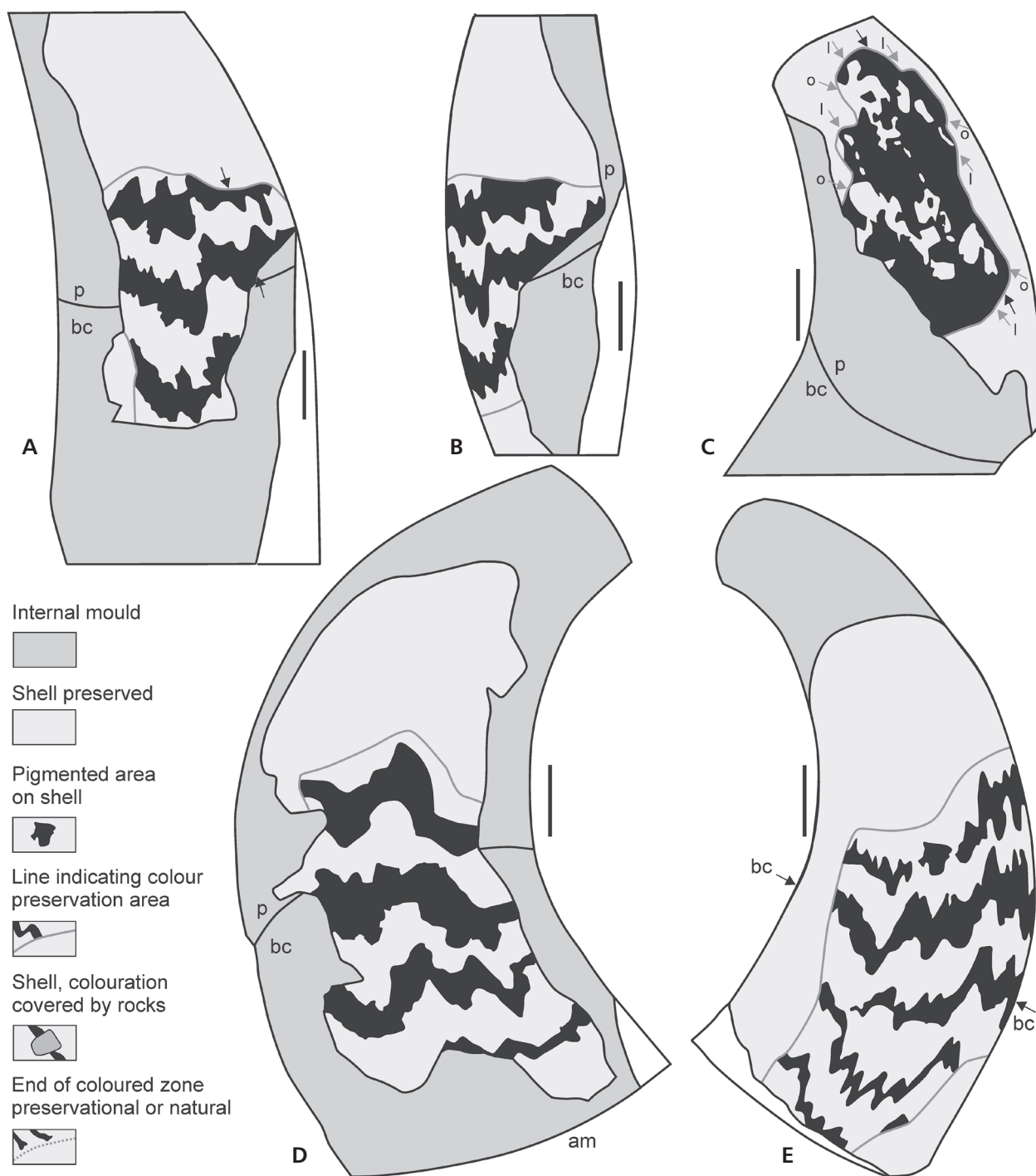


Figure 2. Schematic outlines of colour pattern in *Richardsonoceras forbesi* (Barrande, 1866). Specimens illustrated herein in the Fig. 1; A, B – NM-L 46536, ventrolateral (A) and ventral (B) views; C – NM-L 46535, lateral view; D – NM-L 59873, lateral view; E – NM-L 46534, lateral view. Black arrow indicates ventral axis, dark grey arrows indicate narrow longitudinal (l) and oblique (o) zones with developed patches of coloured or uncoloured shell surface. Abbreviations: am – apertural margin; bc – body chamber; p – phragmocone. Scale bars equal 10 mm.

to rapidly expanding (ae = 18–23°), exogastrically coiled and slightly compressed, with a short body chamber, approximately corresponding to shell height. Cross section of the shell is in shape slightly narrower ventrally than

dorsally. Sculpture consists of fine growth lines forming a shallow and wide hyponomic sinus. Annular elevation displays a distinct buttress; its width gradually increases from the dorsum to the venter. All four studied specimens

are similar in size and probably represent adult individuals as indicated by the increasing shell thickness (up to 0.9 mm) close to the aperture and a slight apertural constriction.

The colour pattern in specimen NM-L 46534 (Figs 1F, G; 2E) was briefly discussed by Turek (1990). The specimen is an incomplete shell with the adapical part of the phragmocone broken off; $sl = 86$ mm, $sh = 36.4$ mm, $sh/sw = 1.2$ (measured in the adapertural part of phragmocone due to weathering of lateral side). Apertural margin is preserved only ventrally, it is broken laterally and dorsally. Due to deep weathering of the specimen dextrally, the colour pattern is preserved only sinistrally and ventrally, both on the body chamber and the adjacent part of phragmocone. The colour pattern is composed of irregular oblique zig-zag bands across the shell. Five colour bands are discernible in this specimen. The coloration consists of brownish bands and is the most intense on the base of the body chamber and adjacent phragmocone chambers. With the exception of the zig-zag bands, the general course of the colour bands roughly follows to the oblique course of growth lines. The fifth band (located most adapically) is interrupted two times laterally while the previous four bands are continuous. The widest colour band (3.5 mm) is present near the base of the body chamber. Unpigmented zones between the individual bands are here markedly wider than the pigmented zones located adapically and adaperturally of this band. The coloration of the neighbouring adapical band is less intense and the band is narrower. Traces of the sixth and seventh discontinuous bands are hardly discernible and subsequently, the colour pattern completely vanishes due to unfavourable preservation. Two narrow zig-zag bands are visible laterally on the adapertural half of body chamber. Their general course differs from preceding bands forming a deep lateral saddle. The bands approach each other ventrally due to the coiling. Intensity of coloration of the two bands situated near the aperture is lower in comparison to earlier bands. This may be a primary feature but decreased brightness of coloration adaperturally, but it is at least partially caused by poorer preservation of the shell. Mid-dorsal relicts of colour bands document the original coloration of the entire circumference of the shell.

Specimen NM-L 59873 (Figs 1B, 2D) is incomplete, strongly damaged sinistrally, $sl = 76$ mm, $sh = 34$ mm, and $sh/sw = 1.2$. Colour pattern relicts are displayed dextrally on the body chamber and the adjacent part of the phragmocone. Four dark grey, oblique irregular zig-zag bands attain the maximum width of 5.3 mm ventrolaterally. The width of the bands decreases towards the aperture. Traces of a narrower last band are discernible dorsolaterally close to the aperture. The bands are separated by a slightly wider unpigmented zone.

Specimen NM-L 46535 (Figs 1A, C; 2C) is an internal mould with relicts of the shell wall on the phragmocone and

distinct muscle scars around the base of the body chamber; $sl = 80$ mm, $sh = 39$ mm, $sh/sw = 1.2$. Dark-grey pigmented zones displayed ventrally and ventrolaterally show a somewhat irregular colour pattern. It forms a transitional type between irregular zig-zag bands and minute isolated patches both within (unpigmented zones) and outside the bands (pigmented zones). Patches are concentrated in three narrow longitudinal zones and two poorly visible transversal zones (Fig. 2C).

Specimen NM-L 46536 (Figs 1D, E; 2A, B) is an incomplete shell with the apical part of the phragmocone broken off. The body chamber is sinistrally and ventrally strongly damaged ($sl = 73$ mm, sh at the base of body chamber is 30.6 mm, $sh/sw = 1.15$). The colour pattern shows three irregular zig-zag bands ventrolaterally and ventrally on the body chamber and the adjacent part of the phragmocone. The bands run obliquely to the growth lines in this part of the shell; the maximum width of the bands is 7 mm. They are markedly bilaterally asymmetrical on the venter.

Remarks. – Shell shape, angle of expansion, length of the body chamber, cross section, slightly contracted aperture in fully grown specimens, position of the siphuncle and its diameter, and sculpture of the studied specimens correspond well to the morphology of the holotype of *Cyrtoceras forbesi* Barrande, 1866 (pl. 115, figs 1–7). The holotype was found at Dlauha Hora e_2 locality. This is the area of the Dlouhá Hora Hill in the proximity to the present day Kosov Quarry, where all specimens described herein were discovered. Classification of this species to the genus *Richardsonoceras* Foerste, 1933 supports the view of Dzik (1984) who assigned the species “*Cyrtoceras*” *haueri* Barrande, 1866 and other species described by Barrande (1866–1877) possessing similar morphology to this genus. *Richardsonoceras forbesi* co-occurs in the Kosov 783 section together with the type species of the genus *Oonoceras* – *O. acinaces* (Barrande, 1866) [= *O. sociale* (Barrande, 1866)].

***Richardsonoceras fraternum* (Barrande, 1866)**

Figure 3B–D

Material. – Specimen NM-L 46537; Kosoř, exact site unknown, most probably an old collector pit close to the Hvíždalka section in the Radotín Valley in the southern part of Prague (Kříž *et al.* 1986); the locality exposes the interval from the upper Ludlow (Ludfordian Stage) to the lowermost Přídolí Series; Kopanina Formation. Based on recently collected specimens, the species *R. fraternum* occurs in the Ludlow Series, uppermost Ludfordian Stage, *latilobus-balticus* and *fragmentalis* biozones.

Description. – The shell of a single specimen of *O. fraternum* with colour pattern is relatively large ($sl = 69$ mm,

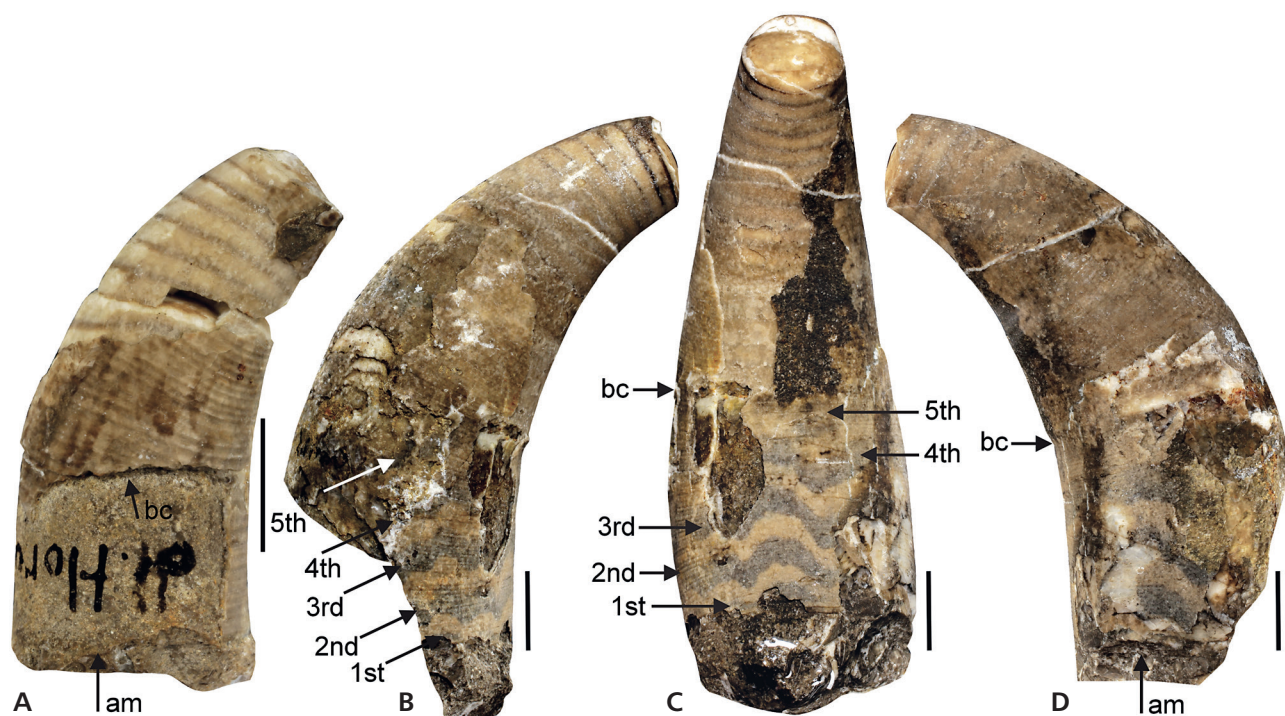


Figure 3. A – *Oonoceras* sp. A; NM-L 46538, Ludlow Series, Ludfordian Stage; Beroun, Dlouhá hora; Kopanina Formation; lateral view; colour pattern in form of narrow zig-zag bands on the adapertural part of the phragmocone. • B–D – *Richardsonoceras fraternum* (Barrande, 1866); NM-L 46537; uppermost Ludlow or lowermost Přidolí series; Praha-Kosoř; Kopanina Formation; dextral (B), dorsal (C) and sinistral (D) views; five broad colour bands visible on body chamber (indicated by arrows). For abbreviations see Fig. 2. Scale bars equal 10 mm.

sh = c. 31 mm, bcl = 35 mm, moderately curved shell, moderately expanding, $ae = 19^\circ$), exogastric and has an almost circular cross section ($sh/sw = 1$). Cross section of the shell is slightly narrower ventrally. The shell surface is smooth with fine growth lines forming a shallow hyponomic sinus. The specimen is incomplete; the adapical part of the phragmocone and the body chamber are broken off ventrally. The colour pattern is well discernible on the dorsum and flanks of the body chamber; traces of the colour pattern are observable also dorsally on the adjacent part of the phragmocone.

Five dark-grey zig-zag bands generally follow the growth line course. The bands are widely V-shaped mid-dorsally. The median tip of this “V” is directed adapically. The bands pass into smaller and narrower “V” dorsolaterally and continue in wide parabolic arches. Zig-zag bands in a small amplitude follow this. The bands are almost of the same width dorsally (3 mm); laterally they attain the width of 4 mm.

Remarks. – Shell morphology of the specimen with colour pattern discussed here corresponds to those of both syntypes of *Cyrtoceras fraternum* (Barrande 1866, pl. 109, figs 22–27). The species is assigned here to the genus *Richardsonoceras*. The species *R. fraternum* has a slightly broader, less curved and smaller shell than *R. forbesi*

(Barrande, 1866). Other morphological characters indicate close relationships between both species (Manda & Turek 2009b), which are known from the uppermost Ludfordian Stage, Kopanina Formation of the Prague Synform sections. *R. forbesi*, however, appears stratigraphically slightly earlier than *R. fraternum* and is more abundant in the light-coloured cephalopod limestones, while *R. fraternum* occurs in more off-shore, distal dark-grey cephalopod limestone (own field data).

Oonoceras sp. A

Figures 3A, 5A

Material. – One specimen NM-L46538 from Beroun, Dlouhá hora (locality indicates Barrande’s inscription “dl. Hora” on the body chamber), i.e. the area of Dlouhá hora Hill near Kosov Quarry. The light-grey skeletal limestone in which it is preserved corresponds to the upper part of the Kopanina Formation, late Ludlow Series (Ludfordian Stage) in age. The specimen was found by V.T. during the revision of Barrande’s material and was not illustrated before.

Description. – The specimen of *Oonoceras* sp. A has a moderately curved, rapidly expanding ($ae = 22^\circ$) exogastric shell with a short body chamber; the shell is compressed with an elliptic cross section, which is narrower ventrally than

dorsally ($sh/sw = 1.3$); the sculpture consists of distinct, transverse growth lines. Hyponomic sinus is very shallow and rounded; $sl = 40$ mm, $sh = 18$ mm, $bcl = 15$ mm.

The specimen is an internal mould with the shell preserved in the adapertural part of phragmocone. The colour pattern is displayed only dextrally. Zig-zag bands with great amplitudes (reaching maximum $\frac{2}{3}$ of sl) and sharp angles can be followed from the mid-dorsal to mid-ventral region. The maximum width of colour bands is about one millimetre. The distance between individual bands roughly corresponds to their width. Two adjacent bands are connected ventrolaterally by a narrow, darkly pigmented zone.

Remarks. – Shell shape, cross section, expansion rate, body chamber length and siphuncle position corresponds to the diagnostic characters of *Oonoceras* Hyatt, 1884. The small size (reconstructed shell length is 45 mm) and widely spaced growth lines near the aperture indicate that the shell may represent an early growth stage. Fragmentary preservation of the studied specimen limited species identification; however, the morphology of the specimen suggested a close affinity to the type species of *Oonoceras* – *O. acinaces* (Barrande, 1866).

Oonoceras geinitzi (Barrande, 1866)

Figures 4, 5B

Material. – Two specimens NM-L 46539, 46540 (leg. L. Zedník); lowermost Přídolí Series, *ultimus-parultimus* Zone, Kopanina Formation, Praha-Lochkov, U topolů section (Manda & Turek 2009b, fig. 1).

Description. – The two specimens are curved shells of moderate sizes (max. reconstructed $sl = c. 70$ mm in NM-L 46539). They are exogastric, with a moderate to large $ae = 19\text{--}21^\circ$ and slightly compressed; the body chamber is very short. Distinct growth lines display a very shallow hypnomic sinus. Both specimens are almost of the same size. Slight expansions of the internal mould near the apertural margin (NM-L 46539) indicates a reduced shell thickness and thus a possible subadult to adult growth stage.

Specimen NM-L 46539 (Fig. 4C, D) represents a body chamber with about $\frac{2}{3}$ of the phragmocone; $sl = 62$ mm, $sh = 19$ mm, $bcl = 22$ mm, $sh/sw = 1.3$. The shell wall is preserved on the phragmocone; the specimen is weathered sinistrally. The faint colour pattern is visible dextrally and ventrally. The typical irregular zig-zag pattern is most distinct ventrolaterally. The general course of colour bands corresponds to the course of growth lines. Close to the centre of dorsum and flanks, colour bands are indistinct. Close to the midflanks, the colour bands reach their maximum amplitude with tips directed adapically. Dark bands are narrower than the unpigmented zones.

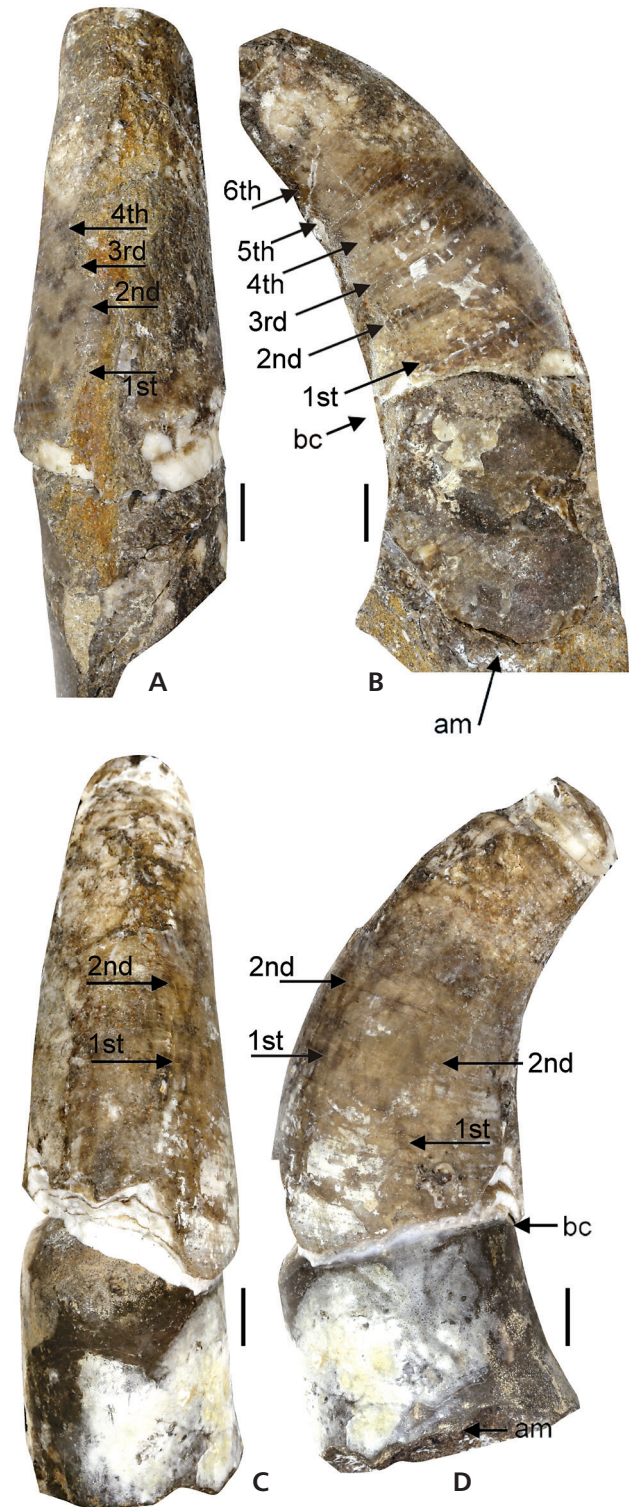


Figure 4. A–D – *Oonoceras geinitzi* (Barrande, 1866), lowermost Přídolí Series, *parultimus-ultimus* Zone, Praha-Lochkov, U topolů section, Kopanina Formation; A, B – NM-L 46540, ventral (A) and lateral (B) views, zig-zag bands (arrows) in the adapertural part of the phragmocone; C, D – NM-L 46539, ventral (C) and lateral (D) views. Narrow zig-zag colour bands indicated by arrows 1st–6th. For abbreviations see Fig. 2. Scale bars equal 5 mm.

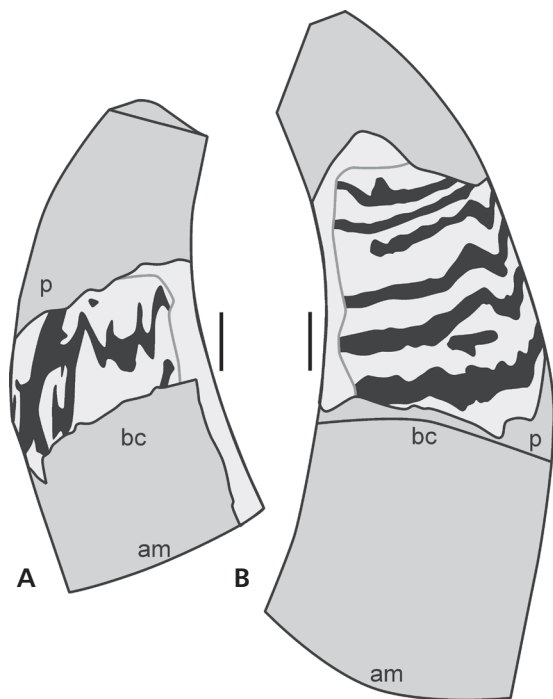


Figure 5. Schematic outlines of colour patterns in *Oonoceras*; lateral views. • A – *Oonoceras* sp. A; NM-L 46538, specimen illustrated herein in the Fig. 3A. • B – *Oonoceras geinitzi* (Barrande, 1866); NM-L 46540, specimen illustrated herein in the Fig. 4B. For abbreviations see Fig. 2. Scale bars equal 5 mm.

Specimen NM-L 46540 (Fig. 4A, B) is a 63 mm long shell fragment with sh = 24 mm, sh/sw at the base of body chamber is 2.4, bcl = 26 mm. The apical part is missing. The shell wall is exfoliated on the body chamber. The colour pattern is displayed sinistrally on the phragmocone. Rather narrow irregular zig-zag bands about 1.5 mm in width increase in amplitude from the dorsum to the venter. Near the median plane, these bands disappear. Their general course is roughly transversal. Light grey interspaces between individual bands are two to three times wider than the bands.

Remarks. – The shell shape, cross section, length of the body chamber and position of the siphuncle conforms to the diagnostic characters of *Oonoceras* Hyatt, 1884. The angle of shell expansion, mode of shell curvature and sculpture corresponds to that of the type material of *O. geinitzi* (see Barrande, 1866, pl. 122, figs 1–8, pl. 208, figs 31–34; Kozořz and Lochkov localities).

?*Oonoceras impatiens* (Barrande, 1866)

Figures 6, 7

Material. – Specimen NM-L 46541; Praha-Lochkov, U topolů section; Přídolí Series, *ultimus-parultimus* Zone, a bed of dark grey cephalopod limestone (packstone) just above

the base of the Přídolí Series (leg. Š. Manda); Kopanina Formation (Manda & Turek 2009b, fig. 1).

Description. – The shell is relatively small (reconstructed sl = c. 49 mm), slightly curved, rapidly expanding (ae = 26°), ventral side more convex than the dorsal side, moderately compressed and exogastric. The shell surface shows distinct transverse growth lines and moderately raised ridges. Hyponomic sinus is very slightly indicated.

Specimen NM-L 46541 (Figs 6, 7) is an incomplete shell with missing apical part of the phragmocone; shell wall on the body chamber is exfoliated. sl = 42 mm, sh = 21 mm, sw = 17.3 mm, lbc = 16 mm, sh/sw = 1.22, ae markedly increase during ontogeny (23–32°). Slight expansion of the body chamber close to the apertural margin may indicate a subadult growth stage of the specimen. Colour patterns are preserved around the entire circumference of the phragmocone. However, the left side of the shell is partly covered by rock. The colour pattern is peculiar and shows sudden changes in its general character. The colour bands are somewhat fragmented with light coloured patches occurring inside dark bands and with narrow bands connecting adjacent bands. The zig-zag pattern is suppressed, and the general course of pigmented zones is transverse. Short and wide transverse pigmented zones are interconnected via thin, finger-like junctions. These thin and short strips are arranged in rows running subparallel to the longitudinal shell axes. Aperturally, the colour pattern displays a striking asymmetry, especially on the dorsum. Close to midflank, the pigmented zone is reduced into narrow strips, which are either interconnected with wide pigmented zones, or isolated. Discontinuous, wide bands are widely W-shaped ventrally.

Remarks. – The cross section with a rounded venter, the thin, subventral siphuncle, elaborated growth lines forming slightly elevated ridges in our specimen are characteristic for *Oonoceras*. By contrast, it differs from *Oonoceras* in having a less curved and a more rapidly expanding shell; the shell curvature decreases apically. Its shell morphology largely corresponds to “*Cyrtoceras*” *impatiens* Barrande, 1866 (Barrande 1866, pl. 120, figs 24–29).

?*Oonoceras* aff. *impatiens* (Barrande, 1866)

Figures 8, 9

Material. – Specimen NM-L 46542; Praha-Lochkov, U topolů section; Přídolí Series, *ultimus-parultimus* Zone, a bed of dark grey cephalopod limestone (packstone) just above the base of the Přídolí Series (leg. Š. Manda); Kopanina Formation (Manda & Turek 2009b, fig. 1).

Description. – Specimen NM-L 46542 (Figs 8, 9) represents an apertural part of a phragmocone partly embedded

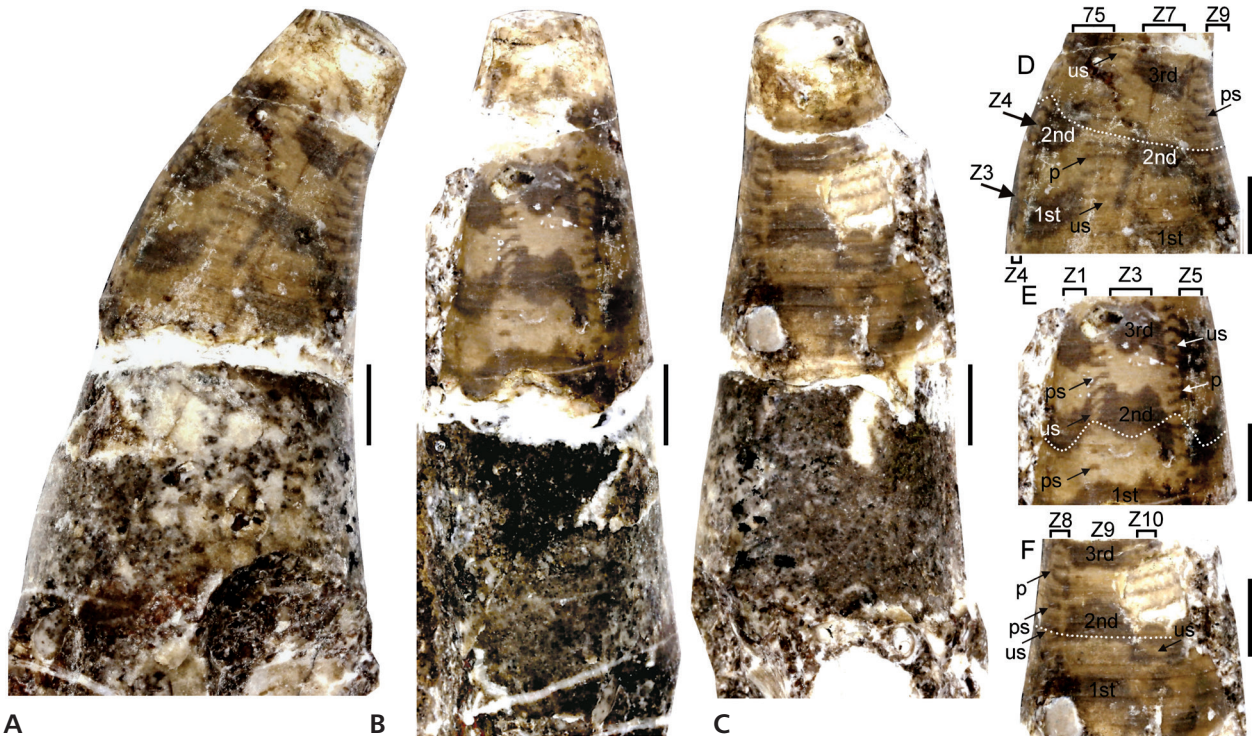


Figure 6. *?Oonoceras impatiens* (Barrande, 1866); NM-L 46541; lowermost Přidolí Series, *parultimus-ultimus* Zone; Praha-Lochkov, U topolů section; Kopanina Formation; lateral (A, detail D), ventral (B, detail E) and dorsal (C, detail F) views; notice unusual colour pattern: wide zig-zags bands (1st–3rd in D–F) reduced into isolated patches arranged in narrow longitudinal zones (Z2, 4, 6, 8, 10) indicated by arrow with grey letters A–E, sometimes interconnected by short narrow bands or spots. Notice also the asymmetry of the colour pattern dorsally. Abbreviations: ps – pigmented spots; us – un-pigmented spots; p – narrow band protrusion. Dotted line indicates the course of colour bands. Scale bars equal 5 mm.

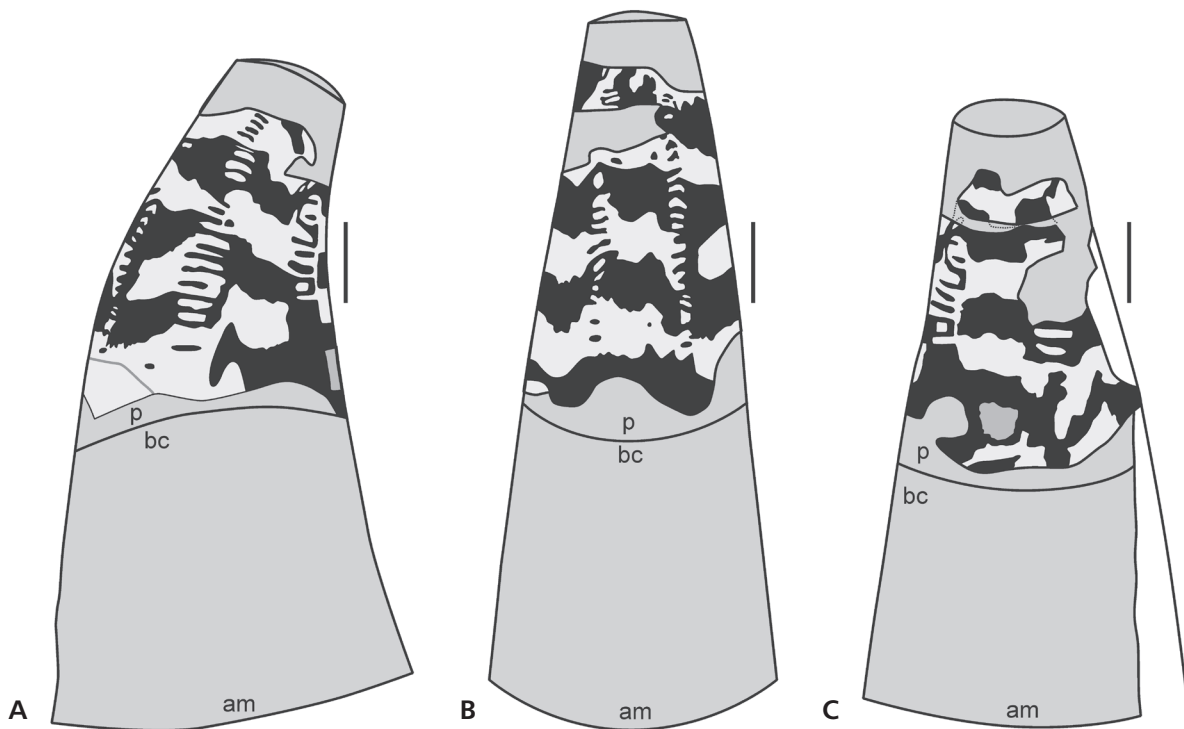


Figure 7. Schematic outlines of colour pattern in *?Oonoceras impatiens* (Barrande, 1866); specimen illustrated in the Fig. 6, lateral (A), ventral (B) and dorsal (C) views. For abbreviations see Fig. 2. Scale bars equal 5 mm.

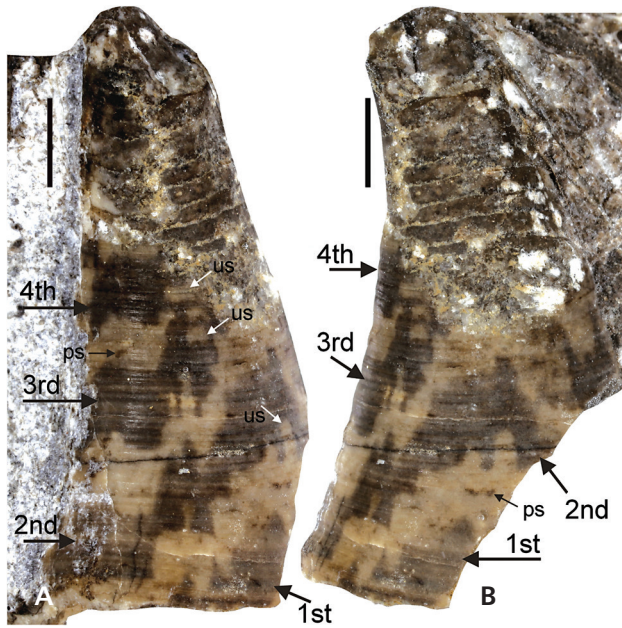


Figure 8. *?Oonoceras aff. impatiens* (Barrande, 1866); NM-L 46542; lowermost Přídolí Series, *parultimus-ultimus* Zone; Praha-Lochkov, U topolů section; Kopanina Formation; dorsal (A) and lateral (B) views; four wide zig-zags in the adapertural half of the phragmocone indicated by arrows. Abbreviation: ps – pigmented spots; us – unpigmented spots. Scale bars equal 5 mm.

in rock. It is adapically exfoliated showing several short phragmocone chambers; sl = 34 mm long, sh = 17 mm, ae = 30°. Four distinct wide colour bands are exposed dorsally and laterally. Their width changes rapidly, attaining maximum width mid-dorsally. Starting mid-dorsally, irregular zig-zags run adapically, obliquely to growth lines; near midflank, the general course of zig-zag bands change and they run obliquely adaperturally (bands thus form a V-shaped pattern). Pigmented and un-pigmented areas on the shell surface are balanced.

Remarks. – Our specimen of *?O. aff. impatiens* resembles *?O. impatiens* (Barrande, 1866) from which it differs, besides differences in colour pattern, in having more

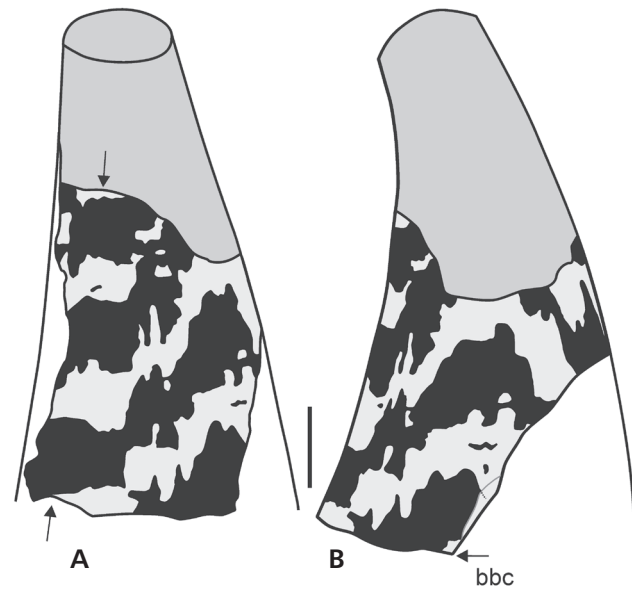


Figure 9. *?Oonoceras aff. impatiens* (Barrande, 1866); schematic outlines of the colour pattern in specimen NM-L 46542 illustrated herein in the Fig. 8, dorsal (A) and lateral (B) views. Abbreviation: bbc – base of the body chamber, arrows indicate the dorsal shell axis. Scale bar equals 5 mm.

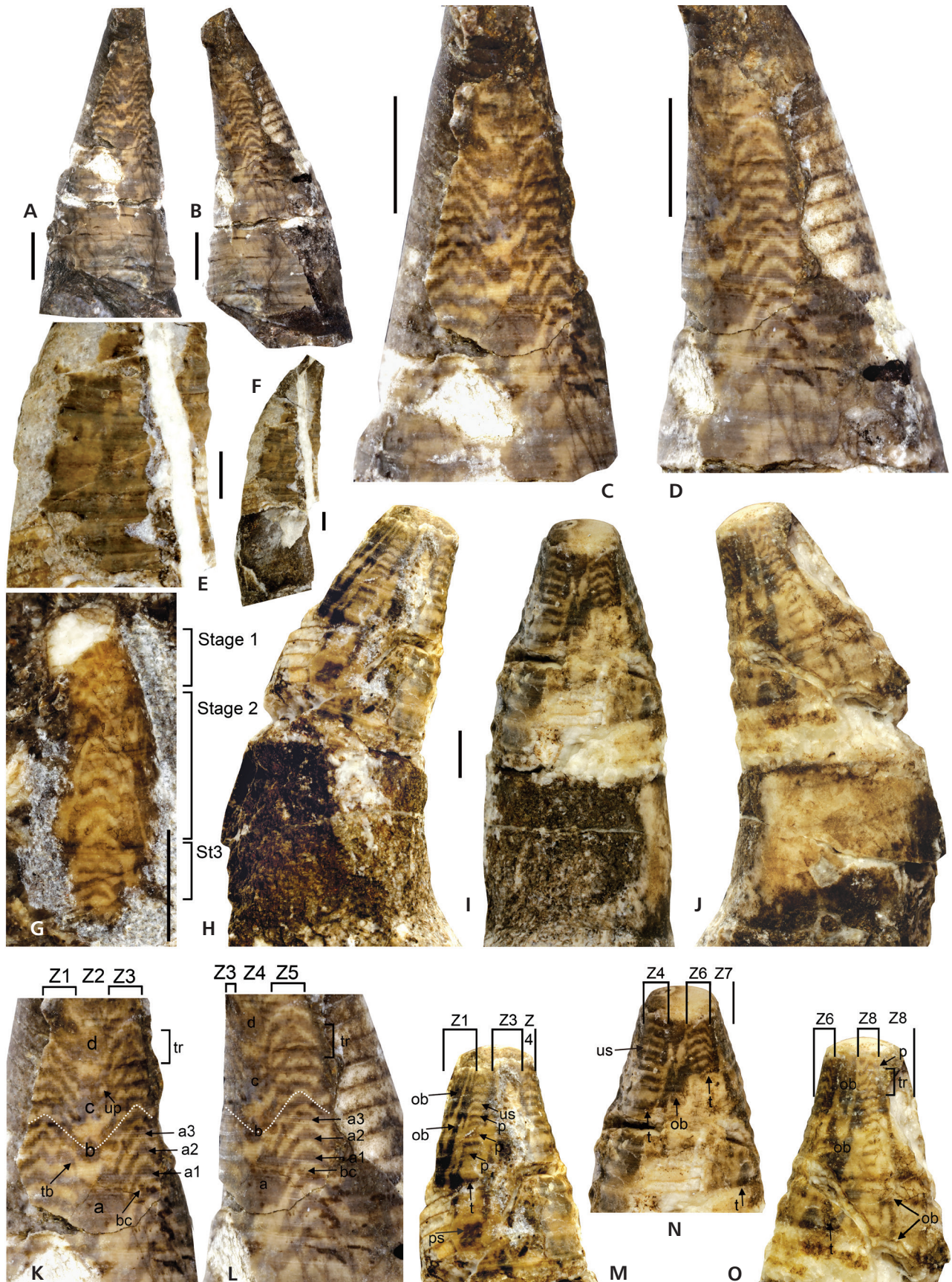
distinct growth ridges. The only specimen available represents an incomplete phragmocone hampering a more precise taxonomic determination. Our specimen of *?O. aff. impatiens* was found in the same bed as *?O. impatiens*; they are at least closely related or conspecific.

***Chromatoceras veteranum* (Barrande, 1866)**

Figures 10–13

Material. – Six specimens showing colour patterns (see Tab. 2 for catalogue numbers and dimensions, for further details see systematic appendix). Barrande (1866, 1877) illustrated two specimens of *C. veteranum* with a preserved colour pattern. Only the venter of the holotype (NM-L

Figure 10. *Chromatoceras veteranum* (Barrande, 1866); A–D, K, L – NM-L 21751 (specimen, Barrande 1877, pl. 514, figs 13–17), lowermost Přídolí Series, Praha-Lochkov, Kopanina Formation, dorsal (A, C) and lateral (B, D) views and details (K, L), a–d indicates four bands branched into narrow bands, e.g. a1–3; E, F – NM-L 10127 (holotype of “*C. sica*” Barrande, 1866, pl. 124, figs 6–11), lowermost Přídolí Series, Praha-Slivenec, Kopanina Formation, lateral views; G – NM-L 46581, lowermost Přídolí Series, *parultimus-ultimus* Zone, Praha-Lochkov, U topolů section, Kopanina Formation, dorsolateral view showing changes in the colouration of the juvenile shell: irregular patches (ip) – (Stage 1), V-shaped bands (vsb) – (Stage 2) and transversal band (tb) – (Stage 3); H–J, M–O – NM-L 46890; lowermost Přídolí Series, *parultimus-ultimus* Zone, Praha-Lochkov, U topolů, Kopanina Formation, lateral (H, J) and dorsal views (I) and details of adapical part of phragmocone, dextral (M), dorsal (N) and sinistral (O) views. Dotted line indicates generalized course of colour bands. Notice peculiar colour pattern – combination of longitudinal zones with densely spaced undulated transversal bands and zones with irregular broad zig-zags, sometimes partly overlapping. Abbreviations: a, b, c, d – indication of uninterrupted colour bands; bb – band branching; bc – band connection; bi – band interruption; bv – band vanishing; da – decreasing amplitude of V-shaped bands passing into transversal bands; ib – irregular band; ob – oblique band; p – protruding part of the band; ps – pigmented spot; t – transversal band; tb – termination of the band; tr – patches arranged in triangular composition; tt – terminal thickening of the band; up – unpigmented spot; us – unpigmented spots; uz – unpigmented zone surrounded by transversal bands; vb – V-shaped band; Z1 to Z12 – short transversal irregular bands arranged into longitudinal zones. Scale bars equal 5 mm.



14298, Barrande 1866, pl. 208, fig. 21) was figured. Another, smaller specimen NM-L 21751 from the locality Lochkov was illustrated later (Barrande, 1877, pl. 514, figs 13–17).

Description. – The holotype (NM-L 14298; Figs 11I–P, 13D–G) is an incomplete shell with partly exfoliated shell wall (for dimensions see Tab. 2). The embryonic shell is missing. Colour pattern is preserved on the phragmocone only. Relicts of the shell wall attached to the internal mould of the body chamber are poorly preserved. The darkly pigmented zig-zag bands are well visible around the whole shell circumference. Their general course is roughly transversal, but the pattern is laterally asymmetrical and markedly changes during growth. Typical zig-zag bands are more distinct in the adapical part of the phragmocone. Adapically, the colour bands become serrate dorsally and resembles fragments of “seismic recordings”. The bands are very narrow and usually less than one millimetre wide. Brownish colour bands are separated by slightly wider light grey interspaces indicating light colouring of the original shell.

Specimen NM-L 21751 (Figs 10A–D, K, L; 12A, B) is an almost complete, small, juvenile shell, which is missing most of its apical part (for dimensions see Tab. 2). The body chamber is ventrally broken off. The shell wall is ventrally and ventrolaterally exfoliated, adapical part of the phragmocone is ventrally abraded and shows the morphology of the siphuncle. The colour pattern is well preserved dorsally (partly also on the body chamber) and dorsolaterally. It consists of rather irregularly developed, narrow zig-zag bands. Some of them disappear mid-dorsally while others merge into irregular patches or form a widely W-shaped pattern. Moderate asymmetry of the colour pattern is well expressed dorsally. Tips of the “W-shape” are directed adorally. Dorsolaterally, the narrow colour bands form oppositely oriented “V”s with the tips directed adapically. The mid-dorsal zone is lighter in colour than the dorsolateral part of the shell. Irregularity and asymmetry of the colour bands increase towards the body chamber; the features are well expressed dorsally. Close to the base of the body chamber, the zig-zag pattern fades out.

Specimen NM-L 46581 (Fig. 10G, 12D) is a fragment of the early juvenile part of the shell. Colour pattern is observable dorsolaterally and documents rapid changes in the course of colour bands during early ontogeny. The bands in the earliest preserved shell part are discontinuous forming more or less isolated patches. Later, the bands form

zig-zag patterns with the V-shaped tips oriented adapically. On the shell fragment located most adapically, the zig-zag pattern is suppressed.

Relicts of zig-zag bands are preserved in NM-L 10127 (Figs 10E, F and 19G, H). The almost complete specimen is, however, strongly damaged. The shell wall is partly preserved on the phragmocone and shows slightly expressed irregular zig-zag bands mid-laterally. Their tendency to coalesce into patches is indicated.

Specimen NM-L 46890 (Figs 10H–J, M–O and 13A–C) represents a complete body chamber and a phragmocone with missing adapical part; the shell wall of the body chamber is exfoliated. The colour patterns show an unusual combination of irregular transverse bands arranged into longitudinal rows and broad zig-zags. Two rows of short, thin and densely spaced bands are located dorsally and one row near the centre of the flanks. Relicts of distinct zig-zag bands with an acute angle are preserved between these rows. These bands sometimes overlap transverse bands, which disappear adapically, while zig-zag bands persist.

The heavily damaged specimen NM-L 46578 (Figs 11A–H, 12C–G) lacks the adapical part of the phragmocone and the adapertural part of the body chamber. It probably represents an incomplete subadult growth stage. Colour patterns are well visible across the entire circumference of the phragmocone. The general pattern closely resembles the pattern in specimen NM-L 21751. It shows two longitudinal rows of short transverse bands vaulted or pointed adapically on dorsum and venter. Between them, darkly pigmented patches occur. Finely serrate undulating bands running roughly transversally cover the flanks. The narrow transverse bands changed adapically from vaulted to transversal. Similar, lighter-coloured zones with patches of dark pigment, as in the centre of ventral and dorsal sides, are developed ventrolaterally and dorsolaterally.

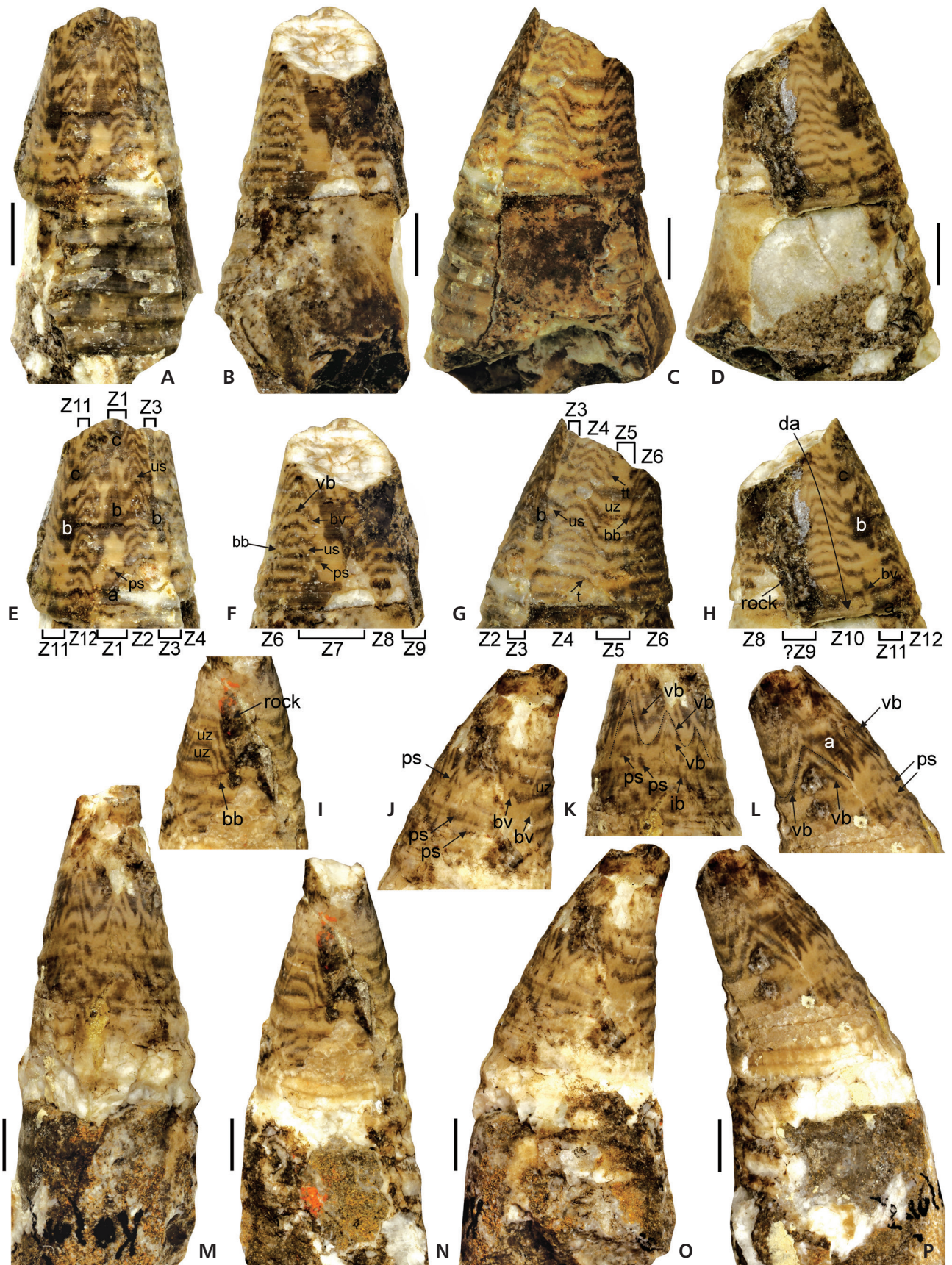
Specimen NM-L 46580 (not figured) is incomplete with missing adapical part of the phragmocone. Relicts of the colour pattern are present dorsolaterally on the phragmocone and show dark grey zig-zag bands. However, due to poor preservation, a more detailed description of the pattern is impossible.

***Chromatoceras constringens* (Barrande, 1866)**

Figures 14, 15, 20

Material. – Two specimens NM-L 669, 46579; for details see the systematic appendix.

Figure 11. *Chromatoceras veteranum* (Barrande, 1866); A–H – NM-L 46578, lowermost Přidolí Series, *parultimus-ultimus* Zone, Praha-Lochkov, U topolů, Kopanina Formation, ventral (A, E), dorsal (B, F) and lateral views (C, G and D, H), a, b, c indicate continuous individual bands; I–P – NM-L 14298 (holotype illustrated by Barrande 1866, pl. 208, fig. 21); lowermost Přidolí Series, Kosoř, Kopanina Formation, ventral (K, M), dorsal (I, N) and lateral views (J, O and L, P). For abbreviations see Fig. 10. Scale bars equal 5 mm.



Description. – The holotype NM-L 669 is an incomplete shell missing the adapical half of the phragmocone (for dimensions see Tab. 2). The shell wall is partly exfoliated. The colour bands are partially visible around the whole circumference of the shell (Figs 14A–D, 15). Its venter shows markedly asymmetric colour patterns. Bands,

generally running obliquely to the shell axis in an angle *c.* 20°, form separated segments, some of them resembling rhabdosomes of graptolites. Wide lateral strips with frayed margins indicate the general zig-zag course of the bands. Disintegrated narrow band segments of similar course as on its venter are discernible also dorsally. Between main

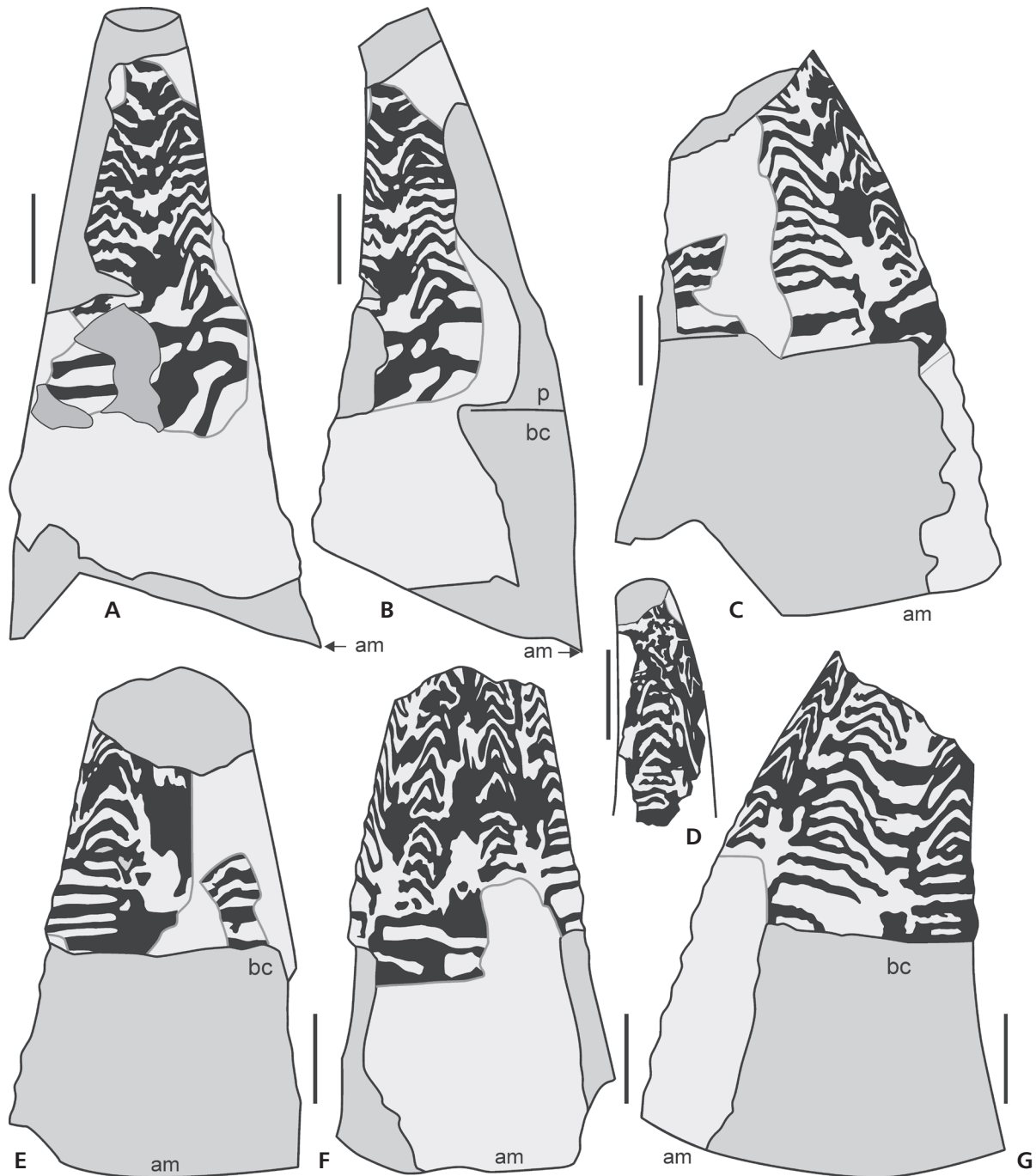


Figure 12. Schematic outlines of colour pattern in *Chromatoceras veteranum* (Barrande, 1866); A, B – NM-L 21751, illustrated in the Fig. 10A–D, dorsal (A) and lateral (B) views; C, E–G – NM-L 46578; illustrated in the Fig. 11A–H, lateral (C, G), dorsal (E) and ventral (F) views; D – NM-L 46581, illustrated in the Fig. 10G, dorsolateral view. For abbreviations see Fig. 2. Scale bars equal 5 mm.



Figure 13. Schematic outlines of colour patterns in *Chromatoceras veteranum* (Barrande, 1866); A–C – specimen NM-L 46890, illustrated herein in the Fig. 10H–J; D–G – specimen NM-L 14298, illustrated herein in the Fig. 11I–P. For abbreviations see Fig. 2. Scale bars equal 5 mm.

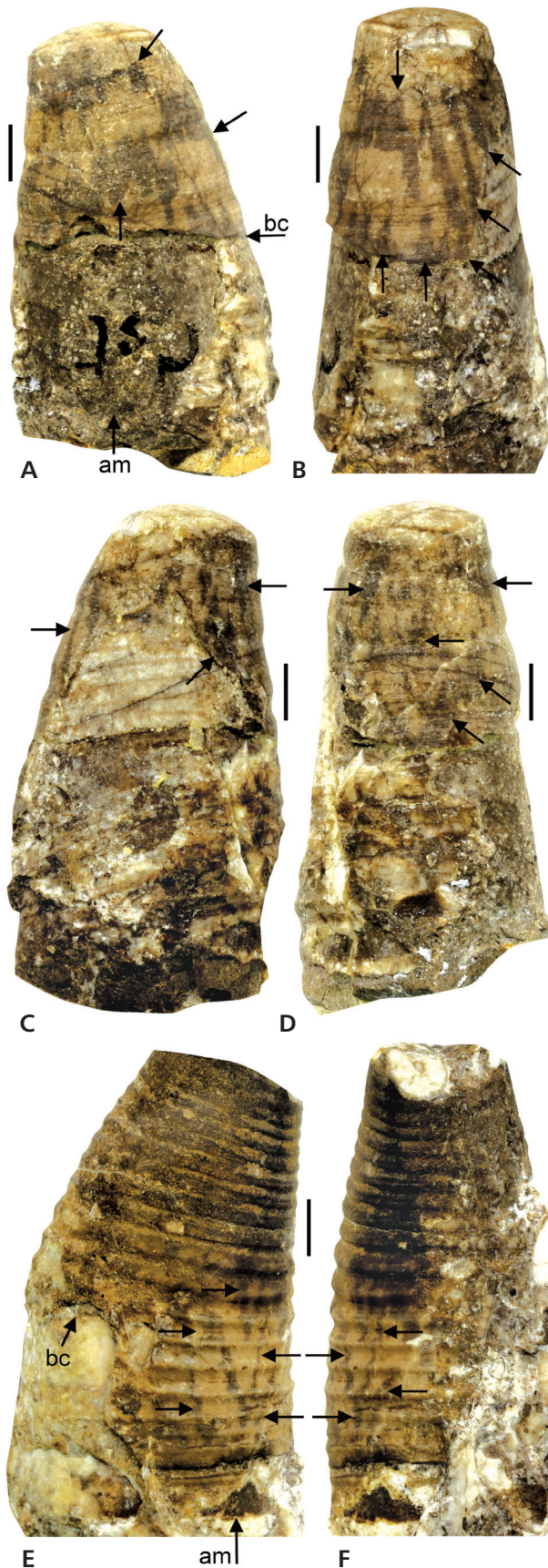
pigmented zones, small pigmented patches are located irregularly.

Specimen NM-L 46579 (Figs 14E, F; 20A–C) displays a well-preserved shell, only the left side of the body chamber is damaged. A zig-zag pattern formed by discontinuous narrow bands is discernible laterally (dextrally) on the body chamber and the adjacent part of the phragmocone.

?*Euryrizoceras decurio* (Barrande, 1866)

Figure 16

Material. – The species is based on the holotype (NM-L 15404) only, illustrated by Barrande (1866) in pl. 240, figs 11–14 (refigured here as Fig. 16); its preservation and sedimentary filling of the body chamber (dark grey cephalopod packstone) indicate Ludlow Series (Ludfordian



Stage, Kopanina Formation) or Přídolí Series (Požáry Formation). The locality “Vallon de Slivenetz”, *i.e.* Slivenec Valley near Praha-Slivenec, is given in the text and figure captions concerning this species (Barrande 1867, p. 69). Nevertheless, Barrande’s original inscription “Gr. Kuchel” (= Gross Kuchel), *i.e.* land registry of Praha-Velká Chuchle, is written in black ink on the specimen. However, both localities lie close to each other in the Slivenec Valley but in different land registries; based on the mode of preservation, the origin from the locality “Vallon de Slivenetz” is more likely.

Description. – The shell of the holotype of ?*E. decurio* is small (sl = 38.6 mm, sh = 19.4 mm), rapidly expanding ae = 22°; length of reconstructed complete shell is about 45 mm), slightly curved and exogastric. Body chamber occupies $\frac{2}{3}$ of the shell length. The shell is moderately compressed, elliptic in cross section (sh/sw = 1.25). The sculpture consists of distinct, transversal growth lines forming a shallow hyponomic sinus ventrally; internal structure of the siphuncle is unknown. The specimen is incompletely preserved, with strongly damaged phragmocone and missing adapertural part. The shell wall is partially preserved on the phragmocone; on the body chamber, it is exfoliated except relicts of dorsolateral shell wall.

The colour pattern is well preserved on the phragmocone dextrally and dorsolaterally (Fig. 16A). Distinct bands in the form of narrow and high parabolas are situated mid-laterally (dextrally); dark-grey bands are widest near apices of these parabolas, which are oriented adaperturally. There, their width reaches three millimetres. Segments of parabolas dorsolaterally form a V dorsally, probably with a small mid-dorsal lobe. Two transversally prolonged patches of dark-grey pigment displayed sinistrally probably do not represent an original colour pattern and are rather of diagenetic origin. Sporadic traces of colour patterns are preserved ventrolaterally. They indicate that originally, the zig-zag colour pattern was present on the entire circumference of the shell. Lighter coloured interspaces are almost of the same width as the darker bands.

Remarks. – The illustration by Barrande (1866, pl. 240, fig. 11) showing wide, dark grey symmetrical V-shaped bands laterally is in this case inaccurate and simplified (see

Figure 14. *Chromatoceras constringens* (Barrande, 1866); A–D – NM-L 669 (holotype by monotypy, illustrated by Barrande 1866, pl. 156, figs 1–6), lowermost Přídolí Series, Kosoř, Kopanina Formation, sinistral (A), ventral (B), dextral (C) and dorsal (D) views. Notice striking asymmetry of colour pattern on ventral side (indicated by arrows); E, F – specimen NM-L 46579 illustrated herein also in the Fig. 20A–C, lowermost Přídolí Series, *parultimus-ultimus* Zone, Praha-Lochkov, U topolů section, Kopanina Formation, lateral (E), and dorsal (F) views. Abbreviation: bc – body chamber. Scale bars equal 5 mm.

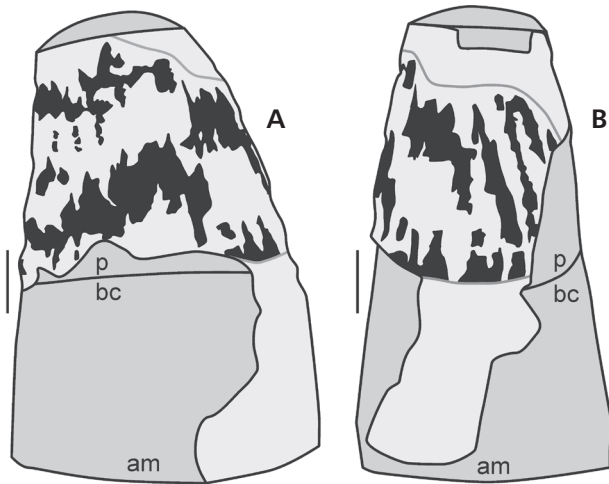


Figure 15. Schematic outlines of colour pattern in *Chromatoceras constringens* (Barrande, 1866); A, B – specimen NM-L 669 illustrated herein in Figs 14A, B and 20D–G, lateral (A) and ventral (B). For abbreviations see Fig. 2. Scale bars equal 5 mm.

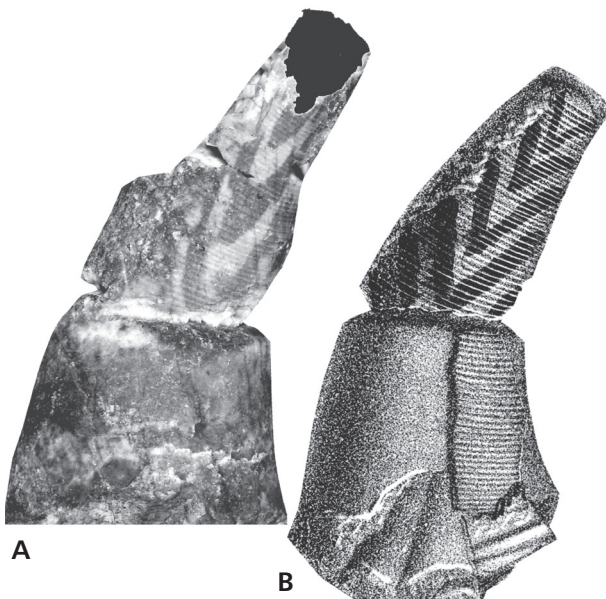


Figure 16. *?Euryrizoceras decurio* (Barrande, 1866), NM-L 15404 (holotype by monotypy), upper Ludlow or lower Přídolí Series, Praha-Slivenec (Vallon de Slivenetz), Kopanina or Požáry Formation, lateral view. Distinct colour pattern in form of narrow parabolas situated laterally (A) and Barrande's illustration of the specimen from the year 1866, pl. 240, figs 11–14 (B). Notice strongly simplified original Barrande's illustration.

Fig. 16A, B). The character of the apertural margin and the rather constant density of growth lines on the entire body chamber indicate that the only known specimen of *?E. decurio* represents very likely a juvenile growth stage, which complicates its taxonomic assignment. Nevertheless, the slightly curved, exogastric, and rapidly expanding shell and the large body chamber equal the characters of

Euryrizoceras Foerste, 1930b; *Euryrizoceras obesum* (Barrande, 1866) ranges in Bohemia from the middle Wenlock up to the upper Přídolí series (Manda & Turek 2009b).

Family Oocerinidae Teichert, 1939

***Oocerina* aff. *lentigrada* (Barrande, 1866)**

Figures 17, 18

Material. – One single specimen NM-L 59875, Karlštejn, Budňany Rock section (Kříž 1992); Přídolí Series, *transgrediens* Zone, Požáry Formation, uppermost bank of cephalopod limestone just below the Silurian–Devonian boundary (Chlupáč *et al.* 1972; beds 40, 41 in Kříž 1992). The specimen was found by V. Turek in 1988 and the colour pattern was briefly discussed by Turek (1990).

Description. – The studied specimen shows the body chamber and the adjacent third of the phragmocone. The shell is a slightly curved, slowly expanding ($ae = 8^\circ$), compressed ($sh/sw = 1.14$) and exogastric; its venter exhibits a faint keel. The body chamber is very short with an adapertural length of 30 mm; the fragment has a maximum length of 68 mm and a maximum height of 28 mm. The shell wall is preserved on the adapertural part of the phragmocone and in relicts also on the body chamber. The shell surface is smooth; fine growth lines form a well-developed, wide and moderately sharp hyponomic sinus. The annular elevation expands from the dorsum laterally, reaching the maximum width of 6.1 mm mid-laterally; the annular elevation is ragged.

The colour pattern is preserved along the entire circumference of the shell (Figs 17, 18). Dark grey transverse, densely spaced bands have a width about one millimetre. They are separated by light-coloured interspaces, which are almost of the same width as the colour bands, or slightly wider dorsally. Their undulation is most pronounced laterally and dorsally in the preserved adapical part of the phragmocone, the undulation is irregular, bilaterally asymmetrical in dorsal view. Ventrally, the course of colour bands corresponds to the growth lines course. Toward the aperture, the pronounced undulation diminishes dorsally and laterally, and bands become straight ventrally. The bands in the adapertural part of the phragmocone are almost straight around the entire circumference of the shell. The three most adoral bands are developed ventrally and disappear laterally.

Remarks. – The studied specimen corresponds to *Oocerina* Foerste, 1926 in shell shape, cross section, expansion rate, presence of a ventral keel and type of sculpture (very fine growth lines or almost smooth shell). Shell parameters of the specimen are similar to parameters of the type species of *Oocerina* – *O. lentigrada* (Barrande, 1866). This species

is, however, documented from the uppermost Ludlow of the Prague Synform, *i.e.* it is stratigraphically slightly older than the above-described specimen. The Silurian species at present assigned to *Oocerina* are in need of a revision. This is why we describe the studied specimen in the opened nomenclature.

Discussion

Colour patterns in cephalopods with distinctive surface sculpture

Shell colour patterns in fossil cephalopods were usually described from Early Palaeozoic forms that are smooth or inconspicuously sculptured (Foerste 1930a, Teichert 1964). Ribbed shells of Palaeozoic cephalopods display shell colouration only very occasionally (Kröger 2011 – Middle Ordovician endocerid *Anthoceras* Teichert & Glenister, 1954; Blake 1882, Manda & Turek 2015 – Silurian orthocerid *Dawsonoceras* Hyatt, 1884; Turek & Manda 2010, 2011 – Silurian nautilid *Peismoceras* Hyatt, 1894). Therefore, the ribbed shell of *Chromatoceras* displaying colour patterns represents a rather exceptional case. This indicates that the colouring occurred in strongly ornamented oncocerids as well. Cowen *et al.* (1973) suggested that such a type of sculpture produced shadows that visually broke up the shell outline and functioned in an analogous manner to pigmentation. Eventually, distinctive surface sculpture replaced colouration (see Mapes & Davis 1996, Westermann 1998). The findings of well-developed colour pattern in nautiloids having ribbed shells, as well as in strongly ornamented ammonoids (Mapes & Larson 2016) and other molluscs, impeach this alternative hypothesis.

Colour pattern as taxonomic character and its evolution

The studied Silurian oncocerids of the family Oonoceratidae carry exogastric, cyrtconic and slowly to moderately expanding shell. Their colour patterns consist of irregular transverse and undulating bands to more angular zig-zag bands. Closely related species with a similar shell shape such as *Richardsonoceras forbesi*, *R. fraternum* and *Oonoceras geinitzi* display also very similar type of zig-zag bands; differences are in the bands course, width and the proportions between pigmented and un-pigmented areas on the shell surface. More irregular, narrow zig-zag bands are documented in *Oonoceras* sp. A, where the colouration is preserved only on a small shell area in an early growth stage. According to Westermann (1998), *Richardsonoceras* and *Oonoceras* were forward moving demersal swimmers

with a hydrodynamically stable shell. Taking the biological position of the shell into account, the general course of colour bands changed during life from horizontal to inclined.

The shell of *?Oonoceras impatiens*, *?O. aff. impatiens* and both species of *Chromatoceras* is less curved and shorter in comparison to *Richardsonoceras* and *Oonoceras geinitzi*, and their shell expansion is somewhat higher. Westermann (1998) speculated that such a shell form was more manoeuvrable and turbulence resistant compared to typical cyrtcones and suggests that the above nautiloids were demersal bottom feeders. The colour pattern in these cephalopods is more complex than in *Richardsonoceras* and certain *Oonoceras*; zig-zags are more or less disrupted by narrow, bilaterally symmetrical longitudinal zones with patches of pigment.

Irregular oblique colour bands in *C. constringens* are locally interrupted and fragmented. The bands are associated with longitudinally arranged rows of small coloured patches and the shell colouration is similar to that in *?O. cf. impatiens*. *Chromatoceras veteranum*, closely related to *C. constringens*, exhibits the most complex colour pattern yet documented in nautiloids. Despite high variations, the pattern displays a combination of zig-zag bands and undulating transverse bands. Both may be disrupted into short segments and arranged into longitudinal zones.

Zig-zag bands sometimes tend to merge into large patches. However, the zig-zag pattern is more or less indicated. The variation of colour pattern in *C. veteranum* is much higher than that of other morphological characters of the species, namely shell shape and sculpture. This is the first documentation of high intraspecific variability in the colour pattern in Multiceratia. Colour patterning in *C. veteranum* possesses some common characters in patterning with *?Oonoceras impatiens*. However, in the latter species, the pattern is less complicated. The discontinuous colour pattern was derived from zig-zag bands known in *Oonoceras* and *Richardsonoceras*.

Concerning the colour pattern in *?Euryrizoceras decurio*, Barrande (1866) published an idealised reconstruction of this pattern showing V-shaped zig-zags bands of constant width. The distribution of the dark grey pigment concentrated in two almost rectangular patches on the opposite side is confusing and may be influenced by diagenesis. However, relicts of the colour pattern on dorsum and venter indicate original colouring surrounding the whole shell. Barrande's idealised illustration was adopted by Ruedemann (1921) in his attempt to use colouration as tool to reconstruct the biologic shell orientation of Silurian brevicones (refigured by Berry 1928 and Teichert 1964); this has later been widely accepted (*e.g.* Stridsberg 1985, Westermann 1998).

In shell shape, *Oocerina* resembles some oncocerids of the family Oonoceratidae and represents a case of

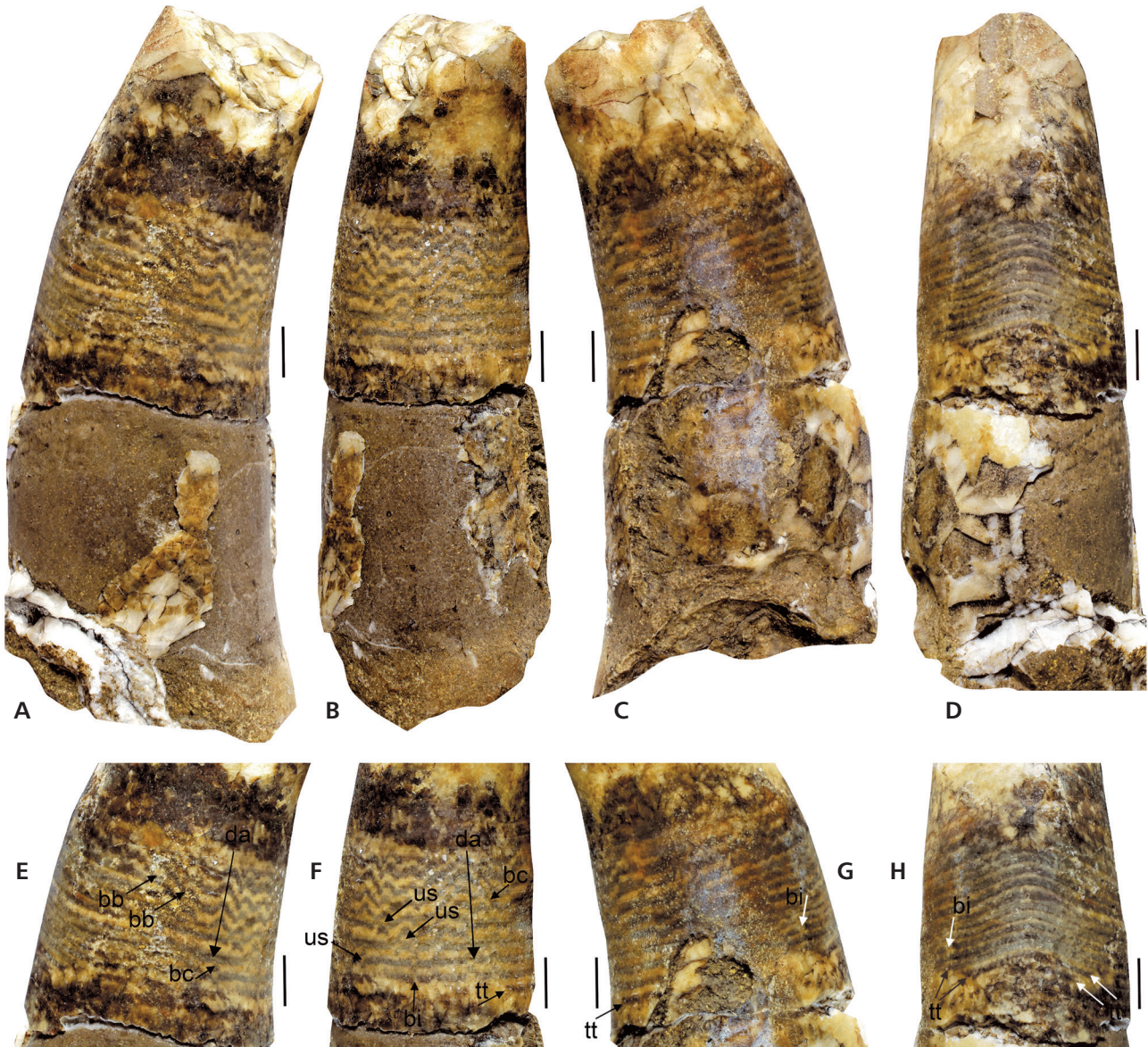


Figure 17. *?Oocerina cf. lentigrada* (Barrande, 1866); NM-L 59875; upper Přídolí Series, *transgrediens* Zone; Karlštejn, Budňany Rock; Požáry Formation; lateral (A, C), dorsal (B), and ventral (D) views, for details see E–H below. Notice changes in course of transversal bands during ontogeny laterally and dorsally. For abbreviations see Fig. 10.

adaptive convergence. *Oocerina* differs from *Oonoceras* in having a more vaulted venter and a wider siphuncle with intrasiphonal deposits. Although the shell shape of *Oocerina aff. lentigrada* resembles *Oonoceras*, the colour patterns are quite different in both taxa. The colour pattern in *Oocerina* consists of narrow, densely spaced subparallel bands. Generally, the bands are transversal, passing into more or less oblique, sometimes branching bands.

There are only a few cases in which it is possible to trace changes of colour pattern in any successive or closely related species. In some cases, species belonging to the same nautiloid genus share a similar colour pattern (e.g. *Peismoceras*, Turek & Manda 2010 and *Richardsonoceras*

discussed in this paper). By contrast, there is evidence indicating that quite different colour patterns occurred within a single genus *Phragmoceras* (see Turek & Manda 2011). Sometimes, closely related taxa display a different colour pattern as documented herein for *Chromatoceras* and *Oonoceras*.

Tracing the evolution of colour pattern based on such an incomplete fossil record is a difficult task. Species of the family Oonoceratidae, *Oonoceras geinitzi*, *?O. impatiens*, *?O. cf. impatiens*, *Chromatoceras veteranum*, *C. constringens* and *Euryrizoceras normata* (Manda & Turek 2009b), co-occur at a single locality that represents a narrow stratigraphic interval in the lowermost Přídolí Series. This

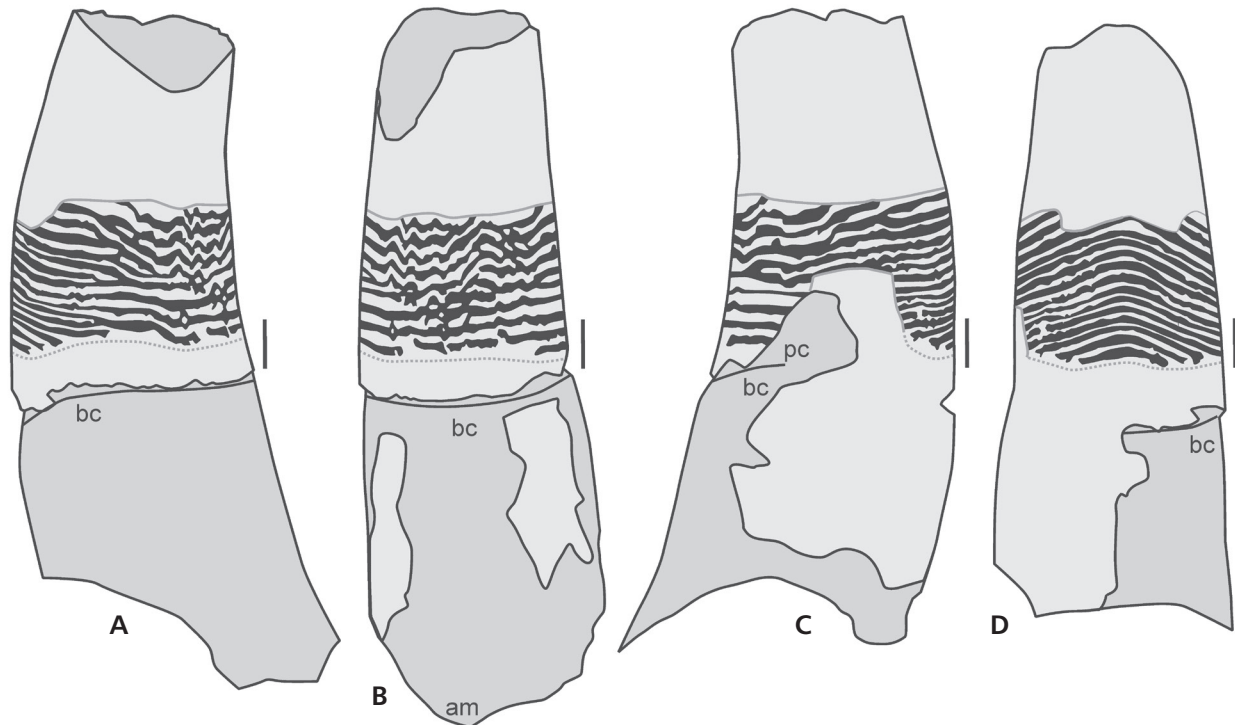


Figure 18. Schematic outlines of the colour pattern in *?Oocerina cf. lentigrada* (Barrande, 1866). Specimen NM-L 59875 illustrated herein in the Fig. 17A–C, lateral (A, C), dorsal (B) and ventral (D) views. Abbreviations: bc – body chamber; pc – phragmocone. Scale bars equal 5 mm.

indicates a high diversity of colour pattern in a cephalopod faunule and implies the possibility of pattern diversification in a monophyletic group. Zig-zag bands in moderately expanding cyrtocoines evolved into an irregular complex pattern appearing in more derived, demersal forms characterised by a more rapidly expanding and much less curved shell. This supports the hypothesis that the pattern was in these cases exposed to a low selective pressure. Similar shell shape in closely related taxa does not necessarily mean that the taxa shared a similar type of colour pattern. Development of quite similar colour patterns in only very distantly related nautiloids (Tab. 1) suggests that this feature appeared repeatedly in evolution just like other morphological features.

Asymmetry of colour patterns

The stratigraphically oldest known nautiloid (Multiceratia) colour pattern in the Middle Ordovician oncocerid *Hedstroemoceras* Foerste, 1930a consists of simple symmetrical chevron bands; regular zig-zag bands appeared in the Late Ordovician with *?Rizoceras* (Tab. 1). Other types of colour patterns are known from the middle and late Silurian (Tab. 2). High disparity and distinct asymmetry of colour patterns in some late Silurian species is documented here. The colour pattern in discosorids

resembles the pattern in other oncocerids and it is known since the middle Silurian. Spiral colour bands and typical zig-zag pattern are known in tarphycerids (Tab. 1). All Ordovician and Silurian straight shelled orthocerids and pseudorthocerids that supposedly lived in the water column (passively floating or actively swimming (Peterman *et al.* 2019) display a rather regular symmetrical colour pattern consisting of longitudinal bands (Ruedemann 1921, Foerste 1930a, Frey 1989, Kröger *et al.* 2009, Manda & Turek 2015, Kröger & Aubrechtová 2019). Longitudinal bands have also been documented from shells of Ordovician and Silurian actinocerids (Foerste 1930a, Kobluk & Hall 1976). In straight-shelled Ordovician demersal endocerids, only irregular and asymmetrical colour bands are known (Balashov 1964, Kröger 2011).

It is a question which type of colour pattern – symmetrical or asymmetrical – is evolutionarily older in cephalopods. Data concerning colour patterns in Late Cambrian cephalopods is still missing and the Ordovician record is still very scarce. The distinct asymmetry of the colour pattern and disruption of colour bands into separate segments or patches that evolved from irregular zig-zags are documented in this paper. The herein accumulated data support the hypothesis that irregular and asymmetrical patterns appeared more frequently in demersal cephalopods while the regular colour pattern was more common in more mobile cephalopods.

Ontogeny of colour patterns

The characteristic colour pattern in *Nautilus* generally appears slightly before or immediately after hatching (Arnold *et al.* 2010, Swan & Saunders 2010). The ventral and ventrolateral parts of the body chamber in mature recent nautilids are white because all these nautilids stop the secretion of the red-brown pigment (Collins & Ward 2010). In Palaeozoic nautiloid cephalopods, the colour pattern was probably usually present over the entire surface of the shell in all growth stages. Similarly to the extant *Nautilus*, the original luminosity of the colour pattern probably changed during the growth of an individual (Stenzel 1964). However, the luminosity of colouring was strongly altered by taphonomy (Mapes & Davis 1996, Mapes *et al.* 2010) and hardly can be objectively judged in the fossil record.

Data concerning colouration of fossil embryonic and juvenile shells are, however, sporadic (Ruedemann 1921, Foerste 1930a, Teichert 1964). Incompleteness of specimens and fragmentary preservation of colour patterns limited tracing of colour pattern changes through ontogeny in Palaeozoic nautiloids. Some of these nautiloids changed their mode of life during their post-embryonic development, which may be reflected in changes of colour patterns. A change in colour pattern during ontogeny was reported in the Silurian oncocerid “*Cyrtoceras*” *parvulum* Barrande, 1865 (Barrande 1865, 1870), in which straight transverse bands close to the apex follow regular zig-zag bands with increasing amplitude. In the early Carboniferous nautiloid *Arcuatoceras* Niko *et al.*, 2009, different colour patterns are developed in juvenile and subadult shells. Niko *et al.* (2009) suggested that these colour patterns are homeomorphic to those of some Silurian oncocerids. If there is a similarity between changing habits and colour patterns between juvenile and sub-adult stages, then this is an argument for an adaptive value. In turn, this raises the question whether this was present in the last common ancestors of these groups or whether this evolved convergently (homoplastic).

The apical part of the shell of *Richardsonoceras forbesi* is coloured with irregularly pigmented patches arranged roughly obliquely to the shell axis (Fig. 2C). Later in ontogeny, obliquely transverse zig-zag bands appeared. The thinning of the three most adoral colour bands is documented in a specimen of *R. forbesi* (Figs 1F, G; 2E); the body chamber was thus somewhat lighter in colour than the phragmocone. Decreased width of the two most adoral colour bands is also developed ventrolaterally in another specimen of *R. forbesi* (Figs 1B, 2D). A weak apertural constriction and a thickening of the apertural edge indicate maturity of these two specimens. Cowen *et al.* (1973) interpreted the decreasing width of colour bands as counter-shading like in modern nautilids. Irregular colour patterns in the apical part of the phragmocone of *Eurizocerinina normata* (Manda & Turek 2009b) probably

changed during growth into zig-zag bands like in *Richardsonoceras*, as well.

The preserved shell part of *Oocerinina cf. lentigrada* displays an increasing regularity in colour patterns through ontogeny. Wavy and sometimes also branching transverse bands pass laterally and dorsally into almost straight bands. Regularly arranged transverse bands on the venter, subparallel to the growth lines, did not change their course. Close to the base of the body chamber, colour bands disappear laterally and bands end with a weak thickening. Fragments of the shell wall on the internal mould of the body chamber indicate that there is the possibility that the body chamber was not pigmented ventrally like in recent *Nautilus*. Except for Cretaceous and recent nautilids, the lack of colour patterns in mature shells is unknown in fossil nautiloids (Mapes & Evans 1995).

The juvenile shell of *C. veteranum* displays irregularly arranged patches of pigment, later passing into disrupted irregular bands; the amplitude of V-shaped bands decreases during shell growth. Finally, in mature shells, irregular transverse bands sometimes surround un-pigmented patches close to the base of the body chamber. Data presented here imply that colour patterns changed throughout ontogeny already in some Silurian nautiloids, often giving the adult body chamber a brighter colour. This suggests a Silurian origin of counter-shading, which makes sense in the light of the Silurian radiation of jawed fish (e.g. Klug *et al.* 2010, Brazeau & Friedman 2015).

Function of colour patterns

The presumption that the colour pattern in *Nautilus* served as camouflage is an important actualistic model for the ecological role of colouration in Palaeozoic nautiloids. Miller (1947) and Stenzel (1957, 1964) suggested a protective function of colouration. Later, Cowen *et al.* (1973) reinterpreted these suggestions in terms defined by Cott (1940) and considered the *Nautilus* colour pattern as an example of disruptive camouflage and counter-shading (see also Packard 1988, who pointed out similarities with colouration in fish). In the most recent synthesis of *Nautilus* biology (Saunders & Landman 1987, 2010) there is, however, just one remark concerning “protective colouration” in juveniles (Arnold *et al.* 2010, p. 390). Ward (1987, p. 196) referred to Cowen *et al.* (1973) and suggested that *Nautilus* populations from New Caledonia and New Hebrides differ in colouration. Because in both areas, *Nautilus* animals “are commonly seen in depth much shallower than *Nautilus* from other areas with warmer surface water...it may be that shallower water habit makes more coloration an adaptive trait” (Ward 1987, p. 196). Mapes & Larson (2016, p. 41) emphasized that modern nautilids “might have lived below the euphotic zone where visibility is extremely

Table 1. List of Early Palaeozoic nautiloids with preserved colour pattern including morphotypes, characteristics of colour pattern, occurrence and corresponding source. Quotation marks indicate taxa that were described by Barrande (1866, 1877) but in fact represent other unrevised species. Abbreviations: * – species in need of a revision that were originally described under morphological genera used in 19th century and are assigned to a genus tentatively; ae – angle of shell expansion; CPT – colour pattern type; IZ – irregular zig-zag bands with changing width; UV – zig-zag bands with a high amplitude that form U-shaped saddles towards aperture and in opposite side V-shaped lobes; CB – chevron zig-zag bands; WB – slightly irregular, narrow, densely spaced wave bands; RB – radial bands; IB – irregular bands; TLB – combination of narrow transversal and longitudinal bands; TB – transversal bands parallel/subparallel with growth lines or ridges; TZB – zig-zag bands, irregular and roughly transversal; W+UV etc. – combination of different types of colour patterns; D, P – material documented by drawing and photographing, respectively, note that colour pattern indicated by drawing can be idealised as shown in the herein re-described *Euryrizoceras decurio*; Q – quality of preservation; A – well-preserved shell colouration; B – colouration preserved on a part of the shell only but it is possible to obtain image of original colouration; C – relict of colour pattern hindering reconstruction of the shell colouration; M – available material; N – number of specimens; ¹ – determined as “orthoceratoid body chamber” by Turek (2009, fig. 2), the specimen probably represents an oncocerid because it has a slightly curved and moderately expanding shell with oblique growth lines (see *Cyrtoceras genium* Barrande, 1877 of the same age), the zig-zag bands resemble those described here in oncoceratids; ² – the single specimen of the Late Ordovician *Discoceras* described by Kröger & Aubrechtová (2019, fig. 5a) exhibits a rather false colour pattern consisting of a dark shell with lighter narrow mid-lateral band and not a darker lateral band on a lighter shell as shown in the drawing on fig. 5c by Kröger & Aubrechtová (2019). For alternative interpretation, see the discussion on the mid-lateral furrow in the Silurian *Discoceras* (Manda & Turek 2018).

Family and species	Morphotype	Colour pattern	CPT	D	Q	M	Occurrence	Source
Discosorida								
Phragmoceratidae Miller, 1877								
<i>Phragmoceras eurystoma flexibile</i> Hedström, 1917	Endogastric curved brevicone, aperture constricted at maturity	Zig-zag bands with changing width; bands form dorsal V-shaped lobe and lateral broad saddle; interspaces about three times wider than bands.	IZ	P	B	N = 4	Gotland, Wenlock	Turek & Manda (2011)
<i>Phragmoceras dubium</i> Hedström, 1917	Endogastric coiled shell, aperture constricted at maturity	Transversal bands parallel with growth lines, locally slightly irregular in width; some bands bifurcated toward dorsum.	TB	P	A	N = 5	Gotland, upper Ludlow	Turek & Manda (2011)
<i>Phragmoceras imbricatum</i> Barrande, 1865	Endogastric curved brevicone, aperture constricted at maturity	Form A: Transversal bands parallel with growth lines, locally slightly varies band width; bands and interspaces are equal in width. Form B: combination of densely spaced longitudinal and transversal bands; transversal bands are narrower and irregularly broken with wider interspaces.	TB	P	A	N = 1	England, uppermost Wenlock	Turek & Manda (2011)
			TLB	P	C	N = 1	Bohemia, lowermost Ludlow	Turek & Manda (2011)
Nautilida								
Lechitrochoceratidae Flower, 1950								
<i>Peismoceras asperum</i> (Barrande, 1865)	Exogastric coiled shell with protruding last whorl	Narrow V-shaped zig-zags.	CB	P	C	N = 1	Bohemia, lower Ludlow	Turek & Manda (2010)
<i>Peismoceras pulchrum</i> (Barrande, 1865)	Exogastric low-spined shell with protruding last whorl	Typical densely spaced zig-zags; in some specimens one lateral side with oblique spiral bands while opposite side with zig-zags.	CB	P	A	N = 40	Bohemia, lowermost Ludlow	Barrande (1865), Turek & Manda (2010)
Oncocerida								
Rizoceratidae Hyatt, 1900								
<i>?Rizoceras bonum</i> Barrande (1865)*	Orthoconic brevicone, ae = 35°	Broad V-shaped zig-zag bands with narrow uncoloured interspaces, 2.5 zig-zags per lateral side.	UV	D	B	N = 1	Bohemia, Silurian, Ludlow	Barrande (1865, pl. 167, figs 20–24)

Table 1. Continued.

Family and species	Morphotype	Colour pattern	CPT	D	Q	M	Occurrence	Source
<i>?Rizosceras chrysalis</i> (Barrande, 1877)*	Very slightly curved brevicone with decreasing angle of shell expansion during shell growth, ae = 28°	Bilaterally symmetrical U- and V-shaped zig-zag bands, much wider than interspaces; contact between colour bands and interspaces disrupted by minute extensions of uncoloured zone entering the bands (toward aperture); 2.5 zig-zags per lateral side.	UV	D	A	N = 1	Bohemia, Silurian, upper Ludlow	Barrande (1877, pl. 506, figs 27–31)
<i>?Rizosceras eurus</i> (Barrande, 1877)*	Slightly curved endogastric brevicone, ae = 30°	Bilaterally symmetrical V-shape zig-zag bands, much wider than interspaces; contact between colour bands and interspaces disrupted by minute extensions of uncoloured zone entering the bands (toward aperture); 2.5 zig-zags per lateral side.	CB	D	A	N = 1	Bohemia, Silurian, upper Ludlow	Barrande (1877, pl. 506, figs 17–21)
<i>?Rizosceras gentile</i> (Barrande, 1877)*	Endogastric slightly curved brevicone, ae = 40°	Bilaterally symmetrical UV zig-zag bands, c. 5x wider than interspaces.	UV	D	B	N = 1	Bohemia, Silurian, upper Ludlow	Barrande (1877, pl. 505, figs 22–26)
<i>?Rizosceras haestians</i> (Barrande, 1877)*	Endogastric, very slightly curved brevicone, ae = 36°	Bilaterally symmetrical UV zig-zag bands, c. 5x wider than interspaces, 2.5 zig-zags per lateral side.	UV	D	B	N = 1	Bohemia, Silurian, Ludlow	Barrande (1877, pl. 505, figs 18–21)
<i>?Rizosceras jubatum</i> (Barrande, 1877)*	Slightly curved endogastric brevicone, ae = 35°	Bilaterally symmetrical UV zig-zag bands, much wider than interspaces; contact between colour bands and interspaces disrupted by extensions of uncoloured zone entering the following band (toward aperture); 2.5 zig-zags per lateral side.	UV	D	A	N = 1	Bohemia, Silurian, upper Ludlow	Barrande (1877, pl. 506, figs 22–26)
<i>?Rizosceras jugale</i> (Barrande, 1877)*	Very slightly curved brevicone, ae = 39°	Shell dark-coloured with irregular short, transversally oriented uncoloured patches.	?	D	C	N = 1	Bohemia, Silurian, Ludlow	Barrande (1877, pl. 506, figs 12–16)
<i>?Rizosceras parvulum</i> (Barrande, 1866)*	Endogastric curved brevicone	Bilaterally symmetrical UV zig-zag bands, c. 5x wider than interspaces, 2.5–3 zig-zags per lateral side. All specimens showing equal colour pattern.	UV	D	A	N = 15	Bohemia, Silurian, upper Ludlow	Barrande (1877, pl. 481, figs 1–15; pls 504, 505, figs 1–17)
<i>?Rizosceras pseudomorphum</i> (Barrande, 1877)*	Orthoconic brevicone with slightly more expanding ventral side, ae = 30°	Bilaterally symmetrical UV zig-zag bands, c. 5x wider than interspaces; contact between colour bands and interspaces disrupted by minute extensions of uncoloured zone entering the bands (toward aperture); 2.5 zig-zags per lateral side.	UV	D	A	N = 1	Bohemia, Silurian, upper Ludlow	Barrande (1877, pl. 506, figs 7–11)
<i>?Metarizosceras cyathus</i> (Barrande, 1866)*	Very slightly curved exogastric brevicone with rapidly expanding ventrum, ae = 45°	Slightly irregular, minute, densely spaced, narrow, wavy bands with width equal to that of interspaces.	WB	D	B	N = 2	Bohemia, Silurian, upper Ludlow	Barrande (1866, pl. 153, figs 24–30; 1877, pl. 507, figs 24–29)

Table 1. Continued.

Family and species	Morphotype	Colour pattern	CPT	D	Q	M	Occurrence	Source
<i>?Metarizoceras intricans</i> (Barrande, 1877)*	Curved exogastric brevicone, ae = 30°	Irregular minute, densely spaced, narrow, wavy bands with width equal to that of interspaces, bands occasionally branch out or merge.	WB	D	B	N = 1	Bohemia, Silurian, upper Ludlow	Barrande (1877, pl. 514, figs 1–7)
<i>?Metarizoceras minoratum*</i>	Orthoconic brevicone, ae = 40°	Slightly irregular minute, densely spaced, narrow, wavy bands with width equal to that of interspaces.	WB	D	B	N = 1	Bohemia, Silurian, upper Ludlow	Barrande (1865, pl. 191, figs 2–6)
<i>?Metarizoceras sinuatum</i> (Barrande, 1866)*	Very slightly curved exogastric brevicone, ae = 40°	Slightly irregular, densely spaced, narrow, broad wavy bands (wave is much longer than high) with width equal to that of interspaces.	WB	D	B	N = 1	Bohemia, Silurian, upper Ludlow	Barrande (1866, pl. 153, figs 9–15)
<i>?Metarizoceras vilitatum</i> (Barrande, 1866)*	Slightly curved exogastric brevicone, ae = 38°	UV-shaped zig-zag bands, much wider than interspaces; contact between colour band and interspaces disrupted by minute extensions of uncoloured zone entering the bands (toward aperture).	UV	D	C	N = 1	Bohemia, Silurian, upper Ludlow	Barrande (1866, pl. 153, figs 1–5)
<i>?Metarizoceras zebra</i> (Barrande, 1866)*	Slightly curved exogastric brevicone, ae = 38°	Narrow bands, ventrally minute wavy band passing dorsally into wide V-shaped band, interspaces slightly wider than bands.	W + UV	D	B	N = 2	Bohemia, Silurian, upper Ludlow	Barrande (1865, pl. 168, figs 34–43)
<i>“?Metarizoceras zebra”*</i>	Orthoconic brevicone, ae = 35°	Slightly irregular minute, densely spaced, narrow, wavy bands with width equal to that of interspaces combined with occasional irregular longitudinal spots.	WB	D	A	N = 4	Bohemia, Silurian, upper Ludlow	Barrande (1877, pl. 481, figs 16–20)
<i>“?Metarizoceras cyathus”*</i>	Orthoconic brevicone, ae = 45°	Slightly irregular narrow, densely spaced, minute wavy bands with width equal to that of interspaces combined with occasional irregular longitudinal spots.	WB	D	A	N = 1	Bohemia, Silurian, upper Ludlow	Barrande (1877, pl. 481, figs 21–24)
<i>?Rizoceras coronatum</i> Foerste & Savage, 1927	Orthoconic brevicone, ae = 30°	Irregular and narrow UV bands with low amplitude.	UV	P	B	N = 1	Manitoba, Upper Ordovician	Foerste (1930a)
Oonoceratidae Flower, 1942								
<i>Oonoceras geinitzi</i> (Barrande, 1866)	Exogastric cyrtocone, ae = 19–21°	Oblique, irregular, narrow zig-zag bands across the shell.	IZ	P	B	N = 2	Bohemia, Silurian, Pfidoli	New data
<i>Oonoceras</i> sp. A	Exogastric cyrtocone, ae = 22°	Oblique, irregular, narrow zig-zag bands across the shell.	IZ	P	C	N = 1	Bohemia, upper Ludlow	New data
<i>?Oonoceras impatiens</i> (Barrande, 1866)	Slightly curved exogastric cyrtocone, ae = 32°	Irregular zig-zag bands fragmented into narrow longitudinal zones.	IZ			N = 1	Bohemia, Silurian, Pfidoli	New data
<i>?Oonoceras aff. impatiens</i> (Barrande, 1866)	Moderately curved exogastric cyrtocone, ae = 30°	Irregular V shaped zig-zag bands.	IZ	P	C	N = 1	Bohemia, Silurian, Pfidoli	New data
<i>?Euryizoceras iridis</i> (Barrande, 1866)*	Exogastric curved, rapidly expanding, ae ~ 15°	UV zig-zag bands, colour bands wider than interspaces.	UV	D	C	N = 1	Bohemia, Silurian, upper Pfidoli	Barrande (1866, pl. 153, figs 16–23)

Table 1. Continued.

Family and species	Morphotype	Colour pattern	CPT	D	Q	M	Occurrence	Source
<i>Pomerantoceras pollux</i> (Barrande, 1866)	Very slightly curved, slowly expanding cyrtocone, ae = 5–8°	Broad radial bands, bilaterally symmetrical. Numbers and width of bands varies between specimens.	RB	P	A	N = 4	Bohemia, Silurian, upper Wenlock–upper Ludlow	Manda & Turek (2009a)
<i>Euryzocera normata</i> Manda & Turek, 2009b	Exogastric cyrtocone, moderately expanding, ae = 17°	Irregularly branching bands variable in width and outline.	IB	P	C	N = 2	Bohemia, Silurian, Přidolí	Manda & Turek, (2009b)
<i>Chromatoceras veteranum</i> (Barrande, 1866)	Exogastric slightly curved shell, rapidly expanding to breviconic, ae = 23–32°	Irregular asymmetric bands broken into narrow longitudinal zones.	IB	P	A	N = 6	Bohemia, Silurian, Přidolí	Revised here and new data
<i>Chromatoceras constringens</i> (Barrande, 1866)	Exogastric slightly curved shell, rapidly expanding, ae = 25–26°	Irregular asymmetric bands.	IB	P	B	N = 2	Bohemia, Silurian, Přidolí	New data
<i>?Euryzoceras decurio</i> (Barrande, 1866)	Slightly curved exogastric shell, rapidly expanding, ae = 22°	Zig-zag bands in form of narrow and high parabolas preserved laterally.	IZ?	P	C	N = 1	Bohemia, upper Silurian	Revised here
<i>Richardsonoceras forbesi</i> (Barrande, 1866)	Exogastric cyrtocone, ae = 19°	Oblique, irregular zig-zag bands across the shell.	IZ	P	A	N = 4	Bohemia, Silurian, Ludlow	New data
<i>Richardsonoceras fraternum</i> (Barrande, 1866)	Exogastric cyrtocone, ae = 18–23°	Oblique, irregular zig-zag bands across the shell.	IZ	P	C	N = 1	Bohemia, Silurian, Ludlow	New data
Hercoceratidae Hyatt, 1884								
<i>Ptenoceras alatum</i> (Barrande, 1865)	Gyroconic exogastric shell	Irregular diagonal zig-zags across the whorl.		P	C	N = 1	Bohemia, Pragian	Turek (2009)
<i>Ptenoceras nudum</i> (Barrande, 1865)	Gyroconic exogastric shell	Probably symmetric zig-zag pattern.		P	C	N = 1	Bohemia, Emsian	Turek (2009)
<i>Ptenoceras</i> sp.	Gyroconic or cyrtoconic exogastric shell	Zig-zag colour bands across the entire circumference. Slightly asymmetric “w” developed ventromedially.		P	B	N = 1	Bohemia, Pragian	Turek (2009)
Family Oocerinidae Teichert, 1939								
<i>Oocerina</i> aff. <i>lentigrada</i> (Barrande, 1866)	Exogastric cyrtocone, ae = 8°	Narrow transversal bands; some bands pass into irregular zig-zags with low amplitude.	TB + IZ	P	A	N = 1	Bohemia, Přidolí	New data
Hemiphragmoceratidae Foerste, 1926								
<i>Hexameroceras panderi</i> (Barrande, 1865)	Slightly curved endogastric brevicone with constricted aperture	Combination of narrow transversal and longitudinal bands; longitudinal bands about two times more densely spaced than transversal bands. Width and density of bands varied.	TLB	P	A	N = 4	Bohemia, Silurian, upper Ludlow–Přidolí	Barrande (1870, pl. 429, figs 14–19), Turek & Manda (2011)

Table 1. Continued.

Family and species	Morphotype	Colour pattern	CPT	D	Q	M	Occurrence	Source
<i>Octameroceras rimosum</i> (Barrande, 1865)	Slightly curved endogastric brevicone with constricted aperture	Broad transversal bands parallel with growth lines (<i>i.e.</i> bilaterally symmetrical), unpigmented interspaces slightly narrower than colour bands.	TB	P	A	N = 1	Gotland, Silurian, upper Ludlow	Stridsberg (1985), Turek & Manda (2011)
<i>Octameroceras sinuosum</i> Stridsberg, 1985	Slightly curved endogastric brevicone, constricted aperture	Broad transversal bands parallel with growth lines (<i>i.e.</i> bilaterally symmetrical).	TB	P	C	N = 1	Gotland, Silurian, upper Ludlow	Stridsberg (1985)
<i>Pristeroceras ?tumidum</i> Ruedemann, 1925	Slightly curved endogastric brevicone, constricted aperture	Slightly irregular, narrow, U- or V-shaped zig-zag bands. Bands separated by much wider unpigmented zone.	UV	P	B	N = 1	New York, upper Silurian	Sweet & Leutze (1956)
Trimeroceratidae Hyatt, 1900								
<i>Pentameroceras mirum</i> (Barrande, 1865)	Orthoconic brevicone, constricted aperture, ae = 35°	UV bands, 3.5 zig-zags per lateral side. Width of colour bands variable.	UV	P	A	N = 2	Gotland, Wenlock	Stridsberg (1985), Turek & Manda (2011)
Family uncertain								
<i>Hedstroemoceras haelluddenense</i> Foerste, 1930a	Orthoconic shell, ae = 17°	Ventrally bilaterally symmetrical chevron pattern, laterally narrow, regular sub-longitudinal bands, interspaces much wider.	C	P	A	N = 1	Öland, Middle Ordovician	Foerste (1930a), King (1999)
<i>Oncocerida</i> gen. et sp. indet. ¹	Probably slightly curved shell, rapidly expanding	Narrow zig-zag oblique bands, transversal close to the aperture.	TZB	P	B	N = 1	Bohemia, Lochkovian	Turek (2009), see remarks ¹
Tarphyoceratida								
Trocholitiidae Chapman, 1857								
<i>Trocholites</i> sp.	Tightly coiled, planispiral, exogastric shell	A longitudinal band mid-ventrally from which diverged zig-zag bands.	LB + TZB	D	B	N = 1	Germany, Middle/Upper Ordovician	Schuh (1920)
False colour pattern								
<i>Discoceras amfjaernense</i> ² Kröger & Aubrechtová 2019	Tightly coiled, planispiral, exogastric shell	A longitudinal band mid-laterally.	RB	P	A	N = 1	Sweden, Upper Ordovician	Kröger & Aubrechtová (2019), see remarks ²

limited or totally lacking and detection by other visual animals may be extremely limited". Only at night, nautilids move into shallower water. However, the daylight is not the only source of light to which nautilids are exposed. Bioluminescence may be similarly important (Muntz 1987, Johnsen 2005). Also, there is still limited data concerning the ecology of *Nautilus* juveniles (Saunders & Ward 1987, Arnold *et al.* 2010). According to the opinion of Ward *et al.* (2016), the stratigraphic range of *Nautilus* is much longer than previously thought (Ward 1987, Teichert & Matsumoto 1987, Saunders *et al.* 1996). Ward *et al.* (2016) argued that some ancient nautilid genera are congeneric with *Nautilus*, which thus originated possibly in the Middle Jurassic or the Early Cretaceous with maximum diversity during the Late Cretaceous. Occurrences in Mesozoic shallow water facies indicate that *Nautilus* inhabited the euphotic zone at that time. Shell colouring may thus be an evolutionary relict with no or little selective value like in some other molluscs (see Williams 2017).

All nautiloids lived in the water column and thus shell colouration was visible if the shell surface was not covered by epizoans (which is likely) and if the animal inhabited the photic zone (which applied likely to many Palaeozoic taxa). The function of colouration should be related to co-occurrences with animals with vision. The shell surface of coloured nautiloids from the Prague Basin is well preserved with no traces of epibionts or attachment traces of epifauna that would hide the colouration. Similarly, in recent nautilids, *syn vivo* encrusters are also very rare (Seilacher & Gisselick 2015). Cephalopod limestone biofacies in the Prague Basin correspond with 2 and upper 3 life position of Boucot's benthic communities (Havlíček & Štorch 1990, 1999). Brett *et al.* (1993) summarised absolute depth indicators in the Silurian benthic communities, which make possible their depth estimation. The boundary between 4 and life position corresponds with the lower limit of the euphotic zone (Brett *et al.* 1993). Cephalopods with coloured shells accordingly inhabited the euphotic zone in the Prague Basin. Nautiloids with preserved colour patterns occur in faunas including both prey and predators with well-developed vision. This is consistent with widely accepted concept that most brevicones have lived in moderate depths anyway (e.g. Westermann 1998).

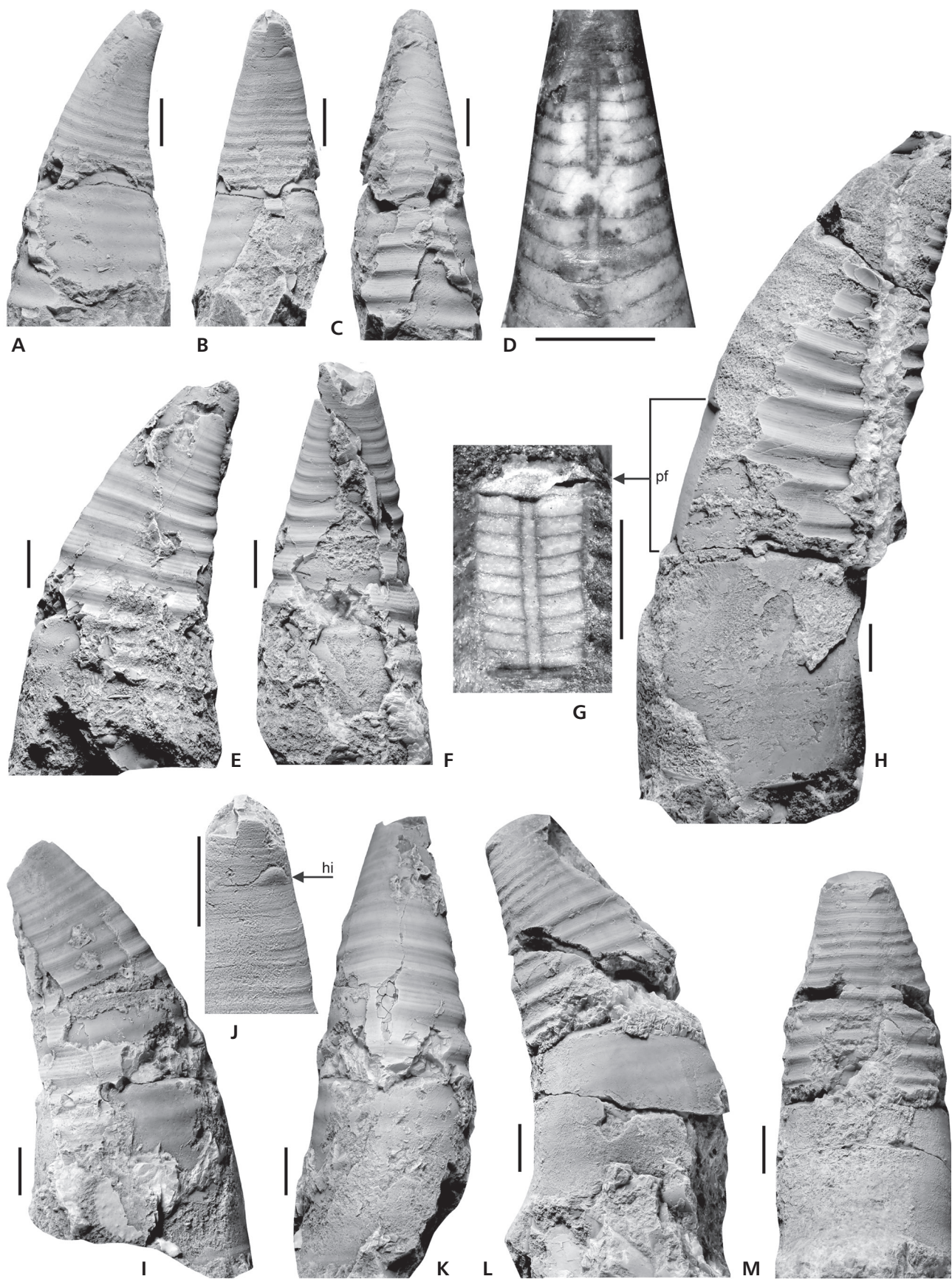
There was likely a strong selective pressure on shell colour and colour patterns serving as camouflage or warning or for sexual display since the Cambrian explosion and the development of the first image-forming eyes, because during the Cambrian explosion, predators evolved better visual acuity and colour vision (Kobluk & Mapes 1989, Aberhan *et al.* 2012). Despite some doubts concerning the function of colouring in recent nautilids, it is reasonable to assume that colour patterns in early Palaeozoic nautiloids served as light screening or camouflage (Stridsberg 1985, Kobluk & Mapes 1989, Westermann 1998). Species-specific colour patterns and their changes through ontogeny in oncocerids with a slightly or moderately curved shell are consistent with a protective function of shell colouration.

Conclusion

1) Among Palaeozoic nautiloids, shell colour patterns are best documented in the order Oncocerida. The pattern is already known in 47 species and they show all types of colour patterns known in nautiloids. The vast majority of oncocerids with preserved colour patterns possess straight or very slightly curved breviconic shells; only very scarce cases of oncocerids with a moderately expanding and curved or coiled shell have been published that show colour patterns. The colour patterns described herein have been discovered in seven Silurian oncocerid species of the families Oonoceratidae and Oocerinidae with cyrtoconic shell.

2) Zig-zag bands represent the characteristic type of colour patterns in oncocerids with cyrtoconic shell of the family Oonoceratidae. The general course of individual pigmented bands is roughly transversal. Differences in zig-zag patterns among individual taxa comprise the width of bands and the amplitude of triangles in the zig-zag bands; bands may split into more or less isolated segments or irregularly bounded patches of dark pigment. Only in one specimen of the family Oocerinidae, the colour patterns form transversal wavelets. The zig-zag patterns, disruptions and other aspects of the colour patterns are characteristic for patterns self-organized by diffusion-reaction processes. Accordingly, the variation also roots in this self-organisation.

Figure 19. *Chromatoceras veteranum* (Barrande, 1866); A–C, J – specimen NM-L 14299 illustrated by Barrande (1866, pl. 208, fig. 22) as *Cyrtoceras fallax* Barrande, 1866, lowermost Přídolí Series, Kosoř locality, Kopanina Formation, lateral (A), dorsal (B), ventral (C) views and detail (J) of a healed injury in adapical region (hi); D – specimen NM-L 21751, illustrated by Barrande (1877, pl. 514, figs 13–17), lowermost Přídolí Series, Praha-Lochkov, Kopanina Formation, phragmocone ventrally polished, showing siphuncle; E, F, I, K – specimen NM-L 14298 (holotype by monotypy; Barrande 1866, pl. 208, fig. 22, refigured herein also in the Fig. 11I–P), lowermost Přídolí Series, *parultimus-ultimus* Zone, Kosoř locality, Kopanina Formation; G, H – specimen NM-L 10127 (holotype by monotypy of *Cyrtoceras sica* Barrande, 1866, pl. 124, figs 6–11), lowermost Přídolí Series, Praha-Slivenec, Kopanina or Požáry Formation, G – a part of siphuncle polished ventrally, H – lateral view; L, M – specimen NM-L 46890 illustrated herein also in Figs 10H–J, M–O and 13A–C, lowermost Přídolí Series, *parultimus-ultimus* Zone; Praha-Lochkov, U topolů section, Kopanina Formation, lateral (L) and dorsal (M) views. Except siphuncle details (D, G), all specimens were whitened with ammonium chloride before photographing. Abbreviations: hi – healed injury; pf – polished part of phragmocone. Scale bars equal 5 mm.



3) New data confirm that the colour patterns in oncocerids originally surrounded the entire shell from early juvenile growth stages to maturity. The ratio between pigmented and unpigmented surfaces is usually close to 1. In the case of *?Oocerina cf. lentigrada*, the venter of the mature shells was rather poorly pigmented without colour patterns.

4) Striking asymmetry of colour patterns in oncocerids has been found especially in the species of *Chromatoceras* gen. nov. Another case of colour pattern asymmetry was documented only in some specimens of the Silurian tarphycerid *Peismoceras pulchrum*, which possesses a low-spired torticone shell (Turek & Manda 2010). Despite the high variation of the colour patterns in some taxa, the general character of the pattern is more or less specific for individual genera or species and thus can be used for taxonomy with some reservation. This variation roots in the self-organisation to a great degree.

5) Changes in colour patterns during ontogeny in some oncocerid species is here documented. Frequently, irregular colour patterns in juveniles changed to more regular patterns in the subadult stage (e.g. *Richardsonoceras*). The decreasing amplitude of zig-zag colour bands throughout post-juvenile growth and the decreasing width of colour bands in the mature shell are documented here. Occasionally, the colour patterns became more irregular again in the subadult stage (*Chromatoceras veteranum*).

6) Dark colour bands in the form of two quite different types of pattern occur in some specimens of *Chromatoceras veteranum*: between isolated segments of zig-zag bands, short and narrow slightly undulated transverse bands are inserted. Due to the suppression of zig-zag bands, a new pattern characterised by transverse bands appeared. The asymmetrical pattern exhibits a high intraspecific variation unknown from other nautiloids

7) The Silurian oncocerids discussed herein inhabited the euphotic zone and it is likely that their colouring served for camouflage. High intraspecific variation of colour patterns in some species and differentiation of colour patterns in closely related taxa possessing similar shell form indicate a weak selective pressure on the evolution of the colour patterns. Asymmetric colour patterns are documented in probably more demersal forms.

Systematic appendix

Subclass Nautiloidea Agassiz, 1847
Order Oncocerida Flower in Flower & Kummel (1950)
Family Oonoceratidae Flower, 1942

Genus *Chromatoceras* gen. nov.

Type species. – *Cyrtoceras veteranum* Barrande, 1866; lowermost Přídolí Series of Bohemia.

Etymology. – Name derived from the Greek word of *chromos* meaning colour.

Diagnosis. – Oonocerid with rapidly expanding exogastric shell with a slightly curved venter throughout ontogeny while the dorsum is curved only in early growth stages; later in ontogeny, the shell is almost straight; shell with prominent more or less regularly spaced transverse ribs; hyponomic sinus very shallow and broad; colour patterns are complex and colour bands are fragmented into individual parts, segments of zig-zag bands, sometimes fusing into irregularly bounded patches alternating with segments of thinner undulating or adapically vaulted transverse bands.

Discussion. – The diversity of oncocerids possessing an exogastric, curved shell and a thin siphuncle is relatively high throughout latest Ludlow and early Přídolí strata of Central Bohemia (Kříž *et al.* 1986, Turek 1992, Kříž 1998). Their phylogenetic relationship is, however, generally poorly studied. Besides widely distributed taxa, there are also some endemic forms with very short stratigraphic range known from this area (Manda & Turek 2009b). *Chromatoceras*, represented by two species, is another example of an oncocerid genus with a very limited geographic distribution, known only from Prague Basin, and a short stratigraphic range. The species of *Chromatoceras* resemble the stratigraphically older *?Oonoceras imperiale* (Barrande, 1866). The exogastric shell in the latter species is curved, moderately expanding, with well-developed ribs and a moderately compressed cross section. With two species of *Chromatoceras*, it shares the following features: decreasing shell expansion and curvature during later shell growth stages and pronounced growth lines arranged into regular elevated zones. Both species of *Chromatoceras* differ from *?Oonoceras imperiale* in having a short and less compressed shell with a dorsum that is only very slightly curved, a vaulted venter and in ribs appearing very early in ontogeny.

Species included. – *Chromatoceras veteranum* (Barrande, 1866) and *C. constringens* (Barrande, 1866).

Chromatoceras veteranum (Barrande, 1866)

Figures 10–13, 19

1866 *Cyrtoceras veteranum* Barr.; Barrande, pl. 208, fig. 21.

1866 *Cyrtoceras sica* Barr.; Barrande, pl. 124, figs 6–11.

- partim* 1886 *Cyrtoceras fallax* Barr.; Barrande, pl. 208, fig. 22.
 1867 *Cyrtoceras veteranum* Barr.; Barrande; p. 571.
 1867 *Cyrtoceras sica* Barr.; Barrande, pp. 529, 530.
 1877 *Cyrtoceras veteranum* Barr.; Barrande, pl. 514, figs 13–17.
 1921 *Cyrtoceras veteranum*. – Ruedemann, p. 80.
 1930a *Cyrtoceras veteranum*. – Foerste, p. 121.

Holotype. – By monotypy, specimen NM-L 14298 figured by Barrande (1866) in pl. 208 as fig. 21.

Type horizon and locality. – Silurian, lowermost Přídolí Series, *parultimus-ultimus* Biozone; Kozoř e₂ by original designation (= Kosoř Village, area of the Hvíždalka Natural Monument, and adjacent area to the south, to the NNE from Kosoř Village).

Material. – Holotype and seven additional specimens (their inventory numbers are listed in Tab. 2).

Description. – Moderately-sized oncocerid with sl = 67 mm, max. reconstructed sh = 27 mm, and maximum reconstructed sl = 77 mm. Slightly curved exogastric shell, rapidly expanding, ae = 23–32°; in fully grown specimens, the angle of shell expansion decreases to about 12° in the body chamber. Venter is much more curved than the slightly curved dorsum. Body chamber length is less than one third of total shell length. Cross section slightly compressed with vaulted venter but flattened dorsum (sh/sw = 1.1–1.3). Suture straight, obliquely oriented with respect to the longitudinal axis of the shell, septa slightly vaulted and

densely spaced. Apical part of the shell is smooth. Densely spaced transverse ribs appear at shell height of 8 mm. Hyponomic sinus is very shallow and broad, in fully-grown specimens almost not visible. Siphuncle narrow, tubular, situated close to ventral side.

Remarks. – In shell shape, cross section, sculpture and colour patterns, “*Cyrtoceras*” *sica* corresponds with other specimens of *C. veteranum*; we therefore regard both taxa as conspecific.

Occurrence. – Silurian, lowermost Přídolí Series, *parultimus-ultimus* Biozone; Kopanina Formation; Praha-Lochkov, U topolů section (a bed of dark grey cephalopod packstone just above the base of the Přídolí; Manda & Turek 2009b, fig. 1) and Praha-Kosoř, Praha-Slivenec, a Barrande locality.

***Chromatoceras constringens* (Barrande, 1866)**

Figure 14, 15, 20

- 1866 *Cyrtoceras constringens* Barr.; Barrande, pl. 156, figs 1–6.
 1867 *Cyrtoceras constringens* Barr.; Barrande, pp. 541, 542.

Holotype. – Holotype by monotypy, specimen NM-L 669 illustrated by Barrande (1866) in pl. 156, figs 1–6 (refigured here as Figs 14A–D, 20D–G).

Type horizon and locality. – Silurian, lowermost Přídolí

Table 2. Shell dimensions in *Chromatoceras*. Abbreviations: sl – maximum shell length; sh – maximum shell height; sw – max. shell width; bcl – body chamber length, sh/sw ratio; sh_{min} – minimum shell height; sw_{max} – minimum shell width; sh2 – shell height at base of body chamber; ae – angle of shell expansion; * – indicates holotype. All measurements in millimetres.

Taxa/inv. number	sl	sh	sw	bcl	sh/sw	sh _{min}	sw _{min}	sh2	ae
<i>C. veteranum</i>									
NM-L 14298*	43.6	19.7	17	16.1	1.16	6.1	6	18	23°
NM-L 10127	66.0	c. 28	c. 20.5	24.5	1.15	11.2	9.5	22.0	–
NM-L 14299	31.7	18.3	17.3	12.2	1.06	4	4	12.7	22°
NM-L 21751	35.2	15.1	14.1	13	1.07	4.9	4	12.5	21°
NM-L 46578	26.5	19.8	15.0	13.6	1.32	10.4	9.3	15.3	26°
NM-L 46580	48.1	22.4	18.1	15	1.24	11.4	11.5	19.3	24°
NM-L 46581	12.6	–	–	–	–	3.8	–	–	–
NM-L 46890	44.0	c. 23	19.5	17.9	1.18	7.9	7.9	20.0	32°
<i>C. constringens</i>									
NM-L 669*	38.0	24.5	21.0	20.2	1.17	12.9	12.2	21.5	25°
NM-L 46579	42.0	25.2	–	18.3	–	13.8	12.6	23.9	26°

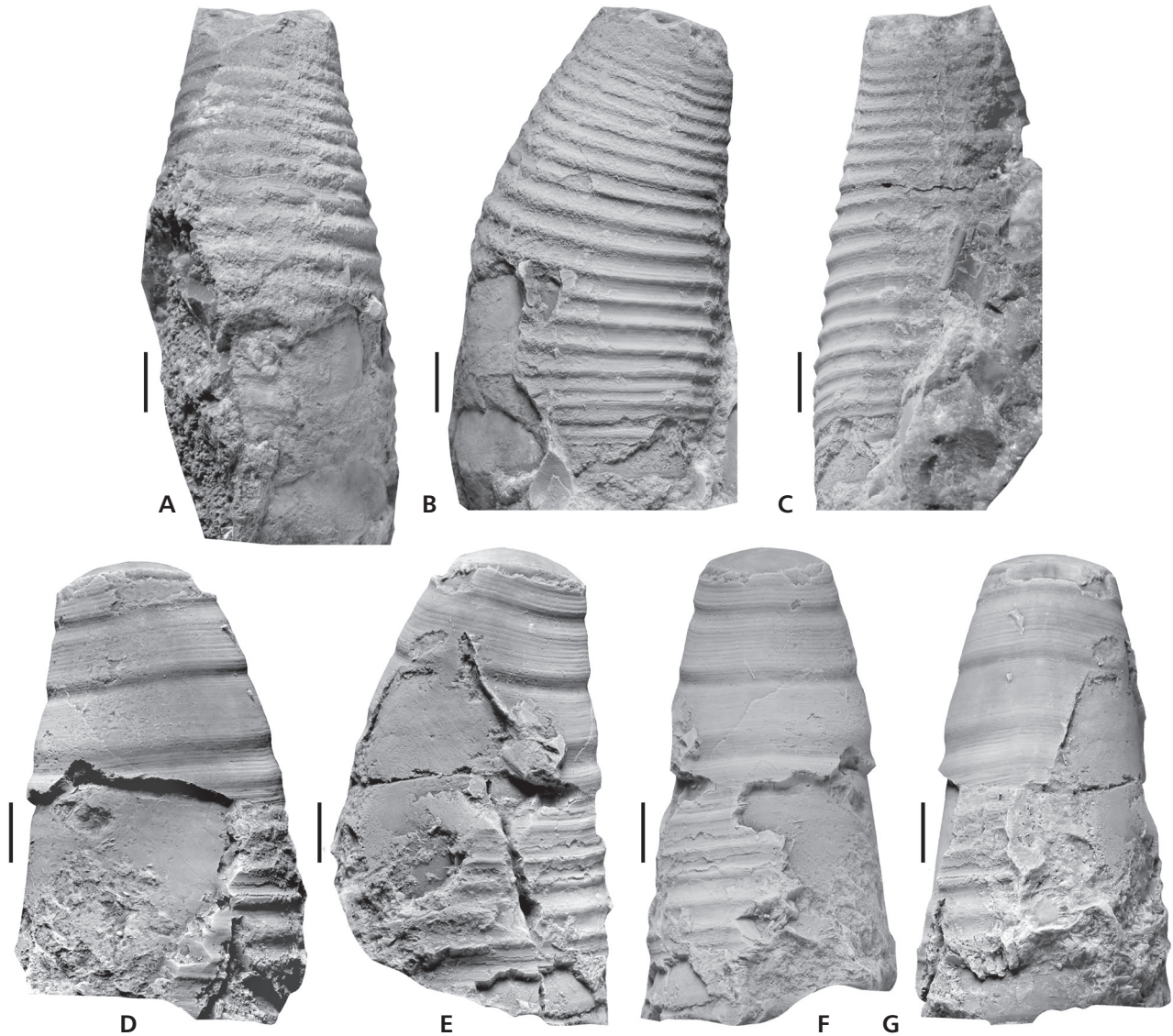


Figure 20. *Chromatoceras. constringens* (Barrande, 1866); A–C – specimen NM-L 46579 illustrated herein also in the Fig. 14E, F, lowermost Přídolí Series, *parultimus-ultimus* Zone, Praha-Lochkov, U topolů section, Kopanina Formation, ventral (A) lateral (B), and dorsal (C) views; D–G – specimen NM-L 669 illustrated herein also in Fig. 14A–D, lowermost Přídolí Series, Kosoř locality, Kopanina Formation, sinistral (D), dextral (E), dorsal (F) and ventral (G) views. Notice anomalous character of shell sculpture. All specimens were whitened with ammonium chloride before photographing. Scale bars equal 5 mm.

Series, *parultimus-ultimus* Biozone; Kozoř e_2 by original designation (= Kosoř Village, area of the Hvíždalka Natural Monument, and adjacent area to the south, to the NNE from Kosoř Village).

Material. – In addition to the holotype only one specimen: NM-L 46579.

Description. – The slightly curved, exogastric shell of *Chromatocera constringens* is small with a sl = 42 mm, sh = 25 mm, and length of the complete reconstructed shell roughly 65 mm. Shell is rapidly expanding, ae = 25–26°.

Body chamber occupies approximately one third of the shell length. Shell is slightly compressed, broadly elliptic in cross section (sh/sw = 1.14). Sutures obliquely oriented with respect to the longitudinal shell axis with shallow lateral lobe; septa moderately vaulted and densely spaced. Shell sculpture on phragmocone consists of fine transversal growth lines forming low and narrow elevations, which are not evident on the internal mould. Growth walls straight, transversal, slightly asymmetric in cross section (adapical part of ribs wider than adoral part). Hyponomic sinus is very shallow and broad. Narrow siphuncle with slightly expanded segments is situated close to venter.

Remarks. – Shell shape and size, thin siphuncle and densely spaced septa, body chamber length and cross section in *C. constringens* correspond to the same features in *C. veteranum*. *C. constringens* differs from the latter species in having lower and more densely spaced ribs.

The shell sculpture of the holotype of *C. constringens* is peculiar; the preserved apertural part of the phragmocone displays two wide segments separated by deep transversal furrows. Their surface is flat, bearing only growth lines. Densely spaced growth lines are typical for *Chromatoceras* and are developed on the body chamber. This sculpture is interpreted as a growth anomaly with respect to the normal appearance of sculpture on the holotype body chamber and the character of shell sculpture in one other specimen assigned to this species. The distinct difference in the colour pattern between *C. constringens* and *C. veteranum* confirms Barrande's concept of two separate species.

Occurrence. – Silurian, lowermost Přídolí Series, *parul-timus-ultimus* Biozone; Praha-Lochkov, U topolů section and Praha-Kosoř, a Barrande's locality.

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