Colour Patterns in Early Devonian Cephalopods from the Barrandian Area: Taphonomy and taxonomy

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Five cephalopod specimens from the Lower Devonian of Bohemia (Czech Republic) preserve colour patterns. They include two taxonomically undeterminable orthoceratoids and three oncocerid nautiloids assigned to the genus *Ptenoceras*. The two fragments of orthocone cephalopods from the lowest Devonian strata (Lochkovian, *Monograptus uniformis* Zone) display colour patterns unusual in orthoceratoids. They have irregular undulating and zigzag strips that are preserved on counterparts of adapertural regions of specimens flattened in shale, despite their original aragonitic shell having been completely dissolved. These are probably the result of the proteinous pigment inside the shell wall, being substituted during diagenesis by secondary minerals leaving only an altered trace of the original shell. Orthoceratoids from sediments unsuitable for preservation of this feature discussed here thus demonstrate an exceptional case of preservation of colour patterns, not only within Devonian cephalopods but also within other Devonian molluscs. Three specimens of *Ptenoceras* that preserve colour patterns come from younger Lower Devonian strata. Oblique spiral adaperturally bifurcating bands are preserved in *P. alatum* from the Pragian and zigzags in *P. nudum* from the Dalejan. Juvenile specimen of *Ptenoceras*? sp. from the Pragian exhibits highly undulating transversal bands—a pattern resembling colour markings in some Silurian oncocerids. Dark grey wavy lines observed on the superficially abraded adapical part of a phragmocone of nautiloid *Pseudorutoceras bolli* and interpreted formerly to be colour markings are here reinterpreted as secondary pigmented growth lines. Other Devonian fossils including a single brachiopod and several gastropods from the Barrandian Area with preserved colour patterns are mentioned. Variety of cephalopod colour patterns, their taxonomic significance, function and significance for palaeoecological interpretation, palaeoenvironmental conditions favouring colour pattern preservation and systematic affiliation of taxa with colour pattern preserved are discussed.

Key words: Cephalopoda, Nautiloidea, colour pattern, Devonian, Bohemia, Czech Republic.

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Introduction

Although colour patterns are rarely preserved among fossil invertebrates, the reported number of specimens exhibiting this feature described since the 1790s, when they were first mentioned (Bruguière 1792), is remarkable. Summaries of data concerning colour patterns are available in the papers by Hoare (1978), Mapes and Hoare (1978), Blodgett et al. (1983), Kobluk and Mapes (1989), Mapes and Davis (1996), and Sun et al. (1999) providing good information about types of colour banding in the geological past. The importance of this morphological feature for palaeoecological implications and taxonomical purposes has been emphasised by these authors.

It is reasonable to assume that many shells and external skeletons of Palaeozoic invertebrates were originally coloured. Two possible mechanisms have been suggested that can colour molluscs shells: insertion of pigment in the shell and absorption and reflections of light wave lengths by the shell ultrastructure (Fox 1972; Kobluk and Mapes 1989; Mapes and Davis 1996). However, in Palaeozoic cephalopods there are no evidence of colours caused by the ultrastructure of their shell, i.e., colours expressed due to diffraction and interference of light on individual layers of the shell from that time span, although such colours have been discovered in Burgess Shale animals (Parker 1998). The original presence or absence of pigment in shells with monochromatic patterns (Gardner and Mapes 2000) that have lost their original colours or in unpigmented shells cannot be determined in their present state. However, all reported colourations in Palaeozoic cephalopods deals with shells in which pigment was deposited in regular or irregular patterns, in which differences in shading suggest the presence of original colour bands. Kobluk and Mapes (1989: table 2) assembled a list of Palaeozoic cephalopod genera with preserved colour patterns in which 16 different genera from the Ordovician to the Devonian are mentioned. With respect to some additional published data and the recent studies of the Bohemian material (references see below), their list of genera can be extended by about 10 genera (*Phragmoceras*, *Ptenoceras*, *Sphooceras*, "*Orthoceras*" indet., *Hexameroceras*, *Oocerina*, ?*Oonoceras*, *Pomerantsoceras*, and two undetermined oncocerids).

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The majority of reported Palaeozoic cephalopods with preserved colour patterns come from Silurian strata, fewer from the Ordovician and very few from the Devonian. The best material with preserved colour patterns was illustrated by Barrande (1865–1877). In this volume, devoted to cephalopods, Barrande figured colour patterns in 22 species (assigned at that time to four genera), Foerste (1930) listed 19 additional species and discussed the issue of colour patterns in detail. Colour patterns in eleven other species were recognised subsequently (Flower 1939; Balashov 1964; Stridsberg 1985; Turek 1990, 2007b). Additional specimens representing five or six species have now been added during recent revision of old material contained in the palaeontological collection of the National Museum, Prague, collection of the Czech Geological Survey and during new field investigations. The present total number of Ordovician–Devonian cephalopod species with presumed colour patterns is now 57 species belonging roughly to 26 genera and the estimated number of coloured patterned nautiloid species from the Palaeozoic of Bohemia is now 32. Some of the latter specimens were previously discussed briefly (Turek 1990, 2004) but detailed documentation of newly discovered specimens, except colour pattern in *Pomerantsoceras* (see Manda and Turek 2009), has not been published. However, there are some specimens in which the dark grey or black pigmentation can reasonably be interpreted as the result of inorganic pigments migrating through the host rock during diagenesis rather than preservation of an original colour pattern. Such pigmentation is usually connected with some raised or depressed elements of surface sculpture (e.g., lirae, striae, ribs). An exact tally of the number of taxa showing original colour pattern is complicated by the fact that a modern systematic revision of Bohemian cephalopods, except for some genera remains to be accomplished. Examples of colour patterns in Palaeozoic cephalopods are known in almost all post-Cambrian nautiloid orders including representatives of endoceratoids and actinoceratoids.

Colour patterns usually have an appearance of dark grey or brownish bands, contrasted by lighter interspaces. The degree of contrast varies from pronounced to almost unnoticeable; most are more visible whenever the shell is covered with fluid. For their preservation in the fossil record, specific favourable conditions must have been required, but these are not fully understood. Basic mechanisms of colour pattern destruction were briefly summarised by Mapes and Davis (1996). Shells usually loose their original colouration in a rather short time after the death of the animal, though, in exceptional circumstances, it can be preserved (Curry 1999). Light and oxygen strongly degrade pigments and exposure of modern coloured shells to either or both results in the colour degrading rapidly (Cheesman et al. 1967). In Recent *Nautilus* the hue and intensity of the brown change rapidly after death of the animal (Stenzel 1964). However, under suitable conditions pigments can survive as molecular fossils, but decay to the extent that they can no longer absorb light at particular wavelengths (Blumer 1965).

In exceptional cases, newly formed minerals replaced the pigments. This condition applies to all four Devonian nautiloids from Bohemia, Barrandian area discussed herein. Three of these specimens (one of the genus *Ptenoceras* and two fragments of unidentified orthocone cephalopods) were found during recent field investigations and two were discovered in old material housed in the palaeontological collection of the Natural History Museum, National Museum, Prague.

Specimens were immersed in alcohol before photographing by an Olympus Camera DP 70 and Camedia C-5050 Zoom. One of them (NM-L 38470) was photographed by Exacta VX1000 camera. Resulting images were processed using CorelDRAW Graphic Suite X3.

Institutional abbreviation.—NM-L, National Museum, Prague, Czech Republic.

Colour patterns in Devonian cephalopods

Among the orthocones a very regular chevron pattern was documented by d'Archiac and de Verneuil (1842) on the species *Orthoceras* (= ?*Michelinoceras*) *anguliferum* from the Middle Devonian of Germany. This is, as Foerste (1930: 132) remarked, "the first record of colour design in fossil cephalopods". Foerste also discussed this example exhaustively and mentioned other specimens from the Middle Devonian of Michigan. He designated the colour-patterned specimens from the Devonian of Michigan as *Orthoceras anguliferum alpense*.

There are only minor differences between the chevron patterns of North American and European *Orthoceras* specimens. Chevrons are present only on the ventral side, and at the mid-lateral position, they fade abruptly (Foerste 1930: pl. 1: 1, 2, pl. 3: 1, 2). However, Furnish and Glenister (1964: 118) assumed that the colour patterns were present only on the upper side, and they concluded that the upper side was in the dorsal position. This conclusion was applied to the majority of longicone orthocones and supports the idea of a predominantly horizontal life position of many orthocerids.

Among cyrtocone and coiled nautiloids with colour patterns, Barrande (1866: pl. 119: 5–9) illustrated dark grey undulated lines on the somewhat abraded adapical region of the specimen *Pseudorutoceras bolli* from Upper Dalejan. He considered these undulating lines as fossilised original colour bands, the interpretation was later rejected by Turek (1990). A specimen with longitudinal revolving bands mentioned by Teichert (1964: K25) as a Devonian *Trochoceras* is in fact a Silurian (Gorstian) *Peismoceras*.

A few additional cephalopods with preserved colour patterns were reported from the Lower Devonian of the Barrandian area (Turek 1990, 2004); none of them have yet been illustrated and described in detail. Our knowledge concerning this feature in pre-Carboniferous cephalopods is very limited. Following the rejection of the dark lines in *Pseudoruto-*

ceras bolli as coloured strips, five specimens discussed in this report, including *Ptenoceras* and two unidentified orthocones belonging probably to different species, are the only Devonian cephalopods from Bohemia exhibiting this feature. Therefore, they provide unique information about the appearance of the pattern of the original pigmentation in two orders of Devonian nautiloids.

Description

Orthoceratoidea

Both fragments of unidentified orthoceratoids (specimens NM-L 38470 and NM-L 38471) represent counterparts in which the shell is completely missing but undulating strips corresponding to original colour banding are well expressed. These specimens come from the lowest Devonian beds (Lochkovian Stage, Lochkov Formation, *Monograptus uniformis* Zone). One was discovered about 1985 in loose material, and the other in the year 2000 directly in the Silurian/Devonian stratotype section at Klonk near Suchomasty; both probably come from one layer—a shale interbed between limestone layers 20/21 (see Chlupáč et al. 1972).

Specimen NM-L 38470 (Fig. 1) is preserved as a counterpart flattened in brown-grey slightly weathered calcareous shale. This fragment of an unidentified orthocone cephalopod shell is from about 20 mm of the adapertural region of the body chamber. The apertural margin is 31 mm long, straight and almost perpendicular to the axis of the shell.

The colour patterning is characterised by diagonal zigzag bands on the entire surface of the fragment. Its central part (along the axis) bears very slightly waved bands, oriented obliquely at an angle of about 25–28° to the axis of the shell. The course of bands markedly changes both dextrally and sinistrally from the axis of shell, passing in an irregular zigzag pattern with the angular inflections having either blunt or sharp tips. The width of bands varies between 0.5 and 2.0 mm. Unpigmented spaces between bands are slightly narrower than the bands. The orientation of the shell is not unequivocally clear. Based on the course of the aperture it could be assumed that either the dorsal or the ventral side of the shell is displayed. The marked asymmetry of the colour markings indicates that lateral compression of the shell occurred in the shale rather than as dorsoventral flattening of the shell. The bands extend to the margin of the aperture as well as laterally. However, the lateral border of the specimen is uneven. A small part is sinistrally broken off and minor parts are probably missing due to sediment compaction. As the whole surface of the fragment bears colour bands, which are most distinct along the lateral edges, it is probable that the whole circumference was originally coloured.

Specimen NM-L 38471 (Fig. 2) is preserved in brownish, slightly weathered calcareous shale. The specimen is associated with two fragments of smaller orthocones and moderately corroded columnals of scyphocrinid crinoids. A small
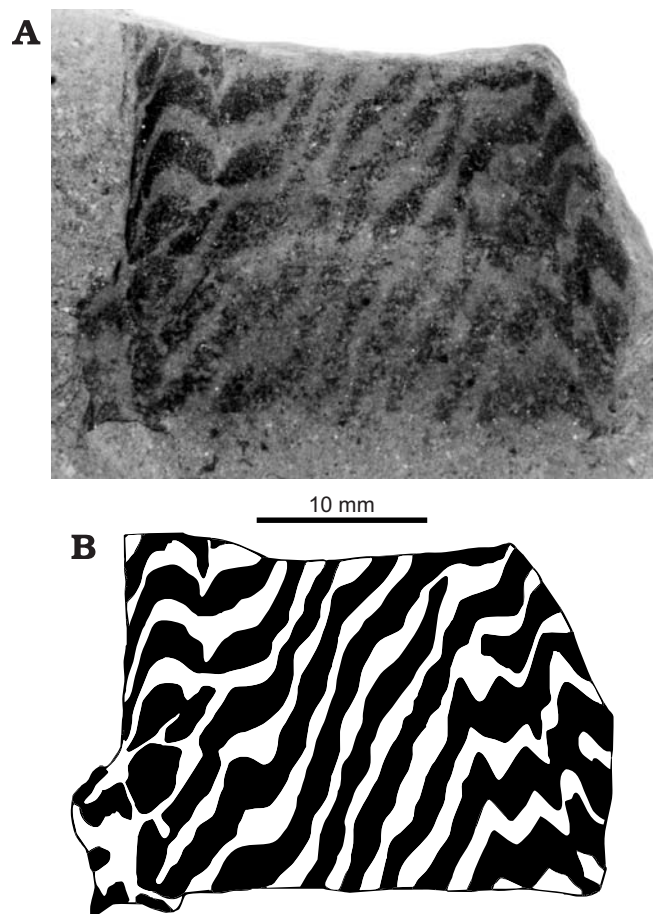

Fig. 1. Adapertural part of orthoceratoid body chamber with preserved colour pattern; counterpart, specimen NM-L 38470. Koněprusy, Klonk section, Lower Devonian, Lochkovian, Lochkov Formation, *Monograptus uniformis* Zone, probably interbed 20/21 (see Chlupáč et al. 1972). **A**. Photograph. **B**. Schematic drawing.

poorly preserved zoarium of a cyclostomate bryozoan (1.5 mm in diameter) is attached in the adapertural region (visible under low angle oblique lightening). On the opposite side of the shale specimen, there is a stem fragment of the vascular plant *Cooksonia*. The counterpart of NM-L 38471 is a 25 mm long fragment of the adapertural part of the body chamber; the apertural margin is 22 mm long. Due to imperfect preservation of the fragment, especially the deformation along both sides and a course of a medium fracture, the specimen resembles a cyrtocone nautiloid more than an orthoceratoid. However, the main longitudinal fracture along the axis is straight, and is bent only 5 mm from the apertural margin, resulting in a taphonomically induced appearance of curvature. Another set of cracks run subparallell to the axis of the shell. An originally cyrtocone form of the shell is also unlikely because cephalopods with curved shells (as well as brevicones which the fragment also resembles) are extremely rare in lower Lochkovian sediments. Preservation of the specimen shows that the shell is well defined dextrally, but marginal parts are broken off sinistrally. In correspondence with this interpretation the course of the aperture is slightly oblique, forming an angle of about 80° to the axis of the shell.
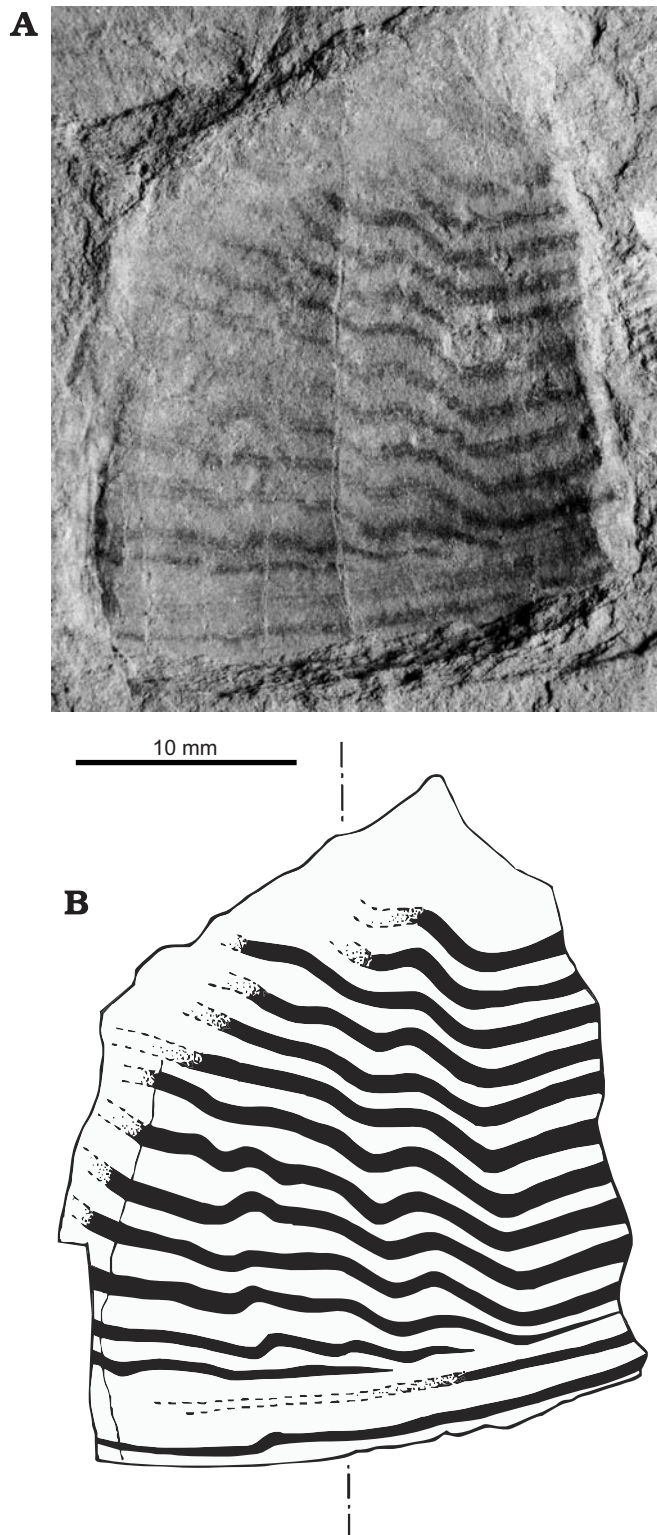
A

10 mm

B

Fig 2. Adapertural part of orthoceratoid body chamber NM-L 38471 with preserved colour pattern; counterpart. Koněprusy, Klonk section, Lower Devonian, Lochkovian, Lochkov Formation, *Monograptus uniformis* Zone, interbed 20/21 (see Chlupáč, Jaeger and Zikmundová 1972). **A**. Photograph. **B**. Schematic drawing; axis of the shell is indicated.

The colour pattern is characterised by transverse bands. The undulating bands extend obliquely to the axis of the shell in the median region forming an angle of about 45° to the axis in the adapical part of the fragment. This angle increases adaperturally; about 5 mm from the aperture, it expands to about 65°. There is a marked change of colour pattern near the aperture. Oblique bands in the central part become thinner and fade out. Sinistrally their undulating course changes into a straight one perpendicular to the axis. A markedly different course of strips is displayed in a narrow zone near the aperture. The last two well-expressed strips are almost straight, concordant with the apertural margin. Strip width is generally about 0.6 mm. Although growth lines on the specimen are faint the character of these striking changes of colour pattern in the adapertural region of the cephalopod does not indicate any damage and repair of the shell. Homology to the black band in Recent *Nautilus* and also observed in some ammonoids (Klug et al. 2007) is possible. Preservation of the pattern indicates that the shell of this orthocone was also originally coloured throughout its entire circumference at this growth stage. The conspicuous asymmetry of the colour markings and the course of the aperture indicate lateral flattening of the shell as more probable than a dorsoventral compression.

Coiled forms

***Ptenoceras alatum* (Barrande, 1865)**.—Specimen NM-L 40726 (Figs. 3B, 4) Lower Devonian (Pragian Stage, Praha Formation, Koněprusy Limestone); locality Koněprusy near Beroun, Zlatý kůň Hill. This nearly complete specimen is preserved in white-grey bioclastic limestone. The body chamber is obliquely dislocated longitudinally and the adapical part is still partly embedded in limestone.

The colour pattern assumes in an irregular diagonal zigzag across the whorl. A faintly expressed symmetric colour pattern was probably developed across the entire surface of the shell similar to other oncocerids with well preserved colour patterns. Traces of colour pattern in *Ptenoceras nudum* (NM-L 40727) observed ventrolaterally supports this assumption. The colour pattern is not visible in the midventral region, perhaps due to incomplete preservation. Curiously, colour bands are better seen under dimmer natural light than under intense artificial light. Dislocated and slightly shifted sinistral and ventral parts of the body chamber are superficially weathered and limonitised and do not show any colour markings.

Faded brownish discontinuous bands in the umbilical region of the body chamber are about 3 mm wide and are not distinctly defined. In the middle part of the dorsal side they form an angle of 60° and they are pointed adaperturally. A marked discontinuity of their course is visible on the last raised growth line situated dorsolaterally, about 15 mm from the apertural margin. Interruption of colour bands in place of broken off ventrolateral wing-like processes is probably a result of post-mortem taphonomic processes. Oblique bands are adaperturaly bifurcated, widening in that direction as well; their course is irregular.
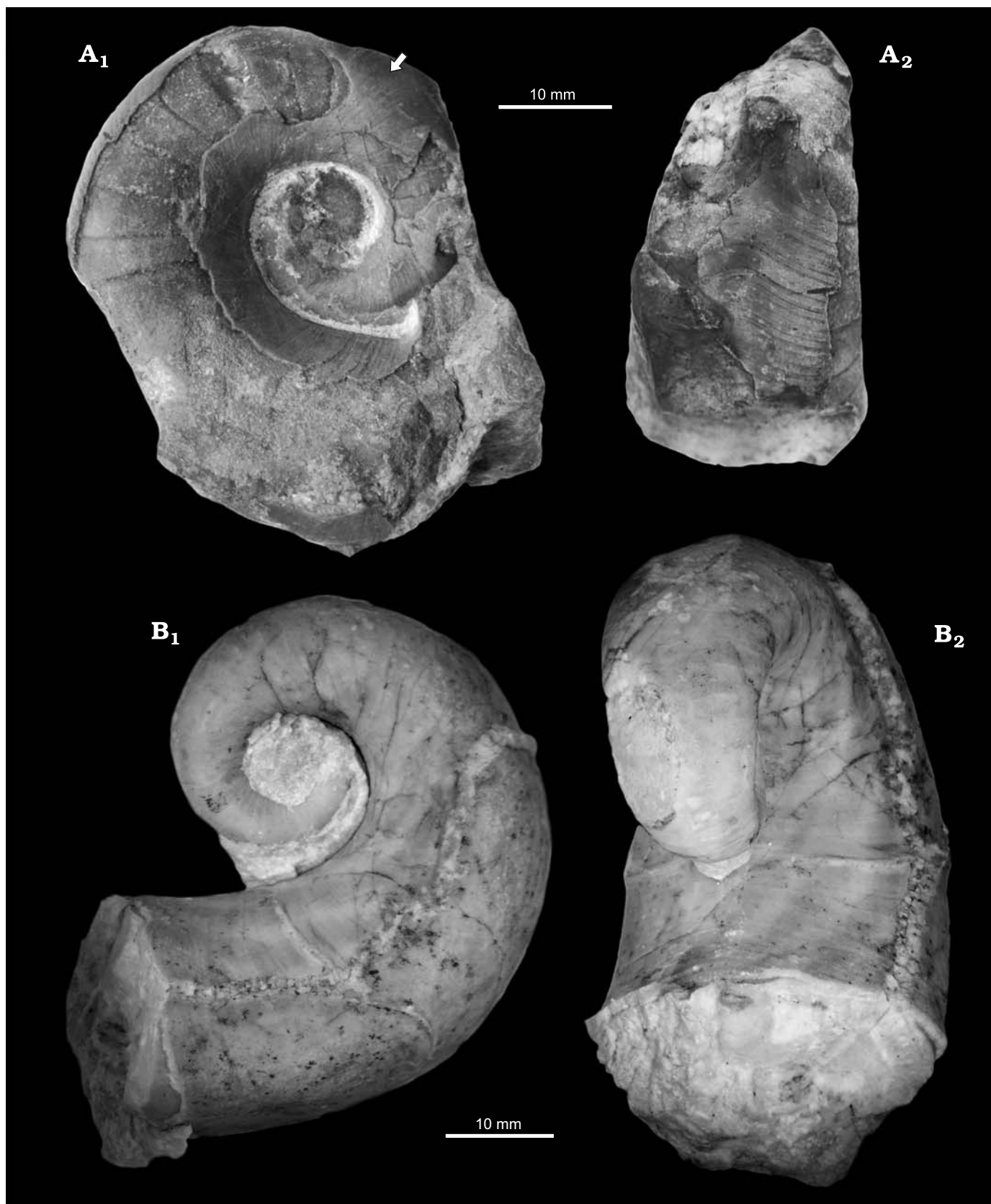
Fig. 3. Colour patterns in Devonian cephalopods *Ptenoceras*. **A**. *Ptenoceras nudum* (Barrande, 1865). Praha-Hlubočepy, Dalejan, Daleje-Třebotov Forma-tion, Třebotov Limestone. Specimen NM-L 40727 in lateral (A₁) and ventral (A₂) views, showing colour bands—zigzags on ventral side of the whorl and a trace of colour band ventrolaterally (indicated by arrow). **B**. *Ptenoceras alatum* (Barrande, 1865). Koněprusy, Pragian, Praha Formation, Koněprusy Lime-stone. Specimen NM-L 40726, in lateral (B₁) and frontal (B₂) views, exhibiting bifurcating colour bands oblique to axis of the shell.
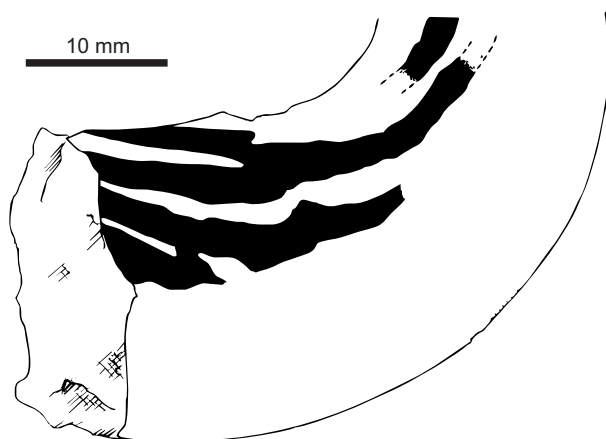
Fig. 4. *Ptenoceras alatum* (Barrande, 1865). Schematic outlines of colour pattern in specimen NM-L 40726, illustrated here on Fig. 3B.
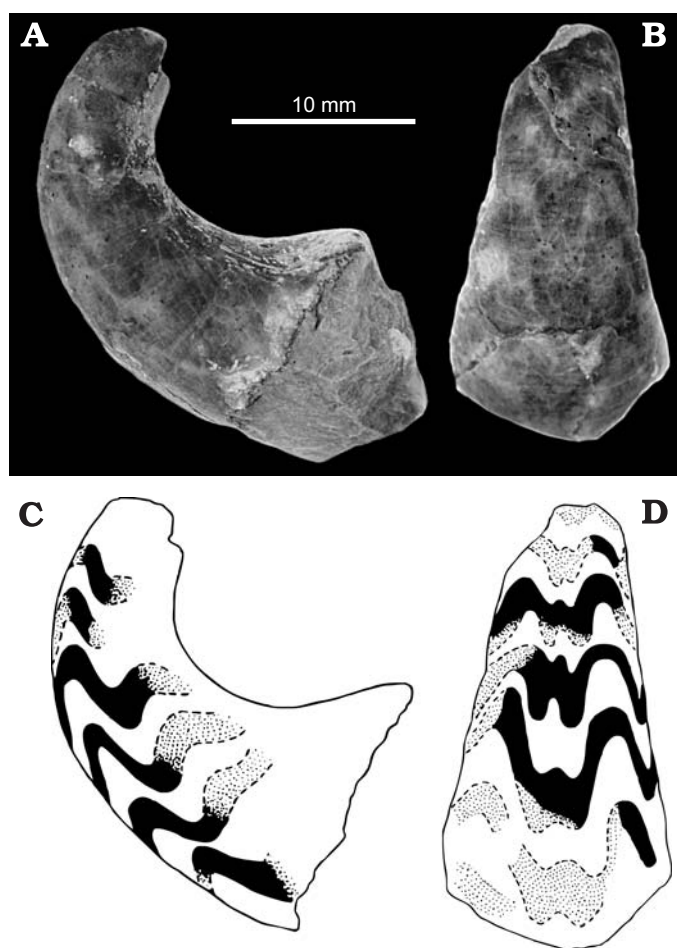

Fig. 5. *Ptenoceras*? sp. Praha-Braník, Pragian, Praha Formation, Dvorce-Prokop Limestone. Specimen NM-L 7644, juvenile shell with preserved colour pattern (**A**, **B**) and schematic outlines of colour pattern (**C**, **D**), lateral (**A**) and ventral (**B**) views.

***Ptenoceras nudum* (Barrande, 1865)**.—Specimen NM-L 40727 (Fig. 3A) comes from the Lower Devonian (Dalejan Stage, i.e., Upper Emsian, Daleje-Třebotov Formation, Třebotov Limestone); locality Praha-Hlubočepy. This incomplete specimen is from an old collection and is preserved in

light grey micritic limestone; the shell is partly exfoliated and, on the left side, deeply weathered. The adapical part of the body chamber is extensively damaged on the ventral side.

The colour pattern is preserved in the ventral and ventrolateral portions of the adapertural part of the phragmocone (1st half of the last whorl). Fragments of shell adhering to the umbilical slope, as well as to the ventral side near the aperture preserve no colour markings. However, brownish dark bands about 2 mm wide are visible on a small area. They exhibit the typical zigzag pattern with centre of the tips directed adapically in the plane of symmetry. The ventromedian angle of zigzags is about 30°; the bands pass into the oppositely directed tips also situated on the ventral side. The further course of bands cannot be followed as the shell is missing.

***Ptenoceras*? sp.**—Specimen NM-L 7644 (Fig. 5) Lower Devonian (Pragian Stage, Praha Formation, Dvorce-Prokop Limestone); locality Praha-Braník. This incomplete juvenile specimen lacks the adapical part of the conch and has a damaged adapertural part of the body chamber. The specimen was recovered with various gastropods in an old Museum collection by Radvan Horný. Its matrix is a dark grey micritic limestone. The shell sculpture is well preserved, except on the internal part of the whorl.

Faint dark grey zigzag colour bands cover most of the entire circumference, except on the damaged internal (dorsal) side of the whorl. The bands in the form of slightly asymmetric "W" are developed ventromedially. A smaller median tip of this "W" is directed adapically. Then the bands pass in parabolic arches ventrolaterally. Their further undulating course around the shell cannot be followed precisely; dorsolaterally they generally follow the course of the growth lines.

This unique juvenile specimen is tentatively assigned to the genus *Ptenoceras* based on the shape and cross section of the shell. However, neither the structure of the siphuncle nor its position are known. In comparison with the type species *P. alatum* some important differences are present. The general course of the growth lines is more perpendicular to the axis of the shell and the growth lines are almost straight, forming a broad, shallow hyponomic sinus. Periodically repeating marked growth lines, that are present on *P. alatum* in comparable growth stages, are not developed on this specimen. Also, the shell expands more rapidly in comparison with *P. alatum* and the colour pattern differs markedly in compared species. The outer morphology of the specimen discussed here resembles *Trochoceras*? *kayseri* (Novák, 1886), but the cross section of the whorl in *T.*? *kayseri* is slightly laterally compressed (not depressed), and the shell expands more gradually.

False colour pattern in *Pseudorutoceras bolli*

Specimen NM-L 449 of *Cyrtoceras bolli* Barrande, 1866 illustrated by Barrande (1866: pl. 119: 5–9; Fig. 6 herein), repre-

Fig. 6. False colour pattern in *Pseudorutoceras bolli* Barrande, 1866. NM-L 449 from Praha-Hlubočepy, Dalejan, Daleje-Třebotov Formation, Třebotov Limestone. **A**. A part of the body chamber with original Barrande's inscription noticing "test", aperture up. **B**. The same specimen in opposite orientation, artificially abraded adapical part with wavy dark lines; ventrolateral view.

senting the type species of newly established genus *Pseudorutoceras* Manda and Turek, 2009, comes from the Lower Devonian (Dalejan, Daleje-Třebotov Formation, Třebotov Limestone); locality Praha-Hlubočepy. A part of the body chamber with Barrande's inscription represents a weathered and slightly deformed internal mould of an incomplete specimen. The entire surface of the specimen is artificially abraded. The specimen is preserved in a light micritic limestone and is limonitised on the surface.

Dark grey thin transverse lines are seen on the adapical part of the phragmocone in the ventral and ventrolateral regions. The lines are sharp with well-defined edges. Their width is 0.1–0.3 mm, and each is separated by wider interspaces, 0.8–1.2 mm across. Their wavy course shows a marked medially situated shallow ventral lobe. It passes into broad saddles, then into ventrolaterally situated lobes. A short continuation laterally indicates a similar course but these lines fade further laterally.

Foerste (1930), when studying this specimen supposed that these lines extended in the same manner around the dorsal side, and he estimated the total number of waves (sine curve) to be six or seven. Though Foerste (1930) accepted Barrande's (1866) opinion dealing with the nature of these lines, the present author proposes that these lines formed by dark grey calcite represent a false colour pattern. Owing to the translucent abraded surface of the specimen it is evident that they represent projections of incremental lamellae growing below the old shell with the surface, and therefore, these features are not a colour pattern (Turek 1990). Unfortunately the shell sculpture is not preserved neither on this specimen, nor in Barrande's (1866) another specimens assigned to the same species. The course of the dark grey calcite lines was compared with the course of growth lines in some Devonian rutoceratids, and the two features seem to be generally concordant. Second-

ary pigmentation showing the concentration of dark pigment in narrow transverse or also in longitudinal ridges has also been observed in some Silurian nautiloids. Darker narrow undulating lines represent more conspicuous lamellae repeating in regular intervals on the surface, as is common in some nautilids. A similar case of false colour pattern has been described in *Bactrites* from the Carboniferous (Mapes 1979). False colour patterns on cephalopod shells have been discussed in more detail by Mapes and Davis (1996) and Klug at al. (2007).

Colour patterns in other Lower Devonian fossils from the Barrandian area

Only a few Devonian fossils with a preserved colour pattern have been reported from Bohemia. They all come from the Lower Devonian strata (Pragian Stage, Praha Formation, Koněprusy and Dvorce-Prokop Limestone). Fossils with colour patterns include invertebrates which have shells originally formed of calcite—brachiopods and some gastropods. It is worth mentioning that of the thousands of specimens collected in the Koněprusy Limestone, only a single specimen of the brachiopod *Merista herculea* (Barrande, 1879) has a preserved colour pattern. The smooth surface of this atrypid brachiopod with a faint concentric growth lines bears brownish radial colour bands (Kříž and Lukeš 1974). These light grey bioclastic limestones originated in the environment of well-oxygenated water associated with Lower Devonian reefs or at the periphery of these reefs. Such palaeoenvironments rarely have brachiopods with preserved colour patterns.

Spiral colour bands have been observed in the Early Devonian gastropod *Praenatica gregaria* (Barrande, 1903), including the synonymous *Platyostoma*? *elaboratum* (Barrande, 1911) (see Horný and Henry 1999). These specimens come from biodetrital Koněprusy Limestone (Perner 1911: pl. 226: 35–38) and pigmented bands were also discovered in this platycerid gastropod in the yellow weathered micritic Dvorce-Prokop Limestone (Horný and Henry 1999: fig. 4A–F). Intraspecific variability of the colour pattern is expressed especially in the distinctness and width of dark spiral bands, which are periodically disrupted by growth lines lacking pigment. Jankovský (2003), examining more than one thousand specimens of this species, estimates that 2–3 % of the specimens display relic colour patterns, with most being only faintly visible. The striking dark grey or black-grey pigmentation commonly observed in this gastropod species has not yet been sufficiently explained. White spots accumulated on the exposed part of the last whorl and was explained as a consequence of attachment of an unknown sessile organism (Jankovský 2003; Figs. 7C, 8D, E) can indicate that the dark grey colour is a remnant of the altered original pigmentation. However, that diagenetic processes could also be considered

as the primary cause of this dark coloured pigments. Dark spiral bands, as yet unillustrated, were also observed in several specimens of the gastropod *Oehlertia* sp. (Radvan Horný, personal communication 2007) recovered from the bioclastic Koněprusy Limestone.

Grey micritic Lower Devonian Třebotov Limestone (Daleje-Třebotov Formation, Dalejan) occurring in and around Prague and containing a diverse benthic and nektonic fauna, were also deposited in a well-oxygenated shallow water environment. This facies appears unsuitable for colour pattern preservation. Except the case of the afore-mentioned nautiloid, colour patterns have not been reported in other fossils from this limestone.

Colour patterns have been documented also in strongly weathered silicified fossils (Yochelson and Kříž 1974). This demonstrates that silicification coming in early diagenesis is not always destructive to colour patterns; such a case was observed also in a Bohemian Palaeozoic nautiloid. Also, weathering processes do not always obliterate colour patterns. In fact, in some cases weathering can enhance the pigmented zones in contrast to the surrounding matrix.

Discussion

Variety of colour patterns.—The available material displaying documented colour patterns in Palaeozoic cephalopods indicates their high diversity (compare Teichert 1964). Examples include longitudinal bands developed either on the entire surface of the shell or on one half only, longitudinal bands combined with transversal ones, regular chevrons or less regular zigzag patterns, either continuous or interrupted, oblique spiral bands sometimes passing into zigzag bands, transverse wavy bands present on the entire surface or transverse bands developed on one (ventral) side only, perpendicular or oblique to the axis, and transverse bands concordant with growth lines. Exceptionally, spots or patches originally produced by periodical activity of isolated groups of pigment-producing cells were reported (Hedström 1917). However, largely non-bifurcating oblique bands, concentrated on the flanks of the shell, and coalesced across the ventral side, are present as in the Recent nautiloid genera *Nautilus* and *Allonautilus*. They have not been reported from Palaeozoic or in stratigraphically younger genera (compare Kobluk and Mapes 1989). Some colour patterns in fossil cephalopods can pass from one into another in a single specimen. Through a combination of these types of colour patterns, either symmetrical or asymmetrical development, there are significant differences in regularity of the arrangement of the patterns as well as differences in width of the bands. Probably there were also variations in colour, which produced a large range of forms and patterns.

Taxonomic significance of colour patterns.—Based on a relatively large number of specimens with colour patterns, together with published data, it can be concluded that some col-

our patterns are characteristic for individual species and probably for some genera. Thus, when they are preserved, they have the potential to be used for taxonomical purposes. Regrettably, except for the two Silurian cephalopod species—the tarphycerid *Peismoceras pulchrum* (Barrande, 1865) and the oncocerid "*Cyrtoceras*" *parvulum* (Barrande, 1866), the limited amount of material prohibits variability analysis of this feature. The former species has more than 40 specimens exhibiting traces of colour markings, and the latter species has about 20 specimens in the available collections. From the other taxa one or two specimens were available and only rarely more, e.g., ortoceratoid "*Orthoceras*" *pelucidum* (Barrande, 1868). Rare occurrence of preserved different growth stages in cephalopods with colour patterns, as well as their incompleteness prohibits evaluation of ontogenetic changes of colour patterns.

Function of colour patterns and significance for palaeoecological interpretation.—Functions of colour patterns in fossil invertebrates has been discussed in many papers (see the references in Mapes and Davis 1986). As in Recent *Nautilus* (compare Stenzel 1964), darker, originally perhaps predominantly brown bands in fossil nautiloids, disrupted the outline of the animal. Based on the rather low intraspecific variability of colour patterns in Palaeozoic cephalopods, it can be suggested that this feature could have served as light screening and camouflage. The majority of cephalopods with preserved colour patterns inhabited shallow waters in the photic zone of the Silurian and Devonian tropical and subtropical seas. In such an environment the colour patterns could have had a functional relationship to confuse the visual systems of predatory organisms.

When colour patterns are present over the entire surface of the orthoceracone shells, this may indicate an absence of primary cameral deposits and vertical life position. Mutvei (2002) proposed this condition and diurnal vertical migration in the water column for the majority of orthoceratoids. As an argument against the existence of primary origin of cameral deposits Mutvei (2002) observed that orthoceratid shells preserved in shale are usually completely flattened. The mode of preservation of orthocone cephalopods in sediments with higher content of calcium carbonate or sand admixture (e.g., in the Upper Ordovician and Middle Devonian shale of the Barrandian area) is frequently different and shows that the adapical part of orthocone shells was more resistant towards overlaying sediment pressure. When present, cameral deposits reinforced this part of the shell so that it is undeformed while the adoral part of the phragmocone without cameral deposits and the body chamber are flattened by diagenetically in shale.

Conditions favourable for colour pattern preservation in the fossil record.—Fossilised colour patterns are usually observed on smooth or striated shells, i.e., those cephalopods that are inconspicuously sculptured. An exception is represented by the annulate tarphycerid (suborder Barrandeocerina) *Peismoceras pulchrum* (see Barrande 1865: pl. 28: 1–3)

and *P. asperum* (unpublished) from the Silurian of Bohemia and by the annulated orthocerid *Dawsonoceras annulatum* (see Blake 1882: pl. 4: 4) from the Silurian of Great Britain. Ribbed nautiloids are not known to display colour patterns. It has been widely accepted that shell pigments are primarily metabolic waste products (Comfort 1951; Cox 1960). However, Hedegaard et al. (2005: 5) emphasised that "molluscs have excellent excretory organs, and incorporating waste into structural supports seems implausible, particularly when secretion is episodic and confined to a thin layer at the exterior of the shell". Considering colour pattern in terms of some usually proposed function as light screening or camouflage (e.g., counter-shading), ribbing of shells in cephalopods living within the photic zone could cause a similar effect as that of "sophisticated" ecologically controlled pigmentation. It is possible some markedly ribbed nautiloids were either essentially coloured over their entire surface or unpigmented, but this has not been documented in the fossil record.

Despite the incompleteness of available data dealing with preserved colour patterns in Palaeozoic nautiloids, the frequency of colour-patterned taxa is remarkably higher in relation to total number of bivalve taxa. As shells in both groups were originally aragonitic, the single reported example in bivalves (Devonian *Leiopteria*, Cox 1969) is surprising. Kobluk and Mapes (1989) explain this phenomenon by the hypothesis that Palaeozoic nautiloids may not have had an entirely aragonitic conch. However, some aspects of taphonomy in Palaeozoic fossils of Bohemia related to the mode of preservation of cephalopod shells encrusted by epizoans with a primarily calcite shell or skeleton (bryozoans, articulate brachiopods, crinoids), fossilised in an environment with a primary deficiency of calcite do not support this hypothesis. Cephalopod shells in such sediments are completely removed, but structures built originally by calcite are well preserved (compare Turek 1983, 1987). Hence a calcite conch, if it existed at all in Palaeozoic cephalopods, would probably have been expected to be preserved. Also, the completely dissolved shell of the fragments of orthocone described herein, but still displaying a colour pattern in the counterpart indicate several different taphonomic mechanisms were responsible for colour pattern preservation.

Certain sedimentary environments most likely played a major role in the preservation of colour patterns. Rapid burial of shells and in some cases cyanobacterial sealing slowed aerobic destruction of colour pigments and favoured their alteration (e.g., by pyrite), similarly to how it could happen with some carcasses under low carbon setting, in which ions diffuse toward a localised carbon source (compare Martin 1999: 140). Rapid burial of shells and low oxygen level on the bottom probably favoured influenced preservation of colour patterns in the majority of Bohemian Palaeozoic cephalopods, which come from pyrite rich sediments. This assumption may be supported by results of analyses of the thin honey-coloured outer layer (?periostracum) in the Silurian bivalves from the Barrandian area (Kříž 1972) which showed that the original conchiolin matter was broken down,

and the pores created were then filled with calcite and pyrite. Considering the rarity of the Devonian nautiloids from the Barrandian area no analytical methods that would damage specimens have been used to test if similar preservation is present. The dark grey or almost black colour in specimens NM-L 38470 and NM-L 38471 could be caused by a carbonaceous substance, microcrystalline pyrite or a phosphatic compound (compare Klug et al. 2007). The extremely small grains of opaque mineral were not amenable to analysis. The results of energy-dispersive spectroscopy and microprobe analysis of coloured Triassic brachiopod *Coenothyris vulgaris* are interesting for comparison purposes (Hagdorn and Sandy 1998). This method has not detected any difference between white and pigmented shell strips. There was no concentration of iron oxide in the darker stripe so that an organic origin is suggested. Almost thirty years earlier Blumer (1965) found organic pigments ("fringelites") causing reddish-violet colour of roots and stems of a Jurassic crinoid *Apiocrinus*. Contrary results of electron probe analysis coupled with more conventional techniques showed that the pink colouration of a Middle Devonian *Chonetes* was not due to original organic pigmentation but to small grains of iron oxide (Zenger 1967).

The unique preservation of colour patterns in two ortocone cephalopods from the very base of the Lochkov Formation appears to be produced by a combination of sedimentological, diagenetic and post-diagenetic processes. The sequence in the stratotype is formed by the alternation of fine-grained mostly dark grey limestone layers and dark grey calcareous shale interbeds. Chlupáč and Hladil (2000) estimated that the average duration of one couplet consisting of dark limestone and calcareous shale (0.25 m thick on the average) may correspond to about 16.4 Ka. The ratio of original shale thickness/recent shale thickness is estimated to be about 6:1 to 8:1 (Jindřich Hladil, personal communication 2007). Fine fractures concordant with the shell axis in specimen NM-L 38470 from the interbed 20/21 indicate that the specimen was compressed before the complete dissolution of its aragonitic shell. Due to the relatively slow deposition rate, the colour patterns could be expected to endure only on the lower (buried) part of the shell. Regrettably, just a fragment of the specimen is available, and it cannot be determined if it is a part of a more complete specimen broken off during collecting or whether fragmentation is a result of taphonomic processes. A dark disaerobic bottom environment was in this case the first favourable condition for long-termed persistence of original pigments because the molecules responsible for shell colouration are sensitive to light and oxygen (Cheesmann et al 1967).

Frequent preservation of colour patterns in one cephalopod species and absence in others experiencing identical conditions suggests that there was differential biochemical predisposition of the pigment for preservation in some cephalopods rather than others or the absence is due to fact that the species did not have a pigment. Perhaps their slower decay on the disaerobic bottom followed by subsequent sub-

stitution by secondary minerals during early diagenesis lead to their preservation. Interestingly, the majority of nautiloids displaying colour pattern are brevicone oncocerids and discosorids that presumably lived close to the sea floor and had limited swimming ability (Miller and Furnish 1937; Stridsberg 1985). Shells of these nautiloids are generally thicker in comparison with other cephalopods (Furnish and Glenister 1964), but colour patterns are known only in selected species within these orders. Therefore, it seems that preservation of colour patterns may be related to shell thickness. If the pigments deposited in their shells were metabolic products derived from the organism's diet (Nuttall 1969; Cox 1960), feeding habits might have influenced the preferences of deposition of more stable pigment molecules in the shell. These pigments may have had a better possibility for their replacement by secondary minerals, which enhanced the preservation potential of the colour pattern. Also, the possibility of production of more stable pigment molecules by the animal must be considered.

Pigments in Recent molluscs are deposited in the outer part of the shell or in the periostracum (Hollingworth and Barker 1991). Preservation of colour patterns may depend on colouration that was purely superficially deposited in only the periostracum or penetrated into the calcareous shell. In present-day *Nautilus* pigment is confined to the outermost portion of the porcelaneous layer of the shell wall (Gregoire 1987). In Palaeozoic nautiloids where deposition of pigments causing colouration would be only in the periostracum, the chances of colour pattern preservation would be greatly restricted, as periostracum usually disappeared during fossilisation processes. Conversely, deposition of pigments in the outer prismatic (porcelanous) layer could be an important preservation factor of colour patterns in fossil nautiloids.

Systematic affiliation of the taxa under consideration.— Preservation of two fragments of the Lower Devonian orthocone cephalopods showing colour patters described above does not allow more precise taxonomic determination. Therefore, attention is paid only to coiled nautiloids. Except for two Recent genera, remnant colour patterns have been reported in three Carboniferous nautilid genera, and three Mesozoic and Cenozoic nautilid genera (Mapes and Evans 1995). Transverse bands were reported in *Liroceras*, longitudinal bands in the genus related to *Stroboceras* (see Mapes and Davis 1996) and irregular spots and bands in *Vestinautilus* (see Teichert 1964). The colour patterns in Mesozoic and Cenozoic taxa are characterised by transverse colour banding running concordantly with growth lines. Their colour patterns differ markedly from both modern genera as well as from Devonian genus *Ptenoceras*.

Ptenoceras was placed by some cephalopod workers in the order Nautilida (Kummel 1964; Teichert 1967; Dzik and Korn 1992). More recently Manda (2001) classified Ptenoceratidae Teichert, 1939 (= Hercoceratidae Hyatt, 1884) as well as Trochoceratidae Zittel, 1884 and Rutoceratidae

Hyatt, 1884 as oncocerids. Turek (2007a) substantiated close affinity of *Ptenoceras* with *Hercoceras* as proposed by Dzik and Korn (1992), but shared the opinion of Manda (2001) concerning the systematic position of these genera within Oncocerida. Overall morphology including the shape and sculpture of embryonic shell, the subventral position of the siphuncle, intrasiphonal deposits as well as torticone shell and constriction of aperture occurring in some genera—all are the features typical for oncocerids. This opinion also support oncocerid types of muscle scars documented in *Ptenoceras* and newly discovered in the type species of *Trochoceras*, simple course of sutures and described types of colour pattern. Assignment of these cephalopods to the nautilids is problematic. Colour patterns are not known with certainty in any other Palaeozoic nautilids.

Conclusions

Very regular zigzags developed on the dorsal side of the shell are only the patterns, which have been documented in Devonian (Givetian) cephalopods (d'Archiac and de Verneuil 1842; Foerste 1930). Our knowledge of this morphological feature is extended due to finding five specimens from the Lower Devonian of Bohemia—Lochkovian and Pragian Stages. Rather irregular colour patterns showing waved bands oriented obliquely to the axis and occasionally transforming into zigzags are unusual among orthoceratoids. Shells of these cephalopods were probably coloured around the entire circumference.

The unusual preservation of colour patterns on the counterparts of the orthocone shells otherwise completely dissolved in shale is unique. It indicates the possibility of additional discoveries of this feature in other fossils preserved in shale. The taphonomy of these phenomena is not well understood and deserves additional study.

The colour pattern in the form of oblique irregular bifurcating bands in the oncocerid *Ptenoceras alatum* can be derived from the pattern known in the tarphycerid *Peismoceras*. The zigzag pattern observed in *P. nudum* and zigzags passing into undulated transversal bands in *Ptenoceras*? sp. resemble colour patterns known in some Silurian oncocerids, but these patterns differ substantially from the colour patterns known in representatives of the order Nautilida. Despite the fact that our knowledge of colour patterns in the Devonian cephalopods is still scanty, these unique cases of their preservation demonstrate a great variety of patterns retained from the ancestral Silurian stock. However, any clearly expressed evolutionary trend concerning colour pattern has not been recognised in Palaeozoic cephalopods.

Formerly reported colour markings (Barrande 1866; Foerste 1930; Kobuk and Mapes 1989)—the dark wavy lines observed on the superficially abraded adapical part of a phragmocone belonging to the nautiloid *Pseudorutoceras bolli*—is a false colour pattern. The pattern probably resulted from secondarily pigmented growth lamellae.

Differences in preservation of colour patterns in different groups of cephalopods may be influenced by (i) deposition of pigments causing colouration in the outer most portion of the outer prismatic layer (as in Recent *Nautilus*), (ii) in the periostracum only, or (iii) deposition of more stabile pigment molecules in the shell obtained from the food or pigments manufactured by the animal.

Acknowledgements

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