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Variability of colour pattern and shell abnormalities in Silurian nautiloid *Peismoceras* Hyatt, 1884

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Abstract. A cephalopod *Peismoceras* Hyatt, 1884 from the Silurian (Gorstian) of Bohemia is the single known nautiloid genus of the suborder Barrandeocerina with a documented colour pattern. However, spiral bands on lateral side of the shell, oblique to the shell axis, illustrated by J. Barrande in 1865 in *Peismoceras pulchrum* and later mentioned in several papers are not typical for this species. Zigzag bands are more common and they are developed either on the entire circumference of the shell or on one lateral side, while the other side retained the above mentioned spiral bands. A marked asymmetry of colour pattern on lateral sides has been observed in several cases, but with no proven relationship to the slight dextral coiling of the shell. Densely spaced longitudinal bands preserved on ventral side of *P. asperum* (Barrande, 1865) are illustrated for the first time. Some unusual shell abnormalities occurring in *Peismoceras* are discussed.
Key words. Nautiloidea, Barrandeocerina, *Peismoceras*, colour pattern, shell abnormalities, Bohemia, Czech Republic.

INTRODUCTION

There are only a few fossil nautiloids with coiled shell displaying a colour pattern (see summary in Mapes & Hoare 1987, Kobluk & Mapes 1989). Among tarphycerids of the suborder Tarphycerina is the colour pattern known in Ordovician *Trocholites* (see in Schuh 1920), among representatives of the suborder Barrandeocerina in Silurian *Peismoceras*. The colour pattern in *Peismoceras pulchrum* was illustrated by Barrande (1865: pl. 28, figs 1–3) in specimen NMP L 8055. Figured specimen having slightly trochoceracone shell displays brownish spiral bands on lateral side, running obliquely to shell axis (Fig. 1G). This type of coloration has been assumed to be a typical one for this species. The specimen was refigured in some basic palaeontological publications including cephalopod volume of Treatise of Invertebrate Paleontology (Teichert 1964: K23). Foerste (1930: 142), publishing a comprehensive summary of known colour patterns in fossil invertebrates known at that time, studied Barrande's cephalopods with preserved colour

Fig. 1. A, E–J. ***Peismoceras pulchrum*** **(Barrande, 1865). Gorstian, Kopanina Fm.,** ***C. colonus*** **Zone, Na břekvici, Praha, Bohemia. A, H–J. Almost complete specimen with preserved zigzag colour pattern, A – ventral view; H, J – lateral views; I – body chamber, dorsal view, NMP L 27400, × 0.9; B – incomplete body chamber with zigzags, dorsal view, NMP L 27401, × 0.8; E, G. Specimen illustrated by J. Barrande (1865) on pl. 28, figs. 1–3. Lateral views showing zigzags on one side and spiral bands on the other side of phragmocone. NMP L 8055, × 0.8; F – anomalous growth of shell and colour pattern (cf. fig. 2C), NMP L 27406, × 0.8; C–D.** ***Peismoceras asperum*** **(Barrande, 1865). Gorstian, Kopanina Fm.,** ***S. chimaera*** **Zone, Vyskočilka, Praha, Bohemia. Part of second whorl showing colour bands; lateral and ventral views. NMP L 10377, × 0.7. All specimens were immersed in alcohol before photographing.**

patterns. Concerning the species of *P. pulchrum* he noted: "... there are longitudinal brick-red color bands which appear equally distributed on all sides of the conch." However, the opposite - dextral side of this specimen shows indications of zigzags. This striking asymmetry of colour markings has also been found in some other specimens, but more typical for this species are zigzags present on the entire circumference. In this paper the colour pattern in Silurian *Peismoceras* is re-examined and discussed in detail. In addition, unusual shell abnormalities, one of which affects shell coiling and colour pattern, are described.

Specimens studied are deposited in the palaeontological collection of the National Museum, Prague (abbreviation NMP), Naturhistorisches Museum, Wien, and Museum of Comparative Zoology, Harvard University.

DESCRIPTION OF COLOUR PATTERN AND SHELL ABNORMALITIES IN *PEISMOCERAS*

A relatively rich material representing about 40 specimens of *P. pulchrum* and displaying colour pattern at least on fragments of the shell has been studied. All specimens come from the Silurian (Gorstian), Kopanina Formation, *C. colonus* Zone, locality Na břekvici near Praha-Butovice, Central Bohemia (see Kříž et al. 1993). The specimens are preserved in dark grey cephalopod limestone, rich in pyrite, forming horizon with nodules embedded in calcareous shales and particularly tuffite.

Discontinuous longitudinal bands oblique to the shell axis appear in the younger growth stages, but such colour pattern persists later only rarely. They represent in fact one part of the zigzag pattern, while the second part forming an angle is suppressed (1E,G). Later growth stages and adult specimens of *P. pulchrum* show usually regular zigzag bands across the whorl. They are best preserved in specimen NMP L 27400 (Fig. 1A,B,H–J). Brownish bands are about 1-1.5 mm wide in the adapertural region of adult specimens. The interspaces between individual bands are about twice as wide laterally, but almost of the same width as bands dorsally and ventrally. In contrast to recent full-grown *Nautilus* specimens, they are present on the entire circumference of the shell and they reach the apertural margin.

In one specimen of *P. pulchrum* (NMP L 27406) very unusual abnormalities of the shell have been found. They are expressed in marked changes of coiling followed by strikingly anomalous growth of the shell. Since the shell of this specimen also shows a colour pattern, it was possible to study changes of the feature during anomalous growth. Similarly to recent *Nautilus* (e.g. Ward 1987), sublethal damage in fossil ectocochleate cephalopods is very common and was discussed in detail e.g. by Mapes & Chaffin (2003), Keupp (2006), Klug (2007) and further references therein. Sublethal damage is usually expressed by local anomalies of growth lines forming a small "lobe" directed adapically or a narrow, deep scar. It reflects small injuries of shell margin during the growth caused either mechanical damage of the shell or, probably much more commonly, by predator attacks. Evoked secretion activity of mantle margin caused rapid healing of the shell margin. Growth lines in the repair of the damaged section are initially widely spaced

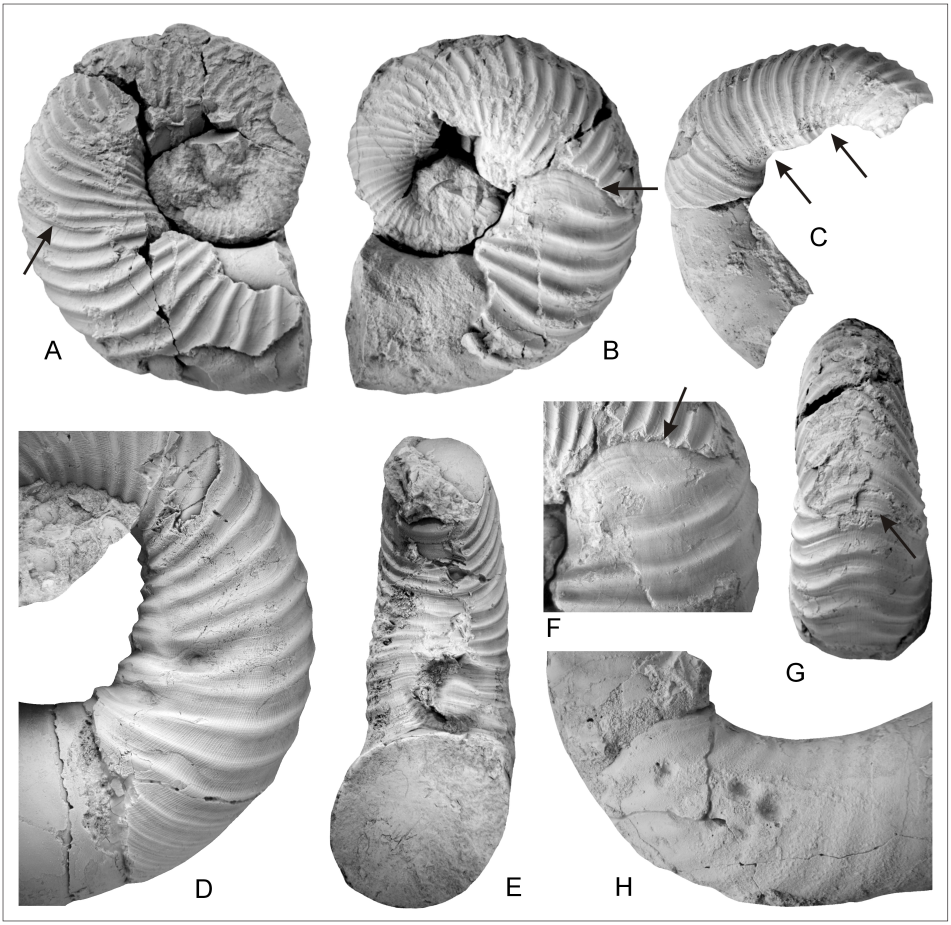

Fig. 2. A, B, F–H. *Peismoceras asperum* (Barrande, 1865). Gorstian, Kopanina Formation, *S. chimaera* Zone. A, B, F, G – Vyskočilka, Praha, Bohemia. Incomplete specimen with preserved shell, heavily damaged in adapertural part of phragmocone (indicated by arrows). A, B – lateral views, G – ventral view, × 1.1; F – repaired part of shell, detail, NMP L 27406; × 1.5; H – Loděnice – Sedlec. Part of whorl, internal mould with pits situated laterally in adapical part of body chamber, NMP L 40801, × 0.9; C–E. *Peismoceras pulchrum* (Barrande, 1865). Gorstian, Kopanina Formation, *C. colonus* Zone, Na břekvici, Praha, Bohemia. C, E – part of whorl showing anomalous growth of shell (cf. Fig. 1F); C – lateral view, × 0.8; E – dorsal view, × 1.5; NMP L 27406; D – pits situated dorsolaterally on shell in adapertural part of phragmocone, NMP L 8056, × 1.7. All specimens whitened with ammonium chloride before photographing.

and follow the contour of damaged edge. As this damaged section is filled in, growth lines gradually resume their normal course. Besides small healed bites well expressed in the course of growth lines in *Peismoceras*, rather frequent (about 10% of population) depressions irregular in shape occur in the umbolateral and lateral regions and on the inner (dorsal) side of the whorl (Fig. 2D,H). They are well expressed both in internal mould (NMP L 40801, NMP L 27399) and outer surface (NMP L 8056).

Shell abnormalities reflecting in a change of spiral coiling or non-uniform growth of the shell are rare. In specimen NMP L 27406 (Fig. 1G, 2C,E) two such shell abnormalities appear. The more obvious one is approximately at the midpoint of the last whorl. Laterally viewed, the spirally coiled shell shows a striking change of growth. The axis here is only very slightly curved in a length of about 20 mm. Then follows a "knee bend" of the shell. Swelling accompanying the first change of the axis course is followed by a constriction of the shell. This anomalous growth is especially well seen on the dorsal side, where there are two immediately adjacent imprint zone depressions, one partially curving around the other. Shell of *P. pulchrum* is generally loosely coiled, with no or very shallow imprint zone. However, in NM L 27406, the plane of the early growth whorl is almost perpendicular to the remainder. The imprint zone crosses the plane of the second whorl almost perpendicularly to shell coiling. It means that the shell growth of the juvenile spire had quite different orientation than the second whorl – the mode of growth resembling growth of shells in some heteromorph Mesozoic ammonoids (Fig. 3). Temporary straightening of the shell axis accompanied by swelling of the shell was probably constrained by anomalous coiling of the first whorl, which formed an obstruction, preventing regular growth of the shell in a logarithmic spiral.

Though a colour pattern is developed on almost the whole circumference of the shell, the best visible portion is on the dextral side of the shell. On the internal side of the whorl, in place of imprint zone, it is not present. The colour pattern is characterized by spiral bands running laterally almost concordantly to the shell axis. Fading indications of zigzags have been observed ventrolaterally in a swollen part of the shell. Bands are also present on the internal (dorsal) side of the whorl. No marked change in the course of brownish bands has been observed in the part of anomalous growth of the shell. In a place of "knee bending" some irregularities and anastomozies between bands appeared. Shell sculpture here shows only a minor anomaly expressed as an indication of bifurcation of the rib.

About the cause of the anomalous growth in juvenile whorl we can only speculate. Damages, which could reflect in anomalous growth of the shell in *Peismoceras*, have been observed especially on the internal side of the whorl. Even thought the shell of *P. pulchrum* is loosely coiled, the space between the whorls is very limited and it seems unsuitable for predator attack. Therefore, attack of some unspecified parasite is considered.

A remarkable large-scale healed injury, rather rare among Early Palaeozoic nautiloids, has been found in the adapertural part of phragmocone of a specimen of *P. asperum* (NMP L 40800). This specimen originating from an old collection comes from the Kopanina Formation, *S. chimaera* Zone, Gorstian, probably from locality Praha-Malá Chuchle, Vyskočilka. It resembles some healed injuries in Mesozoic ammonoids described by Keupp (2006). While ribs show only minor anomaly in their course in right flank and ventrally, appearance of the shell in the left flank is quite different (Fig. 2A,B,F,G). The crack is, however traceable along the entire circumference of the shell, except for the unprepared inner part of the whorl. Along the whole left side it is a loss of a portion of the

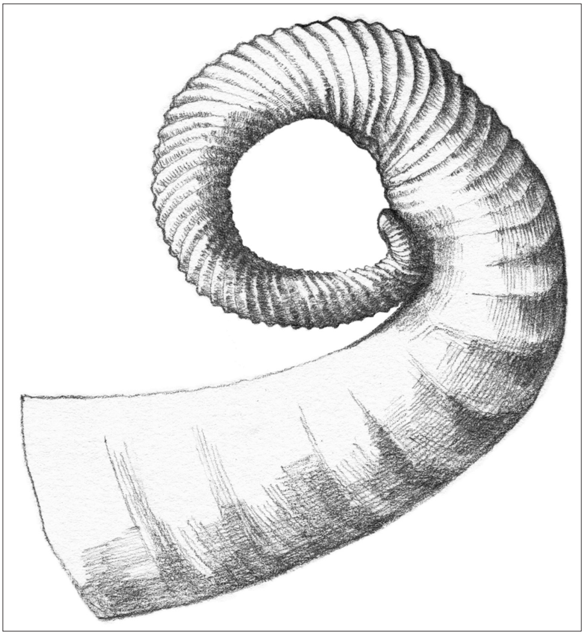

Fig. 3. Reconstruction of anomalous shell of *Peismoceras pulchrum* (Barrande, 1865). Based on specimen NMP L 27406; colour pattern omitted. Drawing by Jan Sklenář.

shell in the form of a wide lobe. The healed part of the shell shows more widely spaced ribs making a sharp angle with previously formed ribs. The last rib before the injury forms an angle of about 30º with the diameter of the shell (measured in the central part of lateral side) and pass to dorsal side, the first rib after the damage is almost transversal and dorsolaterally disappeared.

The character of this injury indicates the pressure action from both lateral sides. Other cephalopods, especially very common orthoceratoids are considered to be probable predators causing this damage. Frequently co-occurring phyllocarid of the genus *Ceratiocaris* are also thought of as potential animals capable of breaking cephalopod shells.

Turek (1990) mentioned densely spaced longitudinal bands on the ventral side of one specimen of *P. asperum* (Barrande, 1865) but the specimen has not been yet illustrated. It comes from Barrande's collection from the locality Praha-Malá Chuchle (Vyskočilka). The specimen is preserved in dark grey cephalopod limestone forming in Vyskočilka Section a distinct limestone bank in calcareous shales of the Kopanina Formation, in early *S. chimaera* Zone in age, Gorstian (Manda & Kříž 2007). Character of the colour pattern observed on the fragment of the shell (Fig. 1C,D) is similar to what has been observed in the ventral region of some specimens of *P. pulchrum,* but the zigzag course was not observed. The bands are about 1 mm wide and the interspaces separating them are almost the same width. Spiral bands frequently passing into zigzags seems to be characteristic for the genus, although we have not found any traces of colouration in other species of *Peismoceras.* It is noteworthy that *P. pulchrum* and *P. asperum* are closely related succeeding species comprising probably an ancestor-descendent line; it is a segment of one of the best evolutionary lineages of tarphycerids traceable from upper Wenlock to upper Přídolí.

CONCLUSIONS

Peismoceras is the only known distinctly sculptured nautiloid in which a colour pattern has been observed. Scarcity of preserved colour patterns in highly sculptured shells may be explained in different ways (see discussion in Turek 2009); taphonomic conditions are presumed to be the most important agent. Although the shell of this tarphycerid is slightly trochoceracone and this fact had to be expressed in living position of the animal (i.e. slightly sub-vertical shell in life), no relationship of colour pattern to asymmetry of the shell has been observed. Asymmetry in colour pattern in some specimens of *Peismoceras pulchrum* is quite unique.

In addition, *Peismoceras* is the only known barrandeocerid with a preserved colour pattern. Barrandeocerids are considered to be an ancestral line for nautilids including present day *Nautilus* (Dzik & Korn 1992, Turek 2008). However, the shell colouration in fossil as well as recent nautilids, i.e. various transversal or subtransversal bands (references see Kobluk & Mapes 1989), strongly differs from *Peismoceras*. On the other hand the zig-zag bands in *Peismoceras* resemble shell coloration in Devonian oncocerid *Ptenoceras* with coiled shell (Turek 2009). Shell coloration, believed to serve a protective function as camouflage (e.g. Cowen et al. 1973), may in many cases represent adaptive convergences, i.e. nautiloids with similar shell form exhibit similar shell colouration (see discussion in Manda & Turek 2009). However, zig-zag colour bands are known only among Early Palaeozoic cephalopods.

Small healed injuries, probably caused by a predator rather than a mechanical agent are very common in *Peismoceras* and indicate a high frequency of predator attacks. Due to preservation of the material in the cephalopod facies, post-mortem phenomena cannot be reliably separated from lethal predation attacks. The most probable predators seem to be either other nautiloids or orthoceratoids; other known co-occurring potential attackers include only phyllocarids of the genus *Ceratiocaris*. Two exceptional heavy shell sublethal damages observed document high regenerative capacity of this tarphycerids. Depressions irregular in shape occurring in the umbolateral and lateral regions and on the inner side of the whorl were probably caused by a parasite attack – a case only occasionally found in fossil nautiloids. The anomalous shell growth observed in one specimen of *P. pulchrum* is unique. It shows a marked change of the plane of spiral coiling and subsequent anomalous growth of the shell. It certainly negatively influenced mobility by increasing the drag coefficient of the animal. Survival of such an anomaly confirms that this species, despite having well-developed hyponomic sinus, was nectobenthic.

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