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Minute Silurian oncocerid nautiloids with unusual colour patterns

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A minute Silurian oncocerid *Cyrtoceras pollux*, from the Prague Basin is assigned here to the genus *Pomerantsoceras*. The only so far known species of this genus comes from the Upper Ordovician (Hirnantian) of Estonia. *Pomerantsoceras* thus represents, except for un-revised poorly understood taxa, the single known oncocerid genus surviving the end-Ordovician extinction events. *Cyrtoceras pollux* is unusual among the Silurian nautiloids because of its small shell. Colour pattern characterised by a few longitudinal bands on the entire circumference of the shell is here reported in oncocerids. Longicone and only slightly curved small shells as in *Pomerantsoceras* are unusual among nautiloids and resemble straight shells of orthocerids and pseudorthocerids, in which the colour pattern consists of straight colour bands. Consequently the shell shape as well as the colour pattern should be regarded as adaptive convergence with orthocerids and pseudorthocerids. It supports the hypothesis that colour pattern functioned as camouflage and its evolution was under adaptive control. In addition, several types of the shell malformations including anomalous growth of septa, shell wall and pits on an internal mould are described.

Key words: Cephalopoda, Nautiloidea, taxonomy, colour pattern, shell size, shell malformation, Silurian.

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Introduction

The extraordinarily highly diverse Silurian cephalopod faunas from the Prague Basin are well known since the seminal work of Barrande (1865–1877) who described 939 species assigned to 11 genera. Hyatt (1883–1884, 1900) started a first generic revision of these widely interpreted genera basing his work primarily on conch shape. It should be noted, that with a few exceptions Alpheus Hyatt and subsequent authors based new genera or revised generic assignments of Barrande's species on descriptions and figures from his work (see Turek 2007, 2008; Manda 2007, 2008). Revisions based on Barrande's types as well as on newly collected material with good biostratigraphical control began with Horný (1956), followed by Marek (e.g., 1971), Turek (e.g., 1975, 1976) and others (see Gnoli 1997). More than one hundred years after printing of Barrande's "Système Silurien du Centre de la Bohême" the majority of the Lower Palaeozoic cephalopods (except goniatites; see Chlupáč and Turek 1983) remain un-revised.

During new research of the Wenlock–Ludlow boundary strata and the Ludfordian Kozlowskii Event, unusually small conchs described by Barrande (1866) as *Cyrtoceras pollux* and *Cyrtoceras pollux* "var. *castor*" were collected. Re-examination of the type material confirms Barrande's (1866) opinion that both taxa represent a single species, which is assigned herein to the genus *Pomerantsoceras* Kröger, 2007 with type species *Pomerantsocera tibia* Kröger, 2007 from the Hirnantian, Upper Ordovician of Estonia. By assigning the Silurian species *Cyrtoceras pollux* to the genus *Pomerantsoceras* it appears that it is the single known oncocerid genus that crosses the Ordovician–Silurian boundary. In addition, the colour pattern and several types of shell malformation have been discovered in *Pomerantsoceras* of Silurian age, and these features along with the exceptionally small shell of *Pomerantsoceras* are described and discussed herein.

Institutional abbreviations.—CGU SM, Czech Geological Survey, Praha, Czech Republic, collection of Štěpán Manda; NM-L, National Museum, Praha, Czech Respublic (Barrande's types).

Material and terminology

Localities where material was collected are shown in Fig. 1. Conventional orientation of the shell is used in descriptions. Terminology is adopted from Teichert (1964), the terms width, height and shell length are used as defined by Stridsberg (1985). Subclass Nautiloidea is used as defined by Teichert (1988), i.e., including orders Discosorida, Oncocerida, Tarphycerida, and Nautilida. In this concept, straight-shelled cephalopods (order "Orthocerida") previously placed

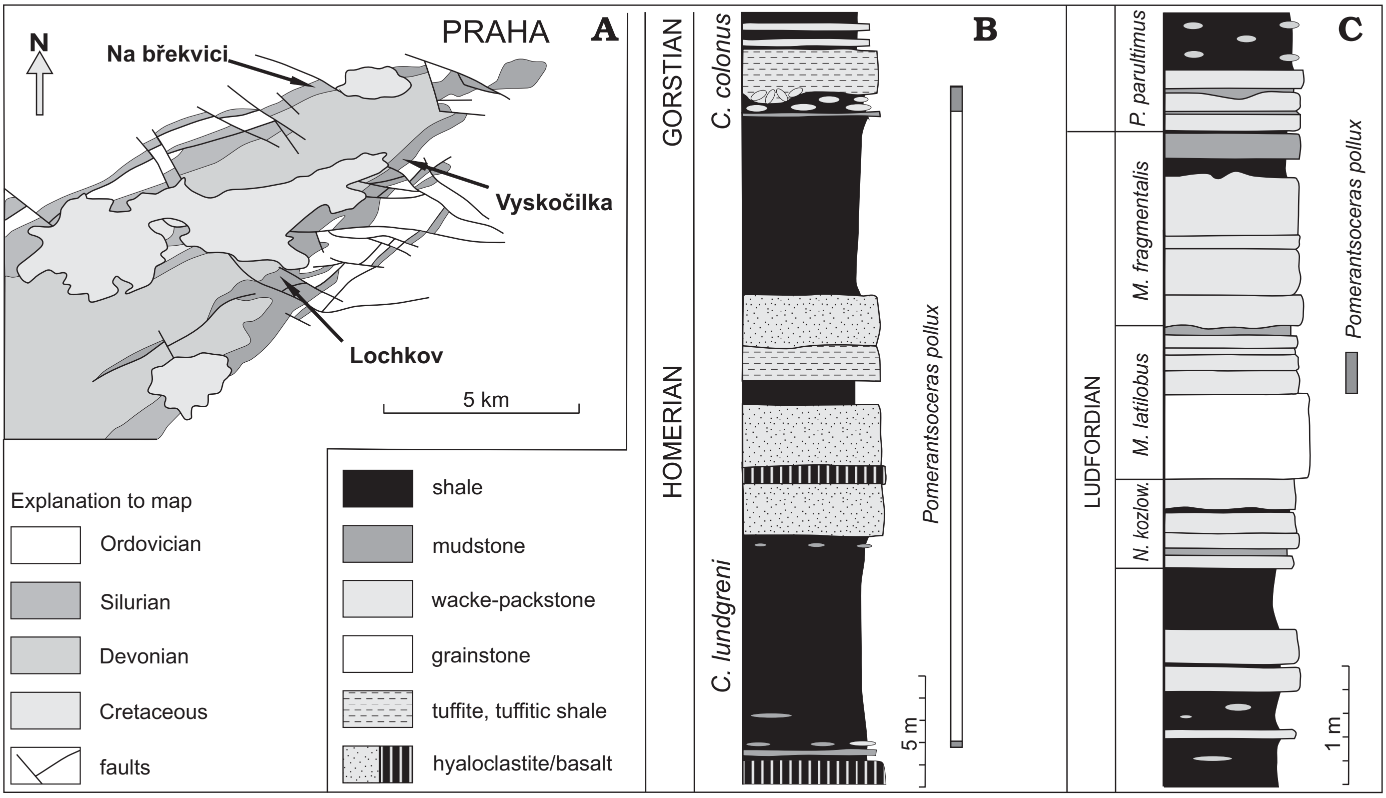

Fig. 1. **A**. Distribution of Silurian rocks in the eastern part of the Prague Synform and position of named localities (see Kříž 1992, Röhlich 2007). **B**. Butovice, Kační Quarry-Na břekvici Section, stratigraphy, graptolite zones, lithology (adopted from Kříž 1992, Kříž et al. 1993) and range of *Pomerantsoceras pollux*. **C**. Lochkov, Nad ubikacemi Section, stratigraphy, graptolite zones, lithology and range of *Pomerantsoceras pollux* (Barrande, 1866). Abbreviations: *C. lundgreni*, *Cyrtograptus lundgreni*; *C. colonus*, *Colonograptus colonus*; *N. kozlow.*, *Neocuculograptus kozlowskii*, *M.*, *Monograptus*; *P.*, *Pristiograptus*.

within the Nautiloidea and commonly incorrectly regarded as "nautiloids" are excluded from nautiloids. Consequently, the nautiloids contain cephalopods with similar general morphologies, embryonic development, and ontogeny as the Recent *Nautilus*; thereby providing the term "nautiloids" with a useful sense in relation to palaeoecological studies and examination of long-term evolutionary trends (Manda 2008).

Remarks on nautiloid shell size

The oncocerid *Pomerantsoceras* from the Prague Basin exhibits a small shell size unusual for Silurian nautiloids. Other Silurian genera, including species with small shells, are *Ophioceras* Barrande, 1865, *Calocyrtoceras* Foerste, 1936 (Tarphycerida) and Mandaloceratidae gen. indet. (Discosorida); see Barrande (1865–1877), and Stridsberg and Turek (1997). Estimated shell length of *Pomerantsoceras* in the largest known specimen is 45–50 mm, height 7 mm and length of the body chamber 12 mm. However, identification of gerontic, shells in nautiloids can be sometimes problematic, aperture constriction and rapid decrease in phragmocone chambers length, increasing density of growth lines and wrinkles in the wrinkled layer as well as thickening of the shell near apertural margin are most indicative. But these changes are not shared by all ectocochleate cephalopods (see Turek 1975; Stridsberg 1985, for summary of mature shell modifications see Ward 1987). Thus, small shells may be simply immature specimens and not a distinct species possessing a small shell. Nevertheless, no larger shell of *Pomerantsoceras pollux* was found during the field work. All collected shells are small and their maximal dimension varies only slightly. Moreover, *P. pollux* exhibits a weak but distinct apertural constriction. The last phragmocone chamber in the holotype of *P. pollux* is shorter than others, which also suggests that the specimen may represent a fully-grown shell. For these reasons, the shell of *P. pollux* is regarded as being primarily small at maturity. The majority of mature nautiloid shells occurring in the Silurian of the Prague Basin are markedly larger than *Pomerantsoceras*. To obtain more precise data about nautiloid shell size the largest available specimens of nautiloids co-occurring with *Pomerantsoceras* were measured (Fig. 2).

Pomerantsoceras is the smallest nautiloid in both localities (see Fig. 3) and is probably one of smallest known Silurian nautiloids. The majority of co-occurring nautiloids have much larger shells. The cephalopod assemblage from Praha-Butovice, Na břekvici Section exhibits a rather continuous distribution of shell size. Nautiloids in this locality exhibited a relatively high juvenile mortality of as pointed out by Manda

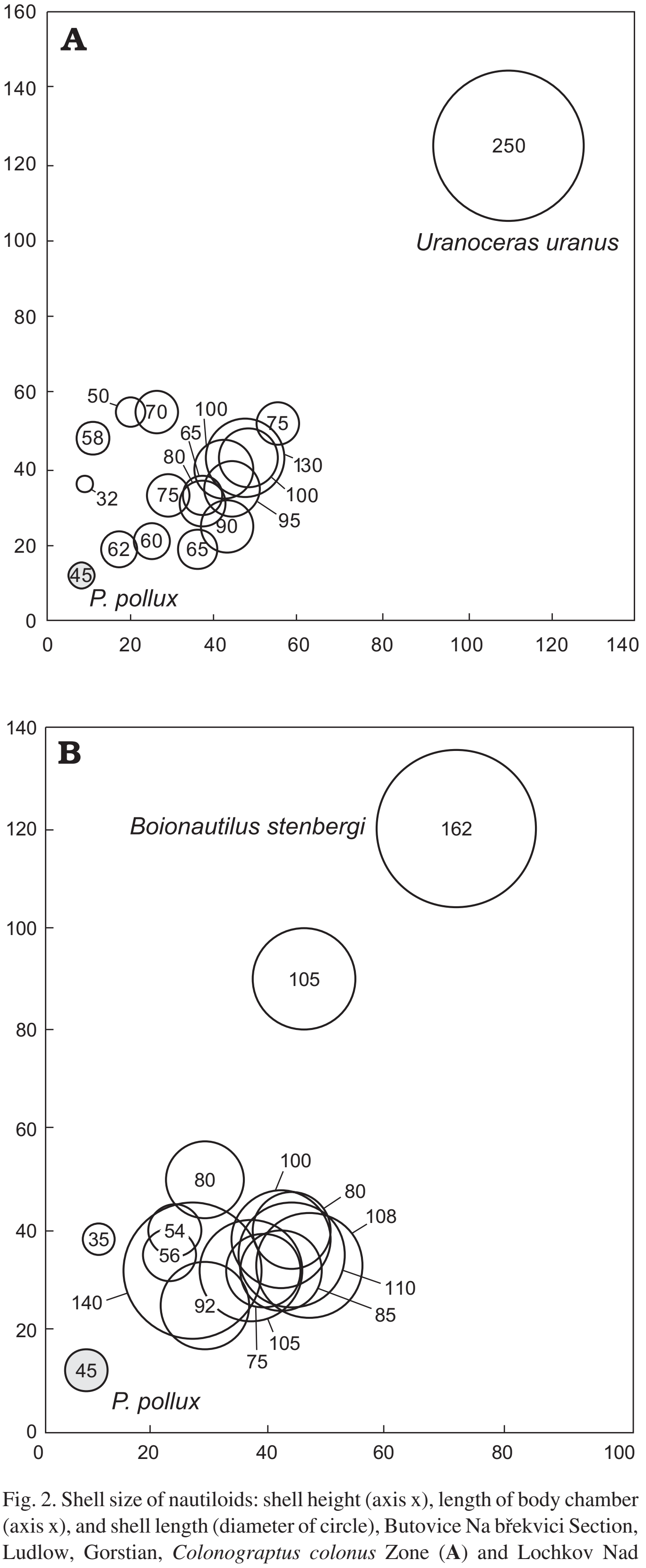

Fig. 2. Shell size of nautiloids: shell height (axis x), length of body chamber (axis x), and shell length (diameter of circle), Butovice Na břekvici Section, Ludlow, Gorstian, *Colonograptus colonus* Zone (**A**) and Lochkov Nad ubikacemi Section, Ludlow, Ludfordian, *Monograptus latilobus* Zone (**B**). Data from Barrande (1865–1877) and author's collection. Note that *Pomerantsoceras* in both assemblages is the smallest nautiloid. The largest present nautiloids, tarpyhcerids *Uranoceras* and *Boionautilus* are all closely related taxa, as suggested by Turek (2008).

(2008) for *Phragmoceras imbricatum* Barrande, 1865. The assemblage inhabited a rather deeper and poorly ventilated environment (less current activity, less oxygenation at sea-floor). This section consists of thin beds of cephalopod limestones intercalated by shales. The assemblage from the Praha-Lochkov, Nad ubikacemi Section occurs in a 40 cm thick bank of light grey cephalopod limestone within a carbonate sequence (Fig. 1). The cephalopod limestone was deposited in shallow well-agitated environment documented by a diverse benthic community including brachiopods, trilobites and corals. The mortality of juvenile nautiloids was low.

Although there are theoretical reasons for selective advantages in having a small size body-shell (for summary see Blanckenhorn 2000), in cephalopods it also means a decreasing fragility of more mature shells against mechanical agents. The majority of nautiloids possess larger more robust shells. It seems that relative rarity of *Pomerantsoceras* suggests that the small shell does not reflect a major selective advance. On the other hand relative stratigraphic longevity of *Pomerantsoceras*, which is unusual among nautiloids, may indicate some adaptive advance of small shell; the type species *P. tibia* appears in the Hirnantian (c. 444 Ma) while *P. pollux* disappeared in the late *Monograptus latilobus* Zone in Middle Ludfordian (c. 420 Ma). Similarly Silurian *P. pollux* in comparison with other Silurian nautiloids from the Prague Basin has a relative long range; appearing in the late Wenlock *Testograptus testis* Zone (c. 425 Ma) and disappearing in the middle Ludlow (c. 420 Ma). Another long ranging species with small and coiled shell is *Ophioceras simplex* (Barrande, 1855), lower Ludlow to latest Přídolí (for data see Stridsberg and Turek 1997). Both *Pomerantsoceras* and *Ophioceras* Barrande, 1865 shared small shell and relative longevity: so if there is a correlation between the shell size and rate of morphological change to stratigraphic longevity it is a promising task for feature study.

Colour pattern of *Pomerantsoceras*

The colour pattern was observed in four specimens which are described separately bellow. The colour pattern is preserved as dark grey or brownish zones on the light-grey re-crystallised shell.

Pomerantsoceras pollux, CGU SM 319, Praha-Butovice, Kační Quarry.—An almost complete specimen but without the dorsal and apical parts of the phragmocone (Figs. 4, 8A). Total shell length is 37 mm, the body chamber is 18 mm long and has a maximum width of 8.5 mm. Shell wall is preserved on the right side of the body chamber and phragmocone and especially on the left side (part of the phragmocone). The colour pattern is well visible on the right flank; on the left it is poorly preserved only on the phragmocone. It is bilaterally symmetrical and consists of six longitudinal colour bands.

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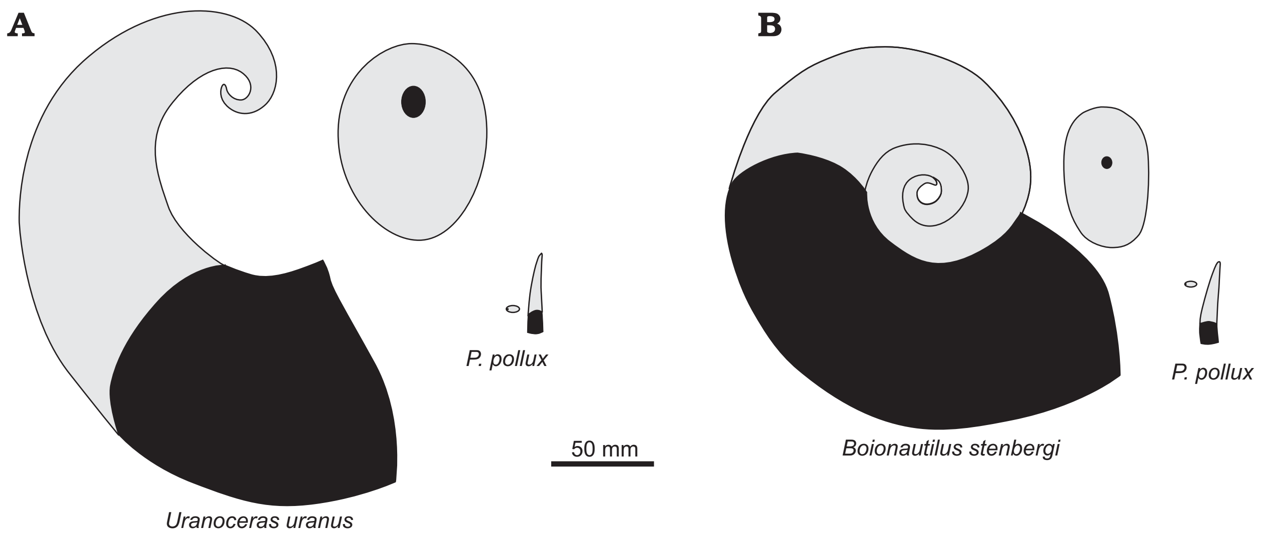

Fig. 3. Comparison of the smallest and largest nautiloids in Butovice Na břekvici Section, Ludlow, Gorstian, *Colonograptus colonus* Zone (**A**) and Lochkov Nad ubikacemi Section, Ludlow, Ludfordian, *Monograptus latilobus* Zone (**B**).

These colour bands occur on the lateral sides and are separated by a narrower zone without colour pigment. The maximal width of colour bands near the aperture is about 3 mm with a maximum distance of about 2 mm on the flanks and the ventral and dorsal un-pigmented zones are about 1.3 mm wide.

Pomerantsoceras pollux, CGU SM 322, Praha-Lochkov, Nad ubikacemi Section.—Incomplete specimen (Figs. 5, 8B) with body chamber with an adjacent part of phragmocone. The shell wall is entirely preserved. Maximum length is 13 mm; the shell height increases from 5 mm to 7 mm. Colour patterning is preserved on the entire circumference of the shell. It consists of four broad colour bands—two lateral and one ventral and dorsal. The colour pattern is bilaterally symmetrical. Width of colour bands increases from 3 to 4 mm. Maximum distance of the lateral colour bands from ventral bands is 1.4 mm and from dorsal bands about 1.8 mm.

Pomerantsoceras pollux, CGU SM 323, Praha-Lochkov, Nad ubikacemi Section.—This fragmentary specimen consists of the body chamber and isolated part of the crushed phragmocone (apical end, few of the youngest septa, part of the venter) (Figs. 6, 8C). Traces of the colour pattern are preserved across whole shell except for a small area on right side of the body chamber. Maximum shell length is 27.5 mm; the height increases from 2 mm up to 6 mm. The colour pattern consists of six bands of almost equal width, three at each lateral side. Width of each band increases from 0.2 to c. 3 mm. Colour bands are separated by slightly narrower zones without pigmentation.

Pomerantsoceras pollux, CGU SM 321, Praha-Lochkov, Nad ubikacemi Section.—Studied specimen consists of body chamber with a part of phragmocone (Figs. 7, 8D). Shell length reaches 20 mm, height increases from 4.5 mm up to 6.5 mm, the body chamber length is 12 mm. Shell is preserved on the left side and particularly also on the right side. Colour pattern is present on the entire circumference of the shell. It consists of three pairs of colour bands which are all about 1.8 mm wide and separated by un-pigmented areas about 2 mm wide on the flanks and about 1.3 mm on venter and dorsum.

Significance of colour pattern of *Pomerantsoceras*—implication for mode of life

The rate of colour pattern evolution is poorly known due to the scarcity of colour preservation in fossil cephalopods (see Foerste 1930). In *Pomerantsoceras pollux* the same type of colour pattern persists (i.e., relatively broad longitudinal bands) from the late Wenlock up to the late Ludlow, an interval spanning about five million years. This suggests relative stability of colour pattern type through time. However, arrangement of colour bands, their width and number varies trough time and even within a palaeopopulation from one locality and bed. The available three shells of *P. pollux* document differing colour band arrangements. In each case the general character, i.e., relatively broad longitudinal colour bands arranged in bilaterally symmetrical pattern is retained. Cowen et al. (1973) pointed out that the colour pattern of Recent *Nautilus* functions as camouflage and together with durable shell structure serves as protection against predators. Later authors (Cowen et al. 1973; but see also Westermann 1998) suggested a similar function for Palaeozoic cephalopods. If this is true, then colour patterns may well be an adaptive feature.

Shells of oncocerids exhibit a complex colour pattern that consists of highly variable zigzag or wave-like ornaments, or a combination of both (Ruedemann 1921; Foerste 1930; Teichert 1964; Kobluk and Mapes 1989; Turek 2009). By contrast, colour pattern of *Pomerantsoceras* consists of longitudinal and relatively broad bands around the entire circumference of the shell.

Data concerning colour patterns in orthoceratoids are still scarce (for summary see Kobluk and Mapes 1989). Longitudinal colour bands present over the entire surface of the shell or only on one side (probably dorsal) seem to be typical for Ordovician and Silurian orthocerids and pseudorthocerids (Ruedemann 1921; Foerste 1930). Colour bands developed only on the dorsal side probably indicates a horizontal position of the shell during life; colour patterns present over the entire circumference of the shell may consequently indicate vertical orientation of the shell during the life of the animal. Longitudinal colour bands, similar to that of *Pomerantsoceras* have been described for example in the orthocerid *Tripterocerina kirki* Foerste, 1935, Upper Ordovician of Wyoming and in Silurian pseudorthocerid "*Orthoceras*" *pellucidum* (Barrande, 1868), Upper Silurian of the Prague Basin (Barrande 1868, Foerste 1930, see also Teichert 1964).

The slightly curved shell of *Pomerantsoceras* resembles the straight or slightly curved shells of orthocerids or pseudorthocerids. Its small shell with low angle of expansion, markedly vaulted septa, absence of cameral deposits, missing traces of hyponomic sinus, and body chamber shorter than phragmocone suggests that *Pomerantsoceras* was a nautiloid with vertically oriented shell, probably pelagic. The vast majority of oncocerids, however, shared demersal habit. It should be pointed out that rather rarely occurring *Pomerantsoceras* has been found in limestones deposited both in shallow and relatively deeper water where no other nautiloids occur (e.g., Praha-Butovice, Kační Quarry; Praha-Malá Chuchle, Vyskočilka Section). Similar distribution pattern occurs among pelagic orthoceratoids, which are usually relatively common. By relative longevity *Pomerantsoceras* also resembles pelagic orthoceratoids comprising usually long-ranging taxa. The shell and colour pattern of *Pomerantsoceras* probably reflect adaptive convergence with some orthocerids and pseudorthocerids with shells oriented vertically during life (Mutvei 2002). Appearance of longitudinal colour bands in *Pomerantsoceras* further supports the suggestion of Cowen et al. (1973) that colour patterns had a protective function and their evolution was adaptive.

Shell malformations in *Pomerantsoceras*

Minute malformations of shell due to the damage of the apertural margin in a living individual are very frequent in Recent and fossil nautiloids and subsequent healing of the shell can often be traced on the shell surface. Sublethal and pathological damage to the shell expressed as anomalies in the growth of the shell and the malformed development of septa have been only rarely documented (e.g., Barrande 1866: pl. 118: 1; Strumbur 1960; Keupp and Mitta 2004; Kröger and Keupp 2004; Klug et al. 2008). The phragmocone is of crucial importance in determining the hydrostatic and hydrodynamic properties of the shell and overall mode of life of the animal. Because septal morphology, including the geometry of the mural ridges and sutures, provide mechanical limits to the depth at which a particular ectocochleate cephalopod could survive without the phragmocone imploding (Hewitt and Westermann 1987) serious damage to the phragmocone was likely to have been lethal to the animal. *Pomerantsoceras* with its small shell was highly vulnerable and despite limited amount of material, four different kinds of malformations have been found.

The holotype of "*Pomerantsoceras castor*" (NM-L 571, Fig. $9C_1$) displays a striking anomaly in the arrangement of septa in the adapertural part of the phragmocone, which was not documented on Barrande's illustrations (1866: pl. 184: 20–23). Abrupt change of course in the suture lines appears in the seventh septum (counted from the body chamber towards the apex). A broad lateral lobe changed into a parabolic lobe. During subsequent growth the septa returned to their normal growth pattern so that the course of last three sutures was not affected by this injury. The anomalous growth of septa in this part of the shell was caused by a sublethal crush to the body chamber in the mid-lateral region of aperture. It is indicated by mid-lateral longitudinal depression shallowing adaperturally. During subsequent shell growth and shifting the body adaperturally, the animal secreted new septa in a narrowed internal space resulting in their change of convexity. Due to exfoliation of the shell in this part of phragmocone, superficial manifestation of this injury could not be observed.

In addition to the anomalous growth of septa, a pair of pits has been observed on internal mould of the last phragmocone chamber in the same specimen. Another larger pit, partially filled with shell material (sparitic calcite), is recognisable on the right side of the shell in the adapical part of the body chamber (see Fig. $9C_2$). No depression is indicated on the cross section of the shell of this single pit. These pits probably correspond to a marked local thickening of the shell wall. This phenomenon was described in detail by House (1960) and Chlupáč and Turek (1983) in Devonian goniatites (see also Klug 2002; Korn and Klug 2002); rather rarely it occurs in nautiloids (e.g., Stridsberg and Turek 1997). House (1960) explained the pitting as pearl-like growth mounds or deposits due to irritation of the mantle by foreign particles that penetrated between mantle tissue and the shell of the animal.

A distinct growth anomaly has also been observed in specimen CGU SM 318 (Fig. 9A). The adapical part of the internal mould of the body chamber is laterally folded to form a false rib. Adaperturally, the internal mould regained its normal smooth form. Due to the absence shell of the body-chamber, the character of injury causing this malformation cannot be determined.

A fragment of the adapical part of the body chamber (CGU SM 316, Fig. 9B), preserved as an internal mould, shows marked elevation situated almost mid-ventrally. It is bordered on both sides by deep furrows. The straight course of this elevation is strikingly disrupted adaperturally probably due to damage of the shell in this part of the body chamber. Morphology of this structure markedly changed here. Instead of elevation there is a mid-ventral groove bordered by relatively wide

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elevated zones. The structure resembles conchal furrow, which may be single or double (Teichert 1964). Conchal furrows, located in the mid-ventral part of the phragmocones and the body chambers of ectocochleate cephalopods, were recently discussed in details by Chirat and von Boletzky (2003) and Klug et al. (2008). According to Chirat and von Boletzky (2003: 167) it represents a taxonomically unimportant developmental by-product originating "from the inner part of the initial, calcified shell apex, in line with the ventral termination of the central linear depression of the cicatrix". However, it should be noted that observed conchal furrow in all members of the family Oonoceratidae, to which *Pomerantsoceras* is here assigned, forms a single shallow depression. Finding the conchal furrow in only one specimen of *Pomerantsoceras* is not surprising as it corresponds to the low frequency of occurrence of this structure at nautiloids (Chirat and von Boletzky 2003). However, it seems more probable that the specimen described here does not display the conchal furrow but rather a malformation caused by an injury inflicted to the mantle margin. This malformation caused the formation of an irregular trace ("Rippenscheitelung"; compare Hengsbach 1996; Keupp 2006) as known from Recent nautilids, ammonoids and bactritoids (Klug 2007).

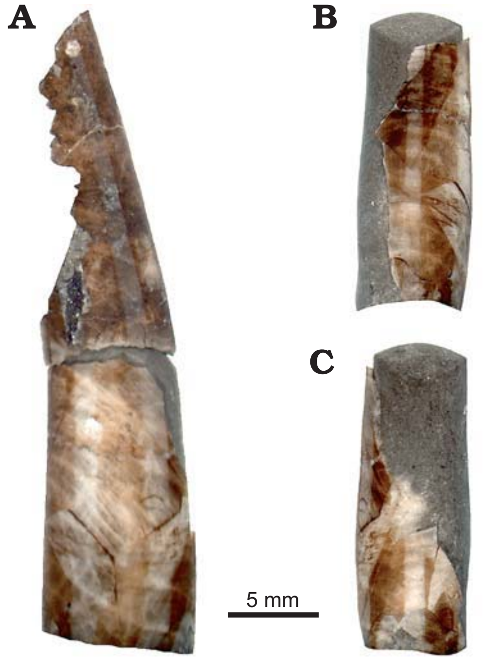

Fig. 4. *Pomerantsoceras pollux* (Barrande, 1866). Specimen CGU SM 319, the body chamber, in lateral (**A**), ventral (**B**), and dorsal (**C**) views. Kační Quarry, *Testograptus testis* Zone, Homerian, Wenlock. Photographed in alcohol.

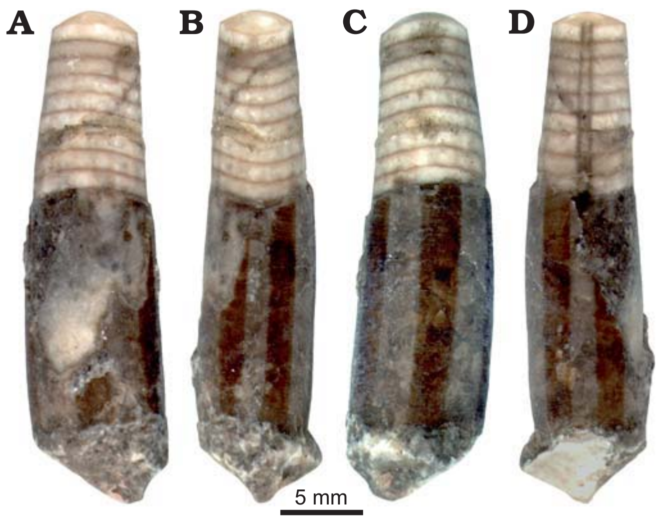

Fig. 5. *Pomerantsoceras pollux* (Barrande, 1866). Specimen CGU SM 322, in lateral (**A**, **C**), dorsal (**B**), and ventral (**D**) views. Lochkov, Nad ubikacemi Section, *Monograptus latilobus* Zone, Ludfordian, Ludlow. Photographed in alcohol.

Systematic palaeontology

Subclass Nautiloidea Agassiz, 1847

Order Oncocerida Flower, 1950

Family Oonoceratidae Flower, 1942

Emended diagnosis.—Oncocerids with an exogastrically cyrtoconic shell; shell curve varies only slightly within an species; siphuncle without deposits, marginal, in later ontogenetic stages slightly sub-marginal; phragmocone chambers are low; suture with broad lateral lobes; hyponomic sinus usually well developed; body chamber relatively short, slightly longer than wider; cross section laterally compressed. Embryonic shell is cup-like, early shell is less curved than adult shell.

Discussion.—Family Oonoceratidae was erected by Flower in 1942, but no diagnosis was given by him. Flower (1942) included three genera in the family, namely *Richardsonoceras* Foerste, 1933 (Ordovician), *Oonoceras* Hyatt, 1884 (Silurian–earlier Devonian), and *Oocerina* Foerste, 1926 (Silurian). However, *Oocerina* in fact belongs to the family Jovellaniidae Foord, 1888 (see Manda 2001). Sweet (1964) synonymised the Oonoceratidae with Oncoceratidae Hyatt, 1884. The diagnosis of the latter family, as refined by Frey (1995), suggests that *Oonoceras* and allied genera cannot by placed here. Late Ordovician species assigned by Flower (1942) to *Oonoceras* probably belong to another genus because they differ from *Oonoceras* in having long body chambers, almost straight sutures and very thin siphonal tubes. The phyletic relationship between *Richardsonoceras* and *Oonoceras* proposed by Flower (1942) and followed by Dzik (1984) is still unclear.

In our view, the family Oonoceratidae contains only *Oonoceras* (Silurian and earlier Devonian) and its allied genera. It should be noted that the majority of taxa are known from the Silurian of the Prague Basin, where the family reached its maximal diversity as well as disparity. New material shows that species grouped within *Oonoceras* in fact belong to other, still undescribed, genera that differ in shell curvature, cross section, sculpture and ratio of phragmocone/body chamber length. At last, two morphologically convergent groups of oncocerids with exogastrically curved shells exist. The Silurian jovellaniids including *Oocerina* differs from oonoceratids by the presence of actinosiphonate deposits. Similarly, Ordovician *Richardsonoceras*–"*Oonoceras*" (sensu Flower 1942) and Silurian *Oonoceras* may represent convergent morphotypes of oncocerids. However, without data concerning early shell ontogeny, the systematic position of *Richardsonoceras* and allied forms remain unclear.

Genera included.—*Oonoceras* Hyatt, 1884 (Silurian, earlier Devonian), *Pomerantsoceras* Kröger, 2007 (latest Ordovician, Silurian), *Pleziorizoceras* Chen, 1981 (middle Silurian), *Shuranoceras* Barskov, 1959 (Silurian).

Genus *Pomerantsoceras* Kröger, 2007

Type species: *Pomerantsoceras tibia* Kröger, 2007. Latest Ordovician of Estonia.

Discussion.—Kröger (2007) placed his new genus in the family Graciloceratidae Flower, 1950. Unfortunately, *Graciloceras* Flower, 1943 (Middle–Late Ordovician) is a poorly known genus. The type species *Graciloceras longidonum* Flower, 1943 has a small exogastric slightly curved shell with relative high expansion rate, moderately compressed cross section, sub-ventral siphuncle, very weakly vaulted septa, and body chamber longer than the phragmocone. The shell of *Pomerantsoceras* expands with a markedly lower angle and during its late growth stage, the angle of expansion further decreases. Its cross section is much more laterally compressed, siphonal tube is in contact with the venter, septa are deeper, and body chamber is markedly shorter than the phragmocone. The sutures of *Pomerantsoceras* consist of broad lateral saddles separated by dorsal and ventral lobes, the ventral being deeper. These morphological features resemble early stages of cephalopods assigned to the genus *Oonoceras* Hyatt, 1884 (Silurian). Consequently *Pomerantsoceras* is transferred to family Oonoceratidae Flower, 1942.

Pomerantsoceras strongly resembles *Pleziorizoceras* Chen, 1981 from the middle Silurian of China (Chen et al. 1981) which is distinct in having shallower lateral lobes at well as ventral-dorsal saddles. *Pleziorizoceras ovatum* Chen, Liu, and Chen, 1981 is based on a single specimen, an internal mould of the phragmocone. Thus, information about sculpture and body chamber is missing. It is possible that *Pomerantsoceras* is a junior synonym of *Pleziorizoceras*, but additional information about the latter genus is needed.

Species included.—The type species and *Pomerantsoceras pollux* (Barrande, 1866) from the Silurian of Bohemia.

Pomerantsoceras pollux (Barrande, 1866)

Figs. 4–10.

1866 *Cyrtoceras pollux* Barr.; Barrande 1866: pl. 148: 16–19.
1866 *Cyrtoceras pollux* var. *castor* Barr.; Barrande 1866: pl. 148: 20–23.
1874 *Cyrtoceras pollux* var. *castor* Barrande 1847; Barrande: 487.
1874 *Cyrtoceras pollux* Barrande; Barrande 1847: 526.

Holotype: By monotypy, specimen NM-L 570 figured by Barrande (1866) on pl. 148: 16–19 and refigured here as Fig. 10B.

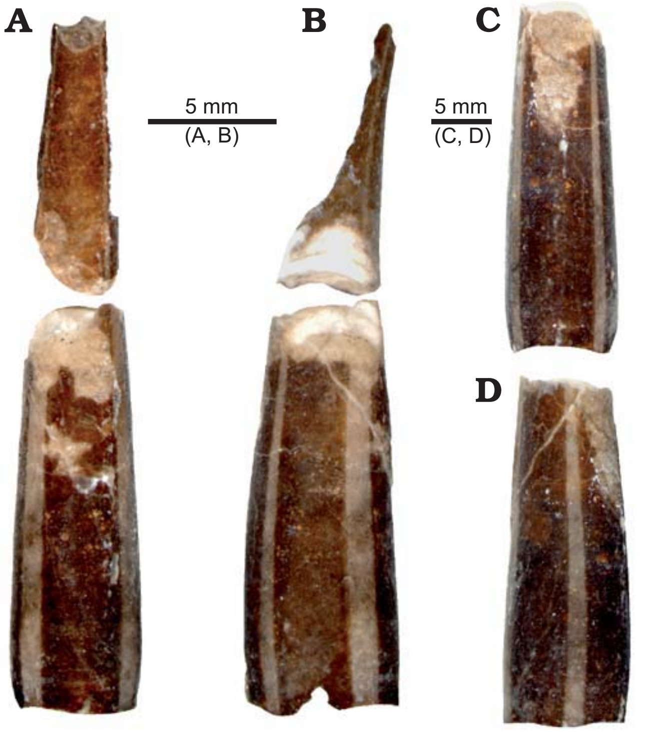

Fig. 6. *Pomerantsoceras pollux* (Barrande, 1866). Specimen CGU SM 323, the body chamber, in dorsal (**A**), lateral (**B**), ventral (**C**), and lateral (**D**) views. Lochkov, Nad ubikacemi Section, *Monograptus latilobus* Zone, Ludfordian, Ludlow. Photographed in alcohol.

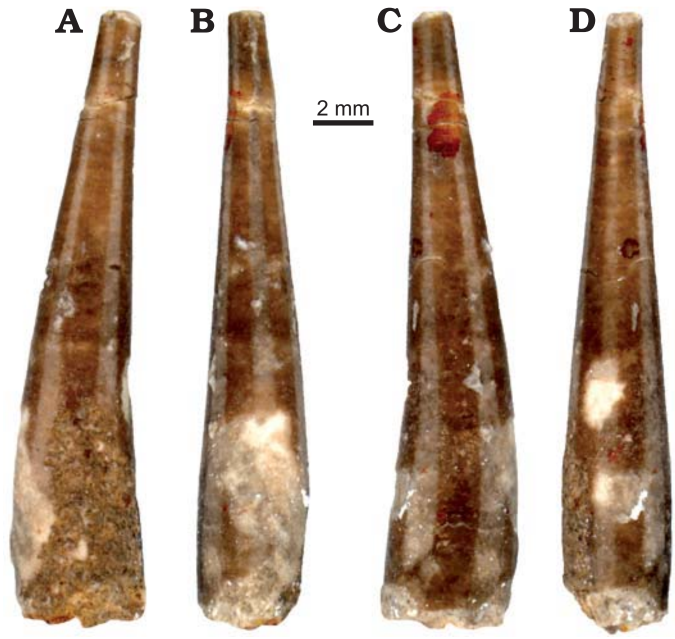

Fig. 7. *Pomerantsoceras pollux* (Barrande, 1866). Specimen CGU SM 321, in lateral (**A**, **C**), ventral (**B**), and dorsal (**D**) views. Lochkov, Nad ubikacemi Section, *Monograptus latilobus* Zone, Ludfordian, Ludlow. Photographed in alcohol.

Type locality: Praha-Malá Chuchle, Vyskočilka e2.

Type horizon: Holotype is a slightly flattened internal mould preserved in dark grey argillite wackestones. Fragments of graptolites and small

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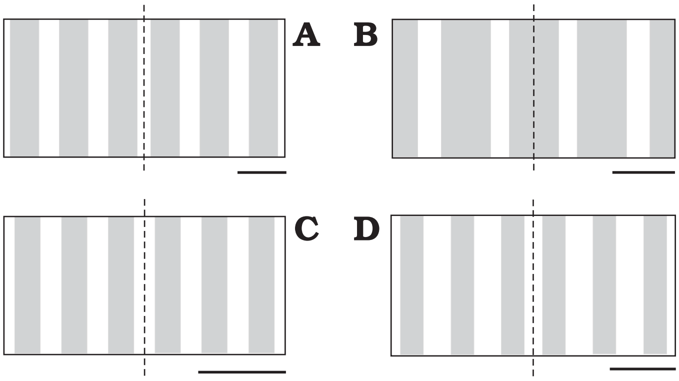

Fig. 8. Sketches of the colour pattern in *Pomerantsoceras pollux* (Barrande, 1866). **A**. Specimen SM 319, Kační Quarry. **B**. Specimen CGU SM 322, Nad ubikacemi Section. **C**. Specimen CGU SM 323, Nad ubikacemi Section. **D**. Specimen CGU SM 321, Nad ubikacemi Section.

shell fragments (juvenile molluscs?) covered by pyrite are visible in the aperture. This mode of preservation is characteristic for the Vyskočilka area in the late Wenlock (Homerian, *T. testis* Zone; unpublished data) and early Ludlow (Gorstian, *C. colonus* and early *L. scanicus* zones; Manda and Kříž 2007) strata.

Material.—Besides the holotype from Barrande (1866), six incomplete specimens with missing apex (NM-L 571, CGU SM 318–323), a body chamber (CGU SM 317), and a fragment of a body chamber (CGU SM 316) are available.

Descriptions.—Shell very slightly curved, exogastric. Angle of expansion low, decreasing with shell growth; in early shell it is about 8°, at fully-grown shell about 4–5°. Cross section elliptical, laterally compressed, height/width ratio varies between 1.2–1.5. Siphuncle ventral, thin with diameter about 0.2 mm at shell height 2.5 mm. Septal necks very short, cyrtochoanitic, connecting rings very thin and very weakly expanding within chambers; on the ventral side they are in contact with shell wall. Suture oblique to the shell axis, with distinct lateral lobes and ventral and dorsal saddles; ventral saddle is deeper than dorsal. Septa moderately concave, with maximum depth is in shell axis; depth of the septa is about 1/5–1/6 of shell height. Phragmocone chambers very low, distance of septa varies only slightly; ratio of shell height and phragmocone chamber length varies between 4.7–6.2. Shell with fine growth lines or smooth. Body chamber relatively short, length of the body chamber is less than 1/4 of shell length. Aperture open, at fully-grown shell very slightly contracted, hyponomic sinus absent. The shell thickness increases up to 0.25 mm (at height 6.8 mm). Maximum measured shell height 7 mm, estimated total shell length 45–50 mm.

Discussion.—Barrande (1866) figured another shell on pl. 148 as figs. 20–23, which he described as "*Cyrtoceras pollux* var. *castor*" (holotype by monotypy; NM-L 571; type locality Butovitz e1, i.e., Praha-Butovice, Na břekvici Section, see Kříž 1992; Ludlow, Gorstian, early *C. colonus* Zone; see Fig. 10A). According to Barrande (1874), "*Cyrtoceras pollux* var. *castor*" differs from *Cyrtoceras pollux* by having a less compressed cross section and slightly deeper ventral and lateral saddles at the suture. The holotype of *Cyrtoceras pollux* is

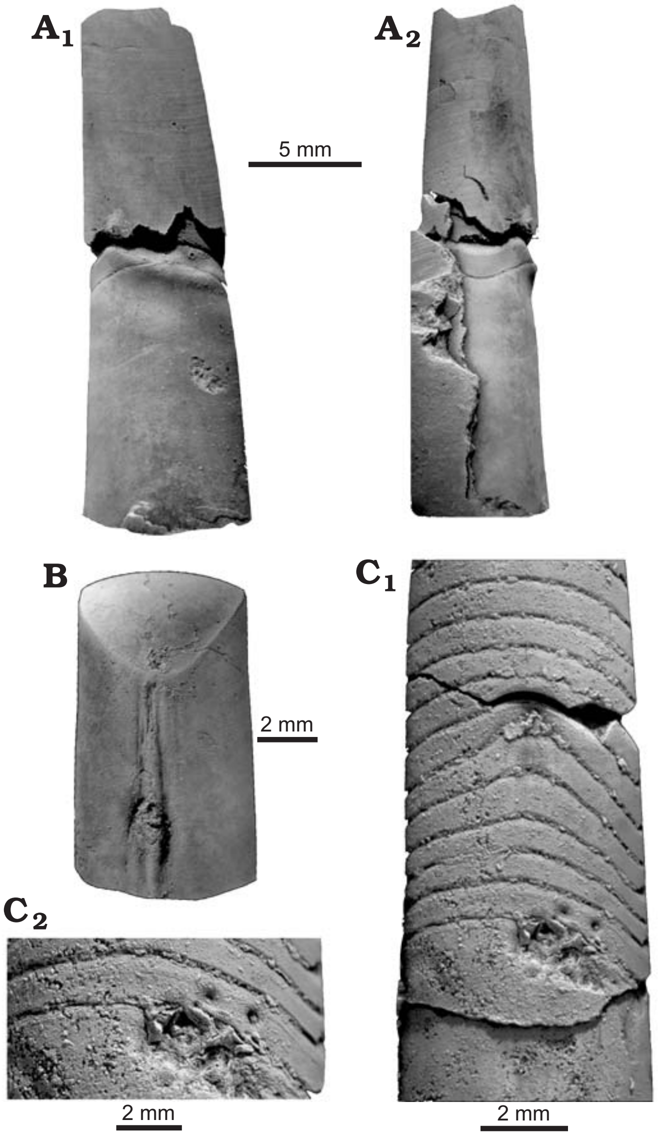

Fig. 9. Shell malformations in *Pomerantsoceras pollux* (Barrande, 1866). **A**. Specimen CGU SM 318 with a false rib at the base of body chamber, in lateral (A_1) and ventral (A_2) views. **B**. Specimen CGU SM 316, body chamber with conchal furrow-like malformation, in ventral view. **C**. Specimen NM-L 571, anomalous septal growth, in lateral view (C_1), and detail of youngest phragmocone chamber with a pair of pits, in lateral view (C_2). All figured specimens come from Butovice Na Břekvici Section, *Colonograptus colonus* Zone, Gorstian, Ludlow. Each specimen is coated with ammonium chloride.

slightly flattened by diagenetic compaction and has slightly deformed original cross section dimensions (Fig. 10B_1). Despite the malformation of the sutures in the adoral part of the phragmocone in the holotype of "*Cyrtoceras pollux* var. *castor"* the sutures and spacing between them are similar in dimension to those in *Cyrtoceras pollux* (Fig. 10A_1). Consequently, suture and cross section differences are the result of shell malformation and diagenesis and thus, "*Cyrtoceras pollux* var. *castor*" is considered synonymous with *C. pollux*.

Silurian species described by Barrande (1866, 1867) as *Cyrtoceras pollux* and *Cyrtoceras pollux* "var. *castor*" exhibit

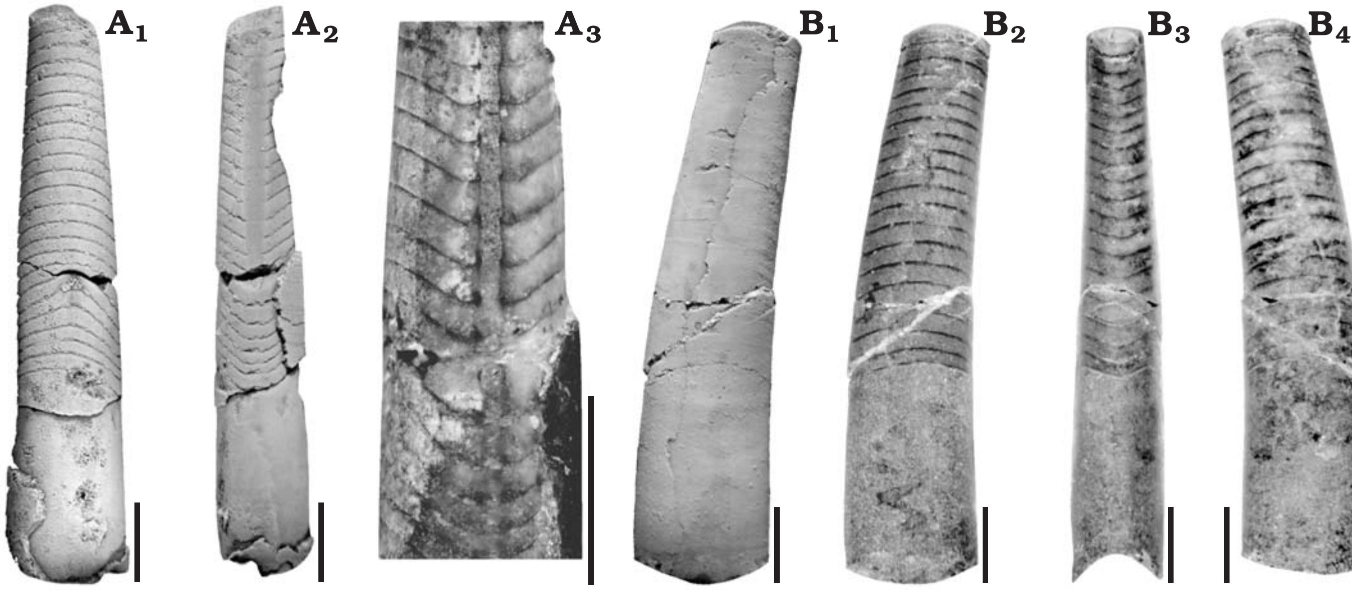

Fig. 10. **A**. Holotype of *Pomerantsoceras pollux* "var. *castor"* (Barrande, 1866). Specimen NM-L 571, in lateral (A_1) and ventral (A_2) views, and detail of the siphuncle (A_3); Butovice Na Břekvici Section, *Colonograptus colonus* Zone, Gorstian, Ludlow. **B**. Holotype of *Pomerantsoceras pollux* (Barrande, 1866). Specimen NM-L 570, in lateral view showing diagenetic rupture of the shell (B_1); and lateral (B_2, B_4) and ventral (B_3) views. Malá Chuchle, Vyskočilka locality, *Testograptus testis*, Homerian, Wenlock. Specimens A_1, A_2, and B_1 are coated with ammonium chloride. Scale bars 5 mm.

a very similar morphology to the Ordovician species *Pomerantsoceras tibia*. These species shared the small slightly curved gently expanding exogastric shell, thin marginal siphuncle, very weakly vaulted connecting rings, laterally compressed shell, relatively short body chamber, very short phragmocone chambers, and sutures with a wide lateral lobe. The Silurian *Pomerantsoceras pollux* differs from *P. tibia* in having cyrtochoanitic rather than achoanitic (see Kröger 2007) septal necks. Despite difference in the shape of septal the necks both of these species are added to genus *Pomerantsoceras*.

Occurrence.—Silurian of the Prague Basin, Bohemia (Czech Republic). Wenlock, Homerian, *T. testis* Zone; Motol Formation; Praha-Butovice, Kační Quarry (Fig. 1, for description see Kříž 1999). Specimen CGU SM 319 was found in a nodule of dark grey cephalopod-graptolite packstone, together with bivalves *Isiola lyra, Cardiola agna*; graptolite *Monograptus flemingi*; and cephalopods *Arionoceras* sp., *Michelinoceras* sp., *Parakionoceras* cf. *originale*, and *Pseudocycloceras duponti*.

Ludlow, Gorstian, *Colonograptus colonus* Zone (i.e., *Neodiversograptus nilsonni* Zone); Kopanina Formation; Praha-Butovice, Na břekvici Section (see Kříž 1961, 1992, 1999; Kříž et al. 1993). Specimens CGU SM 316–318. Cephalopod fauna from this locality was described by Barrande (1865–1977) and perhaps represents the most diverse cephalopod assemblage in the Prague Basin. It includes among others *Sphooceras truncatum*, *Disjunstoceras disjunctum*, *Parakionoceras originale*, *Ophioceras rudens*, *Peismoceras pulchrum*, *Uranoceras uranus*, *Rizoceras robustum*, *Phragmoceras imbricatum*, and *Pseudocycloceras duponti*. Cephalopods occur in nodules of cephalopod wacke-packstone.

Ludlow, Ludfordian, *Monograptus latilobus* Zone; Kopanina Formation; Praha-Lochkov, Nad ubikacemi Section. Specimens of *P. pollux* were found in a 50 cm thick bed of grey cephalopod packsone corresponding with the upper part of "*Ananaspis fecunda* Horizon". Rare bivalves are present which belong to the *Cardiola conformis* Community (Kříž 1998). Among associated cephalopods, *Arionoceras* sp., *Michelinoceras michelini*, *Parakionoceras originale*, *Peismoceras optatum*, *Dawsonocerina dulce*, *Sphooceras* sp., *Pseudocycloceras agassizi*, *Ophioceras simplex*, and *Oonoceras imperiale* are characteristic.

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