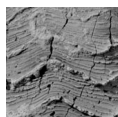


# Revision of the Pragian Rutoceratoidea Hyatt, 1884 (Nautiloidea, Oncocerida) from the Prague Basin

ŠTĚPÁN MANDA & VOJTĚCH TUREK



Superfamily Rutoceratoidea Hyatt, 1884 (Pragian to Frasnian, Devonian) includes nautiloid cephalopods having exogastric cyrtoceracone or coiled shells with periodic walls or raised growth lines (megastriae) forming ridges, sometimes modified in various ways into collars, frills, or different outgrowths. High disparity and intraspecific variability of the shell form and sculpture of the rutoceratoids are conspicuous among Early Palaeozoic nautiloids. Consequently, rutoceratoids are divided according to different patterns of growth structures into three families. Parauloceratidae fam. nov. (Pragian to Emsian) contains taxa with cyrtoceracone shells and simple recurrent ribs with ventral sinus. Family Hercoceratidae Hyatt, 1884 (Pragian to Givetian) comprises forms with periodically raised ridges with three lobes forming ventrolateral outgrowths during shell growth such as wings, nodes or spines. Family Rutoceratidae Hyatt, 1884 (Pragian to Frasnian) encompasses taxa having growth ridges with ventral lobe transforming into undulated frills or distinct periodic collars (megastriae). All of these families had already appeared during early radiation of rutoceratoids in the Pragian. The early radiation of rutoceratoids is, however, adequately recorded only from the Prague Basin. Rutoceratoids become widespread within faunas of Old World and Eastern American realms later during the Emsian and especially Middle Devonian. Three new genera are erected: *Parauloceras* gen. nov., *Otomaroceras* gen. nov. and *Pseudorutoceras* gen. nov. The Pragian *Gyroceras annulatum* Barrande, 1865 is assigned to the genus *Aphytoceras* Zhuravleva, 1974. Rutoceratoids are thus represented by seven genera and eight species in the Pragian Stage of the Prague Basin. In addition, variability of shell coiling among rutoceratoids and its significance for their systematics are discussed. • Key words: Nautiloidea, Oncocerida, Rutoceratoidea, Pragian, new taxa, shell morphology.

MANDA, Š. & TUREK, V. 2009. Revision of the Pragian Rutoceratoidea Hyatt, 1884 (Nautiloidea, Oncocerida) from the Prague Basin. *Bulletin of Geosciences* 84(1), 127–148 (13 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received December 12, 2008; accepted in revised form February 13, 2009; published online March 10, 2009; issued March 31, 2009.

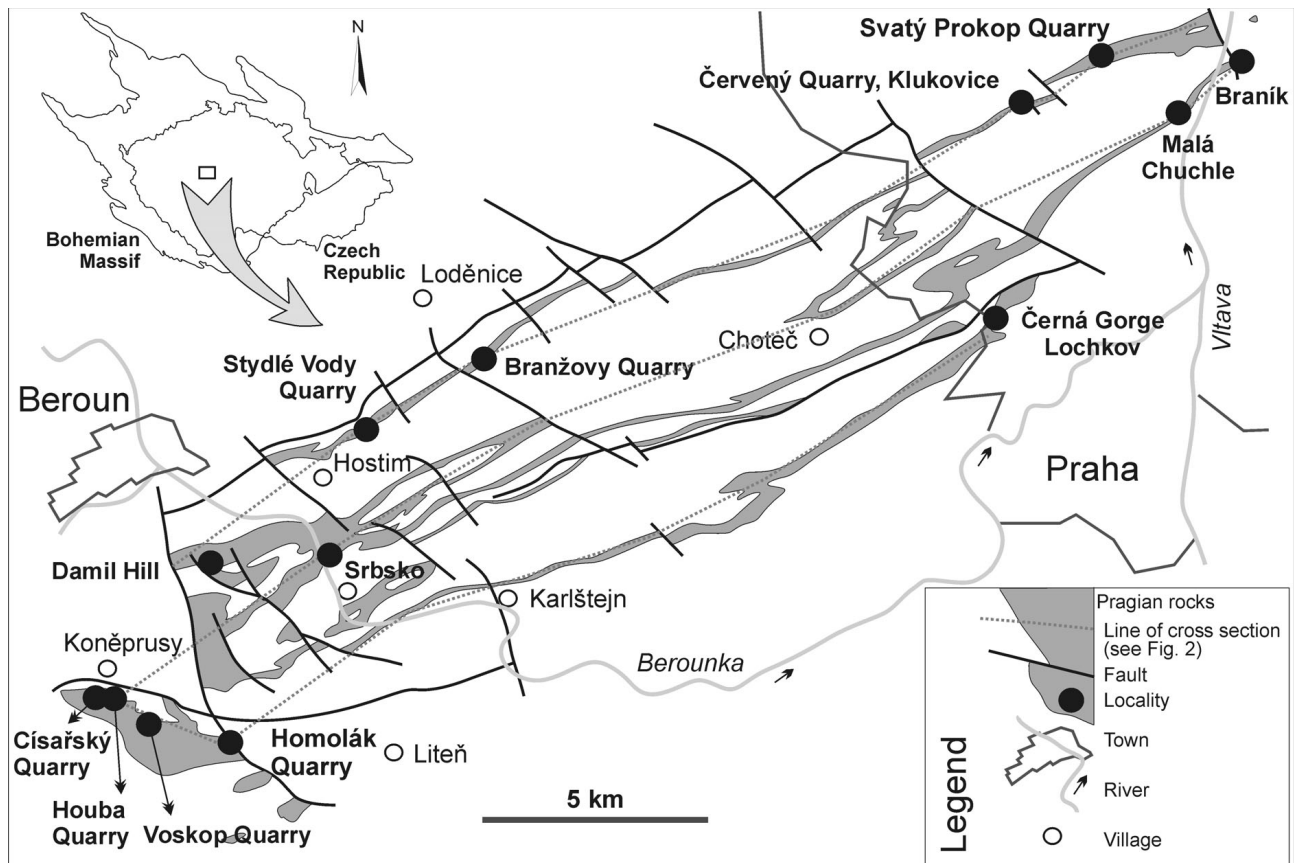
Štěpán Manda, Czech Geological Survey, P.O.B. 85, Praha 011, 118 21, Czech Republic; [stepan.manda@geology.cz](mailto:stepan.manda@geology.cz) • Vojtěch Turek, National Museum, Department of Palaeontology, Václavské náměstí 68, 115 79 Praha 1, Czech Republic; [vojtech.turek@nm.cz](mailto:vojtech.turek@nm.cz)

Like everywhere, cephalopod faunas of the Prague Basin were strongly affected by the extinction at the Silurian-Devonian boundary (one order, one suborder and at last nine families disappeared, see Marek & Turek *in* Kříž *et al.* 1986; Kříž 1998; Manda 2001, 2007). The subsequent diversification of cephalopods from the late Lochkovian to the early Pragian, during which several clades originated, remains poorly understood (Manda 2001, Turek 2007, Kröger 2008).

Late Lochkovian strata of the Prague Basin contains low diversified and poorly preserved cephalopods: orthocerids, pseudorthocerids and oncocerids (Novák 1886, Manda 2001). Cephalopods become a common component in the Pragian faunas in the Prague Basin. The cephalopod faunas of the Pragian of the Prague Basin consist of over fifty described species, representing the most diversified Pragian cephalopod fauna currently known (Barrande

1865–1877, Katzer 1895, Manda 2001, Turek 2007). Most of the cephalopod taxa were previously described and illustrated by Barrande (1865–1877), the vast majority of which have not yet been revised. The most prominent components of the Pragian cephalopod faunas consist of longicone orthocerids and pseudorthocerids. Nautiloids, with few exceptions, occur rarely. Among nautiloids, the oncocerids exhibit the highest diversity and disparity, while discosorids are represented by few taxa, and tarphycerids of the suborder Barrandeocerina by only a single species (Manda 2001).

The oldest known members of the families Nephriticeratidae Hyatt, 1894, Rutoceratidae Hyatt, 1884, Hercoceratidae Hyatt, 1884 and Entimoceratidae Zhuravleva, 1972 have been described from the Prague Basin. Eleven genera have been based on species from the Bohemian Pragian: *Trochoceras* Barrande, 1848; *Ptyssoceras* Hyatt, 1884; *Ptenoceras* Hyatt, 1894; *Gonatocyrtoceras* Foerste, 1926;



**Figure 1.** Distribution of the Pragian rocks in the Prague Basin and position of the mentioned sections (after Havlíček & Vaněk 1998, Röhlich 2007).

• Notes on localities: Braník, Barrande's locality Braník G-g<sub>1</sub>, most probably a small quarry SSE of the Braník Rock, weathered lower part of the Dvorce-Prokop Limestone, earlier Pragian; *Parauloceras pupus*, *Ptenoceras alatum*, *Michelinoceras* sp., *Kopaninoceras barbarum*, *Suloceras pulchrum*, *Cancellispyroceras loricatum* a.o. • Branžovy Quarry, early Pragian (for detail see Fig. 3). • Císařský Quarry, upper part of the Koněprusy Limestone, Pragian (Chlupáč 1955); *Otomaroceras tardum*, *Ptenoceras alatum*, *Suloceras pulchrum*, *Spyroceras patronus* a.o. • Černá Gorge, Barrande's locality Kosorz and Lochkov G-g<sub>1</sub>, lower part of Dvorce-Prokop Limestone, early Pragian (Chlupáč 1957, 1983); *Ptenoceras alatum*, *Aphytoceras annulatum*, *Michelinoceras* sp., *Kopaninoceras barbarum*, *Suloceras pulchrum* a.o. • Červený Quarry, weathered muddy limestone, Dvorce-Prokop or Loděnice Limestone, middle Pragian (Růžička 1941, Havlíček & Vaněk 1998); *Pseudorutoceras* sp., *Goldringia gondola*, other cephalopods un-revised. • Damil Hill, Barrande's locality Damil or Tetin G-g<sub>1</sub>, exact site unknown, upper part of the Dvorce-Prokop Limestone (Chlupáč 1983); *Otomaroceras tardum*, *O. flexum*, *Ptyssoceras alienum*, *Goldringia gondola*, *Spyroceras patronus*, *Michelinoceras* sp., *Kopaninoceras barbarum* a.o. • Houbův Quarry, upper part of the crinoidal Koněprusy Limestone (Chlupáč 1955, Havlíček & Vaněk 1998); *Ptenoceras alatum*, *Otomaroceras flexum*, *Trochoceras davidsoni*, *Spyroceras patronus*, *Calorthoceras pseudocalamiteum*, *Dawsonoceras discretum*, "*Orthoceras*" *woodwardi* a.o. • Homolák Quarry, Koněprusy Limestone, Pragian (Havlíček & Vaněk 1998); *Otomaroceras tardum*, *Ptenoceras alatum*, *Suloceras pulchrum*, *Spyroceras patronus*, *Naedyceras branzenovensis* a.o. • Malá Chuchle, old quarry in the Malá Chuchle Valley, Dvorce-Prokop Limestone, middle Pragian; *Pseudorutoceras* sp., *Spyroceras patronus* a.o. • Srbsko, Šary's locality, exact site unknown, most probably outcrops in the Berounka Valley, Dvorce-Prokop Limestone, late Pragian; *Otomaroceras tardum*. • Stydlé Vody Quarry, Dvorce-Prokop Limestone, late Pragian (Chlupáč in Chlupáč ed. 1986); *Otomaroceras tardum*, *Spyroceras patronus*, *Michelinoceras* sp., *Kopaninoceras barbarum* a.o. • Svatý Prokop Quarry, weathered Dvorce-Prokop Limestone ("yellow bed"), late Pragian (Růžička 1941); *Goldringia gondola*, *Spyroceras patronus*, *Spyroceras* sp., *Thalesoceras amaltheum*. • Voskop Quarry, a large active quarry mining Koněprusy Limestone, Pragian; *Otomaroceras flexum*, *Ptenoceras alatum*, *Suloceras pulchrum*.

*Cayugoceras* Flower, 1947; *Sthenoceras* Flower, 1957 (in Flower & Teichert 1957); *Zooceras* Zhuravleva, 1972; *Calorthoceras* Chen, 1981 (in Chen et al. 1981); *Bohemojovellania* Manda, 2001; *Thalesoceras* Manda, 2001 and *Suloceras* Manda, 2001. However, some of the genera listed above, as well as generic assignments of Barrande's species made by Hyatt (1883–1884, 1894), Zhuravleva (1972, 1974, 1978), Gnoli (1982), Dzik (1984), Manda (2001) and others, urgently need revision. It should be noted that the illustra-

tions published by Barrande (1865–1877), although excellent in quality, sometimes contain Barrande's "interpretation"; in fact, important details may be missing from some of his figures (see Fig. 7). Consequently, conclusions based exclusively on Barrande's published figures may be open to doubt or even wrong. Rutoceratoids from the Pragian of the Prague Basin were partly revised by Manda (2001) and Turek (2007). The remaining species are described and discussed in detail in this paper.

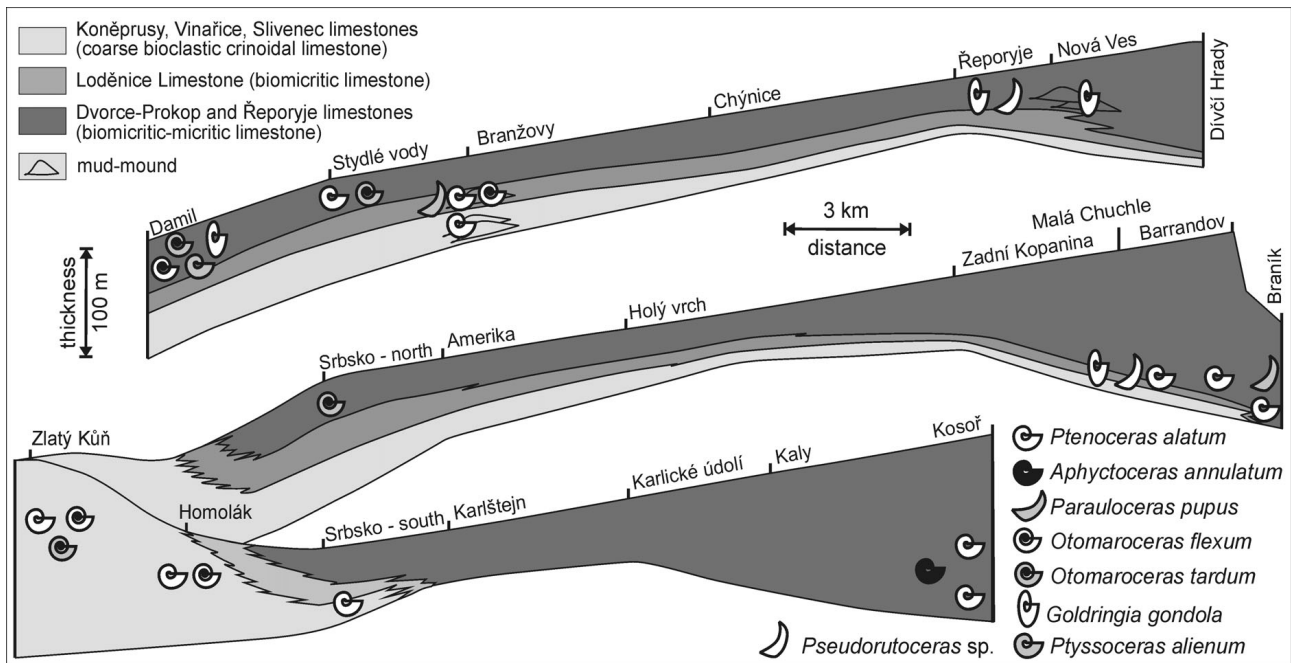


Figure 2. Facies development of the Pragian Praha Formation (modified after Chlupáč 1998) and distribution of rutoceratoids.

We use Pragian stage in its original sense (see Chlupáč 1982). By the new definition of the base of the Emsian at the FAD of *Polygnathus dehiscentis* (GSSP Zinzilban, see Yolkin *et al.* 1997), a prominent part of the former Pragian was included in the Emsian. Consequently, some authors (for summary see Carls *et al.* 2008) have suggested that base of the Emsian needs redefining. Note that the exact position of the base of the Emsian in terms of the current definition in the Prague Basin and peri-Gondwanan Europe is unclear due to missing index taxa.

### Rutoceratoids in the Pragian of the Prague Basin

At least seven genera and eight species from the Pragian strata of the Prague Basin are attributed to the rutoceratoids (Figs 1–3). The Pragian *Ptenoceras alatum* (Barrande, 1865) and *Ptyssoceras alienum* (Barrande, 1865) were previously assigned to the rutoceratoids by Kummel (1964). Manda (2001) described the oldest known species of *Goldringia* Flower, 1945, *G. gondola* Manda, 2001, from the late Pragian Dvorce-Prokop Limestone. Turek (2007) also reported the latter species from the earliest Zlíchovian (Emsian) strata of the Prague Basin (see Fig. 13A).

Some other Pragian rutoceratoids are described in this paper. The new genus *Parauloceras* gen. nov. is based on *Cyrtoceras pupus* Barrande, 1887, previously assigned by Manda (2001) to the genus *Uloceras* Zhuravleva, 1974, of the family Trochoceratidae Zittel, 1884. The presence of distinct ribs suggests that it in fact belongs to the Ruto-

ceratoidea Hyatt, 1884. The juvenile shell of *Parauloceras pupus* differs from other rutoceratoids (*i.e.* Rutoceratidae and Hercoceratidae), and thus the new family Parauloceratidae is proposed to include rutoceratoids with relatively simple shell morphology.

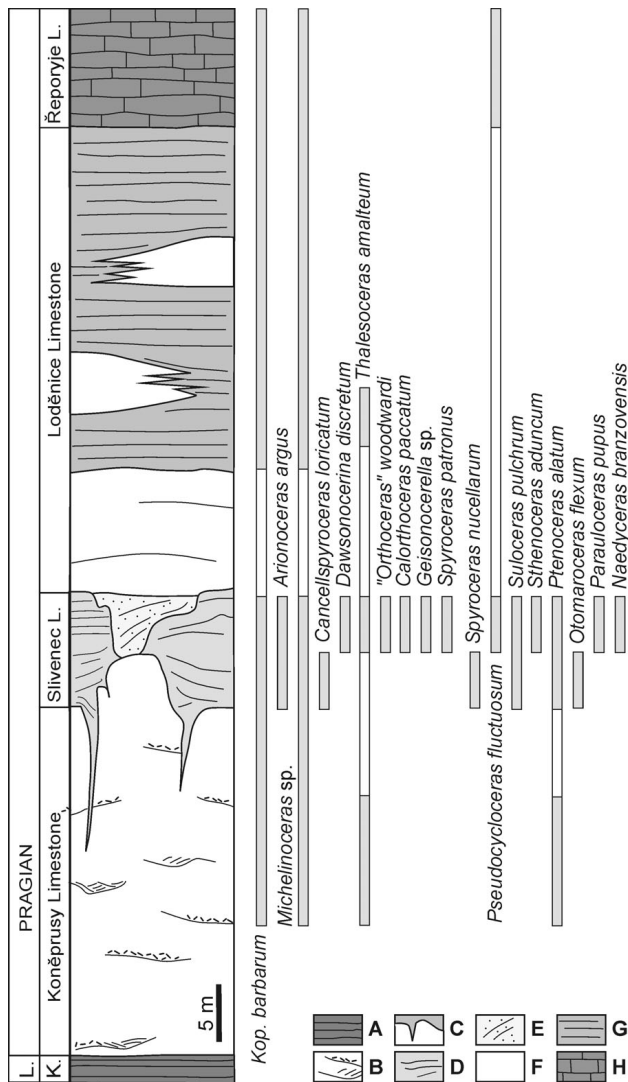
The Bohemian species *Trochoceras flexum* Barrande, 1865 and *Trochoceras tardum* Barrande, 1865 were assigned by Hyatt (1894) to the genus *Ptenoceras*. Zhuravleva (1974) considered these species to be rutoceratoids, but she listed these species without indicating their generic assignment. Examination of some previously unknown specimens of *T. flexum* as well as *T. tardum* suggests that they represent an independent clade within the hercoceratids and thus *Otomaroceras* gen. nov. is introduced based on *Trochoceras flexum*.

*Pseudorutoceras* gen. nov. is based on the late Emsian *Cyrtoceras bolli* Barrande, 1866 from the Prague Basin. *Pseudorutoceras* sp. is described from two shell fragments from the Pragian Dvorce-Prokop Limestone; one of which, Manda (2001) previously incorrectly regarded as *Goldringia gondola*. *Gyroceras annulatum* (Barrande, 1865) is re-described and transferred to the genus *Aphytoceras* Zhuravleva, 1974.

### Taxonomic value of the mode of coiling in Rutoceratoidea Hyatt, 1884

Two known species of *Otomaroceras* gen. nov. share growth ridges (megastriae) with three distinct lobes. *Otomaroceras tardum* has an almost planispiral shells while





**Figure 3.** Early Pragian deepening up sequence exposed in Branzovky Quarry, earliest Pragian corresponds with low stand followed by transgressive tract. An instructive example of cephalopod succession in the Pragian strata of the Prague Basin. Note facial dependence of cephalopods and restriction of diverse cephalopod assemblages to relatively thin levels. Most diverse assemblage occurs in coarse grainstones filling submarine depressions close to mud-mounds (see E). Only few cephalopods exhibit continuous distribution across the sequence, namely pelagic orthocerids (*Kopaniceras*, *Michelinoceras*) and nectobenthic pseudorthocerid *Pseudocycloceras*. • A – platy grey wackestone. • B – massive white limestone with thin cross-bedded levels of the trilobite packstone filling small submarine depressions and channels (mud-mounds). • C – erosive surface of the Koněprusy Limestone, neptunian dykes. • D – coarse cross-bedded trilobite packstone of the Slivenec Limestone (*Platypeltis-Kolihapeltis* Assemblage, fauna from this bed was described by Chlupáč & Šnajdr in 1990). • E – white coarse trilobite-gastropod grainstones with cryptalgal structures filling shallow submarine depressions, gastropod fauna was described by Horný (1995). • F – white-grey massive limestone, local accumulations of bioclasts (mud-mounds). • G – platy grey fine-grained mudstone-wackestone. • H – thinly bedded reddish and grey fine-grained wackestone with large cephalopod shell. After unpublished data of Š. Manda and J. Frýda. Abbreviations. L. – Lochkovian; K. – Kotýs Limestone, *Kop.* – *Kopaniceras*.

*Otomaroceras flexum* exhibits a helicoid shell. We suggest that the mode of coiling and subsequent change in shell symmetry was rapidly changing during evolution and thus does not represent a very important diagnostic character. Hyatt (1883–1884, 1894), Flower (1945) and Zhuravleva (1974) overemphasised the taxonomic value of minor differences in the mode of shell coiling and used these differences to establish new genera of rutoceratoids. Turek (2007) noted that the intraspecific variability in shell coiling ranged from gyrocones to very low torticones (both sinistrally or dextrally coiled) in the Pragian *Ptenoceras* Hyatt, 1894 and the late Emsian *Hercoceras* Barrande, 1865, and consequently he synonymised some taxa that had been established based on minor differences in coiling. In contrast to the rutoceratoids, the majority of other oncocerids display rather low variability in shell shape. The nautiloid orders Nautilida Agassiz, 1847 and Tarphycerida Flower, 1950 exhibit only slow changes in shell coiling during their evolution (e.g., Sweet 1964, Kummel 1964).

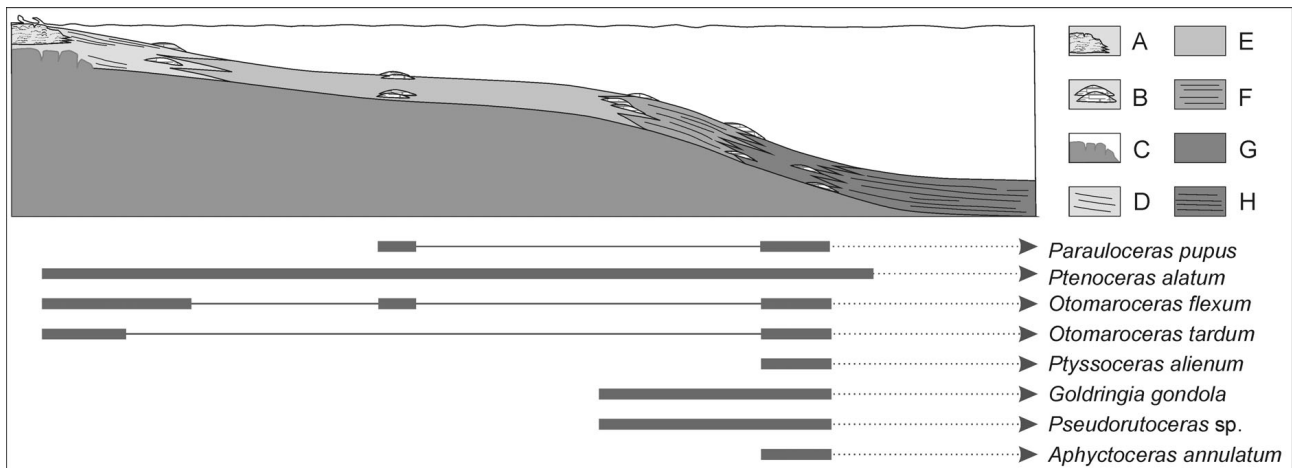
The high evolutionary disparity and intraspecific variability of shell coiling in rutoceratoids are remarkable. It should be noted that the morphological plasticity of shell form in respect to the mode of coiling in rutoceratoids represents an evolutionary novelty enabling adaptation to a variety of niches, and thus enhancing the evolutionary success of rutoceratoids during the Early Devonian. Almost all cephalopod clades, including species with coiled or curved shells, disappeared or were strongly impoverished by the Silurian-Devonian boundary event. Surviving groups rediversified and new clades originated in the Early Devonian.

### Morphological constraints of the nautiloid shell

Raup (1966) analyzed the theoretical morphospace for mollusc shells. However, real ectocochliate cephalopods do not populate the whole of this morphospace, but are unevenly distributed within it. The geometrical form of the shell should be constrained by other factors. Early Palaeozoic (Cambrian–Devonian) nautiloids occupied a wide range of morphospaces; however, post Early Palaeozoic ectocochliate cephalopods, with the exception of heteromorph ammonites, were largely limited to planispiral shells.

The dominance of these morphotypes may be explained by their hydrostatic properties (buoyancy and poise) and hydrodynamic properties, and how these affected swimming. Nevertheless, it is remarkable that these shell forms did not prevail during the Early Palaeozoic when nautiloids with planispiral or nautilicone shells had already appeared.

Of the Early Palaeozoic cephalopods with coiled shells, the majority of them are bilaterally symmetrical, i.e. the conch axis is coiled in a single plane. Tarphycerids and



**Figure 4.** Distribution of the Pragian rutoceratoids of the Prague Basin in relation to the facies (depth) zones. • A – reef core limestone (Koněprusy Limestone *s.s.*). • B – mud-mounds. • C – eroded Lochkovian Kotýs Limestone functioned as submarine cliffs during the earliest Pragian. • D – white-grey coarse cross-bedded crinoid limestone (Koněprusy Limestone *s.s.*). • E – white grey, grey and reddish crinoid limestone (Koněprusy Limestone *s.l.*, Sliveneč Limestone). • F – thinly bedded biomicritic limestone with thin skeletal (mostly crinoids) accumulations (Loděnice Limestone). • G – grey platy trilobite wackestone (Dvorce-Prokop Limestone, *Odontochile-Prokopia* Biofacies *sensu* Havlíček & Vaněk 1998). • H – grey platy mudstone with tentaculites and pelagic orthocerids (Dvorce-Prokop and Řeporyje limestones).

oncocerids exhibited such shells. Nevertheless, shallow torticonic shells in which the translation of the conch axis in the third dimension is so low that only the outermost whorl is visible in a ventral view (crypto-torticonic) may be found in the tarphycerids of the suborder Barrandeocerina (*e.g.*, Lechritrochoceratidae Flower, 1950, Nephriticeratinae Hyatt, 1894) and the oncocerids (Hercoceratidae Hyatt, 1884). Nautiloids with planispiral shells were more or less actively forward swimming animals with the shell in a vertical position and the aperture oriented anteriorly (Westerman 1998). A small deviation of the conch axis from the plane of coiling probably does not affect such a mode of life. This is corroborated by the high intraspecific variability in shell coiling reported in the Pragian *Ptenoceras* Hyatt, 1894 or the Ludfordian lechritrochocerid *Kosovoceras* Turek, 1975 (Turek 1975, 2007).

Only a few genera belonging to the suborder Barrandeocerina have torticonic shells in which the whorls are in contact and invisible from the posterior view (*e.g.*, *Lechritrochoceras* Foerste, 1930a, *Magdoceras* Turek, 1976, *Sphyradoceras* Hyatt, 1884). The mode of life of these nautiloids is largely unknown. Westermann (1998) suggested that shallow-torticonic shells have low stability and suggested a planktonic mode of life for them, but further studies to test this hypothesis are needed. Nevertheless, nautiloids with shallow-torticonic shells usually exhibit a small area of dispersion as well as facial dependence, which contradicts this supposed planktonic mode of life.

The oncocerid *Foersteoceras turbinatum* Hall, 1852 with a high-torticonic shell was described from the middle Silurian of New York. There is some apparent confusion in relation to this genus. All figured specimens (Grabau 1910, Ruedemann 1925) are poorly preserved. The reconstruc-

tion published by Ruedemann (1925, pl. 21, fig. 1) and refigured in the “Treatise” by Sweet (1964, K298, fig. 212.2) appears to be an “artistic” rendering rather than representing the actual form as should be seen in the figured specimens (see Grabau 1910: pl. 31, fig. 3; Ruedemann 1925: pl. 19, fig. 1, pl. 20, fig. 1, pl. 21, fig. 2).

The shell of *Otomaroceras flexum* is torticonic and loosely coiled. Among cephalopods, similar shell forms are almost completely restricted to heteromorphic ammonoids. Shells described here are termed helicoid, and Arkell *et al.* (1957, p. L4) defined this form as “coiled in regular 3-dimensional spiral form with constant spiral angle, as in most gastropods”. Amongst nautiloids this morphotype is otherwise only known in *Lorieroceras lorieri* (Barrande, 1870) from the Devonian of France (see also Foerste 1926). The only known specimen is a part of a large shell with two whorls that are not in contact. The mode of coiling of the juvenile part of the shell is unknown and thus the overall shell morphology is insufficiently known. Therefore, *Otomaroceras flexum* and perhaps *Lorieroceras* represent the only examples of nautiloid cephalopods possessing fully helicoid shells. In summary, high torticonic or helicoid shells are known only in the oncocerids *Otomaroceras* gen. nov. (Hercoceratidae Hyatt, 1884), *Lorieroceras* (Nothoceratidae Fischer, 1882) and perhaps *Foersteoceras* Ruedemann, 1925 (“Brevicoceratidae” Flower, 1941). All of these genera are monospecific, exceptionally rare, and were probably endemic.

The majority of nautiloids are probably constrained to planispiral coiling because post-hatching nautiloids have bilaterally symmetrical shells. Thus, the transition from planispiral coiling to the 3-dimensional spire has to take place through shell transformation after hatching. Helicoid

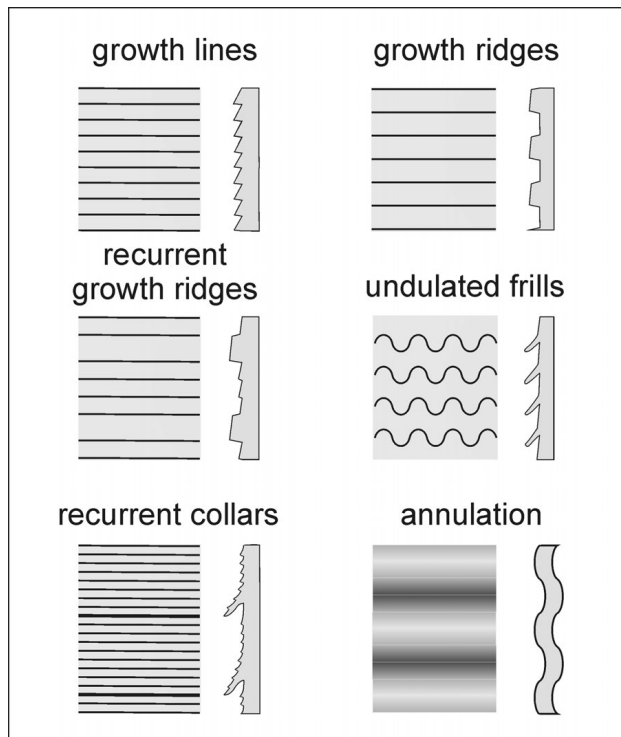


Figure 5. Classification of growth structures among rutoceratoids.

or highly torticone “gastropod-like” shells were probably less suitable for active horizontal swimming. The shape of the shell, however, could have been favourable for food captures on the sea floor owing to the downward orientation of the aperture (see Westermann 1998). However, the majority of early Palaeozoic nautiloids were bilaterally symmetrical brevicones and cyrtocones with more or less downward oriented apertures. Thus, it is possible that high competitive pressure acted as a barrier to the development of nautiloids with helicoid shells.

### Systematic palaeontology

Morphological terminology is largely adopted from the “Treatise on invertebrate paleontology” (Teichert 1964). The terms height, width and length are used as defined by Stridsberg (1985). For the terminology of growth structures see Fig. 5. All specimens except those figured in Figs 9K–M, 11C, F and 13A were coated with ammonium chloride prior to photographing.

*Institutional abbreviations.* – Studied specimens are deposited in the Czech Geological Survey, Praha, collections of Š. Manda (prefix CGU SM), Palaeontological collection (prefix CGU p); National Museum, Praha (prefix NM L); and Museum of Comparative Zoology, Harvard University, Cambridge (prefix MCZ).

Subclass Nautiloidea Agassiz, 1847  
 Order Oncocerida Flower, 1950  
 Superfamily Rutoceratoidea Hyatt, 1884

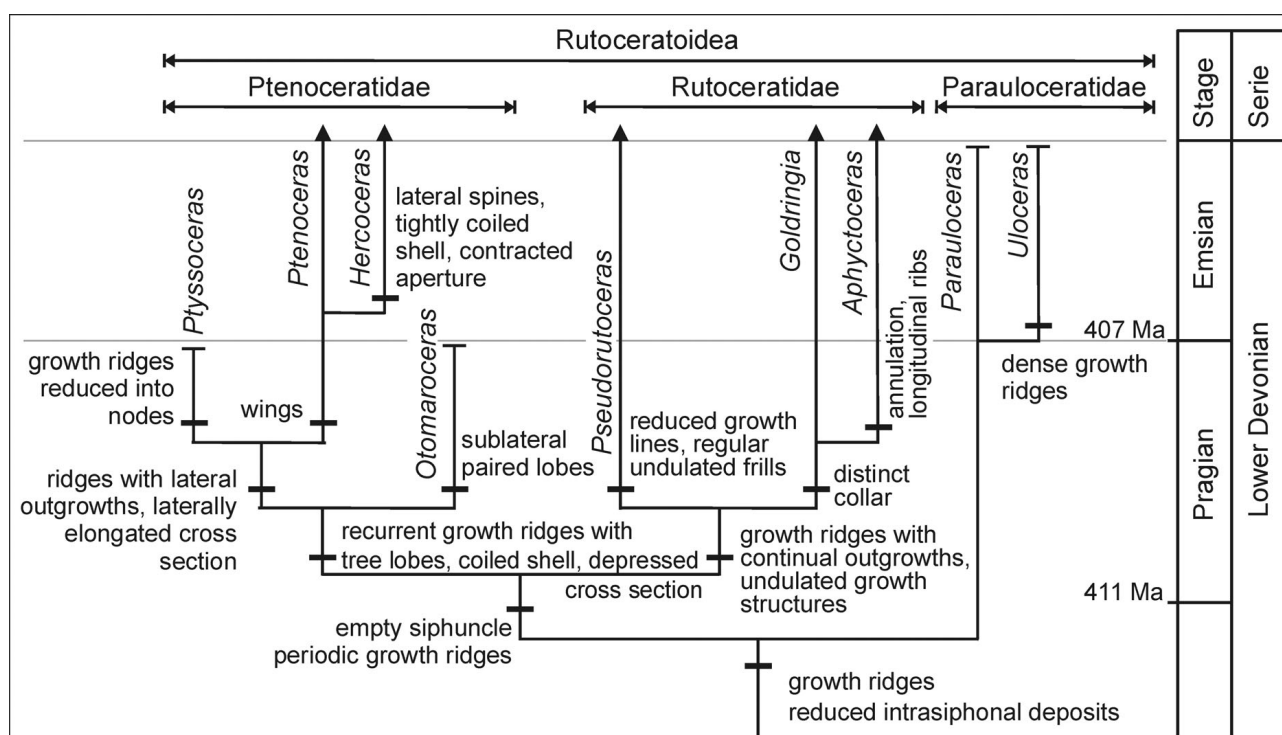
*Diagnosis (emended).* – Oncocerids possessing a nearly straight, cyrtoceraconic or coiled exogastric shell, circular or depressed in cross section. Siphuncle tubular, situated ventrally or sub-ventrally, usually empty or with poorly developed actinosiphonate deposits; septal necks short. Sutures simple. Sculpture consists of recurrent growth ridges, which are frequently transformed during shell growth into spectacular outgrowths; oncocerid type of muscle scars.

*Discussion.* – All taxa grouped within the superfamily Rutoceratoidea share distinct and variously modified growth ridges or ribs, *i.e.* megastriae (Fig. 5). Simple growth ridges are present in the representatives of the family Parauloceratidae. Periodically accentuated growth lines in Rutoceratidae are transformed into collars or undulated frills around the whole shell. In Hercoceratidae the recurrent emphasized growth ridges changed during ontogeny into auricle-like, spine-like or wing-like ventrolateral outgrowths. The aperture in fully grown shells may be widely opened or constricted. Intraspecific variability of the shell form, shape of aperture and outgrowths of the shell is high (Fig. 6). Rapidly changing shell morphology in Rutoceratoidea contrasted with a relatively low rate of change in siphuncle morphology (position, diameter, shape of septal necks and connecting rings).

Three issues concerning rutoceratoids need to be resolved: (1) the monophyly of rutoceratoids, (2) their affinity to the orders Nautilida and Oncocerida, respectively, and (3) their taxonomic ranks.

1. *Monophyly of rutoceratoids.* – In the original concept of Hyatt (1884, 1894, 1900), representatives of the superfamily Rutoceratoidea (as considered here) were placed within two superfamilies of the suborder Orthochoanites. Ruzhentsev *et al.* (1962), Zhuravleva (1974) and Dzik (1984) followed Hyatt’s concept of two independent clades and placed the family Rutoceratidae within the Oncocerida and the family Hercoceratidae (= Trochoceratidae Zittel, 1884) within the Nautilida. By contrast, Flower (1950, 1955) and Kummel (1964) considered the rutoceratoids as a monophyletic group, and this concept is followed here. Similarly, Dzik & Korn (1992) suggested a common ancestor for the *Halloceras*, *Hercoceras* and *Ptenoceras* groups (*i.e.* rutoceratoids).

2. *Position of rutoceratoids.* – As noted above, Ruzhentsev *et al.* (1962), Zhuravleva (1974) and Dzik (1984) placed the family Hercoceratidae in the Nautilida Agassiz, 1847 and family Ptenoceratidae (Rutoceratidae in Dzik) in the Oncocerida. Kummel (1964) considered all rutoceratids to be nautilids.



**Figure 6.** The Pragian-Emsian radiation of the rutoceratoids in the Prague Basin. Note that in the latest Pragian, and especially in the early Emsian, rutoceratoids migrated into other regions of the Old World Realm (Baltica, Laurentia). Some poorly known genera (*e.g.*, late Emsian *Adelphoceras* Barrande, 1870 from the Prague Basin) as well as the Emsian genera recorded outside the Prague Basin are not considered.

R.H. Flower, in various papers, suggested rutoceratids were oncocerids or an independent order from which the nautilids diverged (*e.g.*, Flower 1950, 1955, 1964, 1988). Dzik & Korn (1992), Manda (2001) and Turek (2007) concluded that the position of all rutoceratoids within the order Oncocerida is supported by the presence of a ventral siphuncle, cup-like embryonic shell without nepionic constriction, annular elevation with multiple paired muscle scars and the frequent occurrence of modified apertures in fully-grown specimens.

3. Taxonomic rank. – Various authors have classified rutoceratoids as family, super-family, sub-order and order rank taxon. The rutoceratoid material from the Pragian strata of the Prague Basin nevertheless shows that at last three major clades may be distinguished within the “Rutoceratidae” in Kummel’s concept (1964). Consequently, the two families proposed by Hyatt (1884, 1894) are accepted here and grouped together with the new family Parauloceratidae into the superfamily Rutoceratoidea. The relationship of rutoceratoids to the Middle Devonian nautilid *Centroceras* Hyatt, 1884 (see Flower 1952) and the Late Palaeozoic nautilids is doubtful. Consequently, the grouping of rutoceratoids with them in the order Rutoceratida Flower, 1950 or suborder Rutoceratoidea Hyatt, 1884 is thus questionable.

*Families included.* – Hercoceratidae Hyatt, 1884 (Prag-

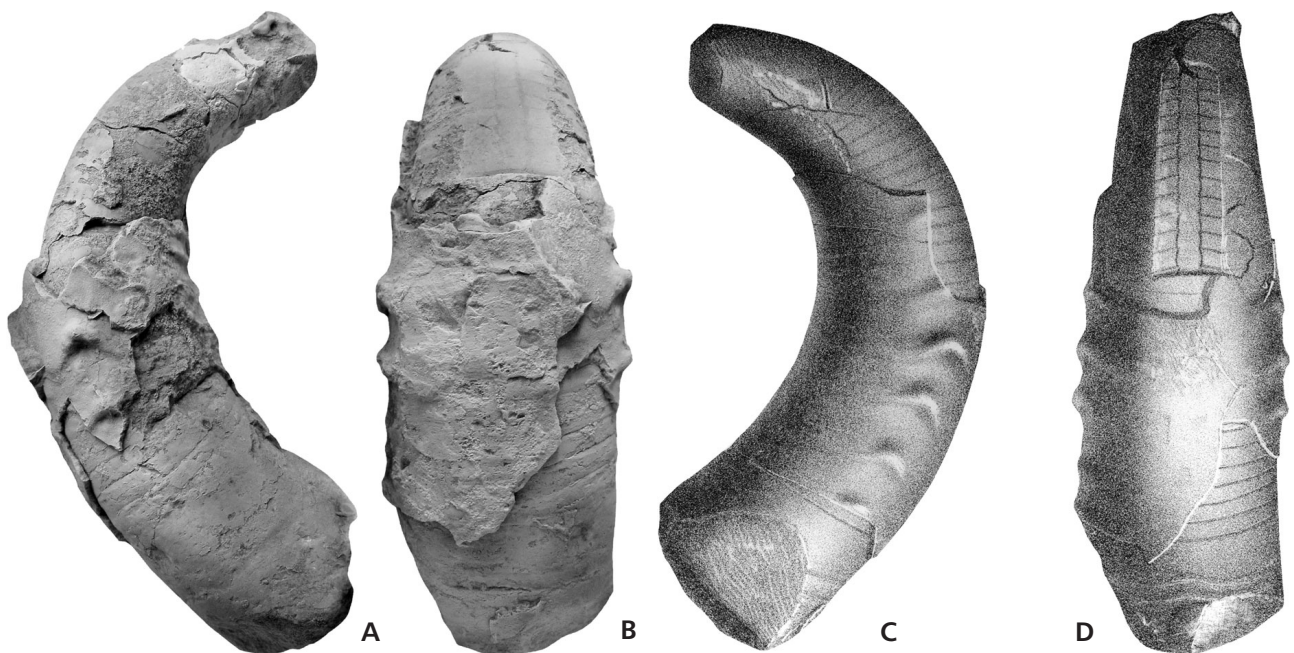
ian-Givetian), Rutoceratidae Hyatt, 1884 (Pragian-Frasnian) and Parauloceratidae fam. nov. (Pragian-Emsian). Family Trochoceratidae Zittel, 1884 (see Dzik 1984) perhaps also belongs to the superfamily Rutoceratoidea, but revision of the type species *T. davidsoni* Barrande, 1865 is necessary to resolve this problem.

Family Parauloceratidae fam. nov.

*Diagnosis.* – Shell cyrtoceracone, exogastric, exhibiting marked changes in morphology during shell growth, juvenile shell is less curved than adult portion. Intrasiphonal deposits present, but disappear in later growth stages. Prominent growth ribs with ventral lobe present in fully grown shells.

*Discussion.* – *Parauloceras pupus* is characterised by a distinct change in shell morphology during shell growth. The juvenile shell is moderately curved, smooth or with fine growth lines. In contrast, the adult shell exhibits distinct growth ridges, which are intercalated with simple growth lines. The ribbed adult shell strongly resembles shells of other rutoceratids in which growth ridges in early shells were later transformed in various ways. Thus, the Parauloceratidae are here considered to form the basal clade of rutoceratoids.





**Figure 7.** *Ptyssoceras alienum* (Barrande, 1866). • A, B – Holotype, lateral (dextral) and ventral views;  $\times 1.1$ ; NM L 40507, Damil Hill near Tetin; late Pragian; Dvorce-Prokop Limestone. • C, D – the same specimen, lateral (sinistral) and ventral views, adopted from Barrande (1866), pl. 127, figs 1, 2.

*Genera included.* – *Parauloceras* gen. nov. (Pragian-Emsian), *Uloceras* Zhuravleva, 1974 (Emsian).

**Genus *Parauloceras* gen. nov.**

*Type species.* – *Cyrtoceras pupus* Barrande, 1877. Early Devonian, Pragian, Prague Basin.

*Diagnosis.* – Rutoceratoid with slightly curved exogastric shell, early shell smooth, fully-grown shell with regular transversal ribs in body chamber.

*Name.* – Combination of the Latin prefix *para-* and the genus name *Uloceras*.

*Discussion.* – Manda (2001) assigned *Cyrtoceras pupus* to the genus *Uloceras* Zhuravleva, 1974. The type species of this genus *Uloceras insperatum* Zhuravleva, 1974 comes from the Emsian of the Pechora River Basin. *Cyrtoceras pupus* differs from the type species *Uloceras insperatum* in having a more complex morphology. *Uloceras insperatum* exhibits a slightly curved shell with regular transverse ribs that are sub-quadrangle in cross section. Their distance is, however, markedly higher than in *U. pupus*. The hyponomic sinus is shallower, septa more convex, and siphonal tube narrower.

*Species included.* – In the Devonian strata of the Prague Basin, *Parauloceras* is represented by an evolutionary lineage containing two closely related species; *Parauloceras pupus*

(Barrande, 1877) from the Pragian, and *Parauloceras* sp. nov. (= *Cyrtoceras pupus* in Barrande 1877, pl. 464, figs 8–10) from the Upper Emsian Třebotov Limestone.

***Parauloceras pupus* (Barrande, 1877)**

Figure 8A–D

- 1877 *Cyrtoceras pupus* Barr.; Barrande, pl. 464, figs 5–7 (non figs 8–10; = *Uloceras* sp. nov.).
- 1877 *Cyrtoceras nepotulus* Barr.; Barrande, pl. 465, figs 13–20.
- 1877 *Cyrtoceras pupus* Barrande; Barrande, pp. 41, 42.
- 1877 *Cyrtoceras nepotulus* Barrande; Barrande, pp. 35, 36.
- 2001 *Uloceras pupus* (Barrande, 1877). – Manda, pp. 270, 271, pl. 1, figs 2–5; text-fig. 1.

*Lectotype.* – A specimen figured by Barrande (1877) on pl. 464 as figs 5–7 (specimen designated by Manda 2001, NM L 21502).

*Type locality.* – Praha-Braník (Prague Basin, Bohemia).

*Type horizon.* – Dvorce-Prokop Limestone, Praha Formation, Early Pragian strata.

*Material.* – Five specimens, NM L21502, NM L13795, NM L13796, CGS SM3, one specimen (5429) is deposited in Palaeontological Collection, Faculty of Science, Charles University.



*Description.* – See Manda (2001), pp. 270, 271.

*Occurrence.* – Early Devonian, lower-middle Pragian. Braník, lower part of the Pragian Dvorce-Prokop Limestone, grey wackestone. Section Branžovy, middle Pragian, Loděnice Limestone, coarse grainstone (CGS SM 3).

Family *Hercoceratidae* Hyatt, 1884  
(syn. *Ptenoceratidae* Teichert, 1939)

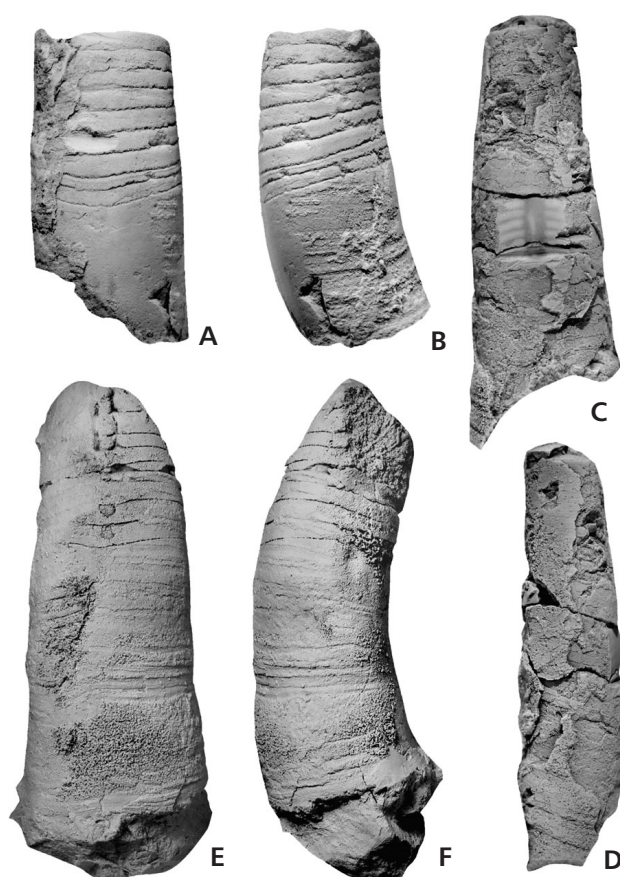
*Diagnosis (emended).* – Exogastric cyrtoconic to coiled shells, possessing recurrent growth ridges with ventral lobe and two sub-lateral lobes. Ridges may pass into different outgrowths such as auricles, wings, spines or nodes during ontogeny. Cross section depressed, siphuncle subventral, thin to moderately wide, without intrasiphonal deposits.

*Discussion.* – Three genera of the *Hercoceratidae* are known from the Pragian of the Prague Basin: *Ptenoceras* Hyatt, 1894, *Ptyssoceras* Hyatt, 1884 and *Otomaroceras* gen. nov. These genera also represent the oldest known members of the family.

Barrande (1865) and Turek (2007) examined about one hundred specimens of *Ptenoceras alatum*. The protoconch is cup-like and possesses fine straight growth lines (Fig. 12B–D). Shallow hyponomic sinus and lateral lobes appear just after the embryonic chamber. Later in ontogeny, the growth lines become differentiated into two orders and recurrent raised growth ridges appear (*i.e.* megastriae). Subsequently these marked ridges form ventrolateral lobes. One or two characteristic wings appeared near the aperture of fully-grown shells. In late Emsian *Hercoceras* ventrolateral auricles (wings) appear in the juvenile shell (Fig. 12G) and are usually transformed into hollow spines during shell growth. The line of *Ptenoceras-Hercoceras* clearly exhibits an evolutionary trend from loosely to closely coiled shells (Manda 2001, Turek 2007) and the extension of lateral outgrowths (Dzik & Korn 1992). These lateral outgrowths may represent a selective advantage in hercocerids.

*Ptyssoceras alienum* (Barrande, 1865), based on the holotype only (Fig. 7), probably possessed a cyrtoceraconic shell with elongated, ventrolaterally situated V-shaped nodes. The cross section of the shell is slightly depressed, and the siphuncle is ventral. In cross-section, the position of the siphuncle in *Ptyssoceras* resembles *Ptenoceras*. Additionally, the elongated nodes are similar in shape to the lobes on raised ridges in *Ptenoceras*. Thus, both genera probably shared a common ancestor.

The new genus *Otomaroceras* shares similar types of growth ridges with three lobes with *Ptenoceras*. *Otomaroceras*, however, differs in having ridges without outgrowths, while recurrent growth ridges appeared later during ontogeny and the distance between them is greater.



**Figure 8.** *Parauloceras pupus* (Barrande, 1877). • A, B – ventral and lateral views (a specimen figured by Barrande on pl. 465, figs 13–16 as “*Cyrtoceras nepotulus*” Barrande, 1877); × 1; NML 13795; Braník locality, Early Pragian; Dvorce-Prokop Limestone. • C, D – ventral (× 1.3) and lateral (× 1.2) views, specimen CGS SM 3; ×; Branžovy Section; middle Pragian; lowermost Loděnice Limestone. • E, F – ventral and lateral views; × 1.3; a specimen deposited in the Palaeontological collection of Faculty of Sciences, Charles University under number 5429; Braník locality, early Pragian; Dvorce-Prokop Limestone.

The whorl cross-section is less depressed than that of *Ptenoceras*.

Ordovician and Silurian oncocerids usually exhibit a bilaterally symmetrical shell with circular, sub-circular or compressed elliptical shell cross-sections. The Devonian hercoceratids show sub-circular or more commonly depressed cross-sections, which are usually elliptical, quadrate or even sub-polygonal. In addition, the cross-section is often slightly asymmetrical as the shell is weakly turned to the left or less frequently to the right from the plane of symmetry. A similar morphological trend in the lateral extension of the shell is achieved in some other Devonian nautiloid clades, *e.g.* in the Entimoceratidae (see Zhuravleva 1972). Lateral extension of the shell might have improved stability during swimming and jet propulsion. Similarly, the recurrent growth ridges may have acted to modify turbulence and change drag during swimming.

*Genera included.* – *Ptenoceras* Hyatt, 1894 (Pragian-Eifelian); *Adeloceras* Zhuravleva, 1974 (Emsian) [= *Dolerocheras* Zhuravleva, 1972; see Turek 2007, p. 9]; *Anepheloceras* Zhuravleva, 1974 (Emsian); *Capricornites* Zhuravleva, 1974 (Emsian); *Centrolitoceras* Flower, 1945 (Middle Devonian); *Diademoceras* Flower, 1949 (Emsian); *Hercoceras* Barrande, 1865 (Emsian-Eifelian) [including *Bastindoceras* Zhuravleva, 1974 (Eifelian), *Piratoceras* Zhuravleva, 1974 (Emsian) and *Spanioceras* Zhuravleva, 1974 (Eifelian)]; *?Megaloceras* Zhuravleva, 1974 (Emsian); *Moneroceras* Zhuravleva, 1996 (Emsian); *?Nassauoceras* Miller, 1932 (Middle Devonian)]; *Nozemoceras* Zhuravleva, 1996 (Emsian); *Otomaroceras* gen. nov. (Pragian); *Ptyssoceras* Hyatt, 1884 (Pragian); *Pleuronoceras* Flower, 1950 (Middle Devonian); new unnamed genus (based on *Rutoceras eospinosum* Zhuravleva, 1974, Emsian of the Pechora River Basin. This unnamed genus possesses recurrent growth ridges with lateral lobes as in *Ptenoceras*, but the shell is only slightly curved).

#### Genus *Otomaroceras* gen. nov.

*Type species.* – *Trochoceras flexum* Barrande, 1865; Early Devonian, Pragian; Bohemia, Prague Basin.

*Name.* – In honour of the Czech palaeontologist Otomar Pravoslav Novák (1851–1892).

*Diagnosis.* – Oncocerid with open-coiled exogastric shell possessing recurrent raised growth ridges having three lobes – a ventral lobe and two ventro-laterally placed lobes; ridges without outgrowths.

*Discussion.* – The holotypes of *Trochoceras flexum* Barrande, 1865 and *Trochoceras tardum* Barrande, 1865 are both poorly preserved internal moulds. *Trochoceras tardum* was figured by Barrande on pl. 26 as figs 9–12 and *Trochoceras flexum* on pl. 44 as figs 1–3. Although these taxa were described as separate species (see Barrande 1867), the figure explanation of *Trochoceras tardum* Barrande, 1865 includes the additional remark that *Trochoceras flexum* is perhaps identical with *Trochoceras tardum*. They were also considered as separate taxa within the genus *Ptenoceras* by Hyatt (1894) and family Ptenoceratidae Zhuravleva (1974). Further support for this assignment is given by the raised ridges running around the shell with three lobes and a quadrate to sub-quadrate cross-section.

*Species assigned.* – *Otomaroceras* is so far known only from the Pragian strata of the Prague Basin where it is represented by *O. flexum* Barrande, 1865 and *O. tardum* Barrande, 1865.

#### *Otomaroceras flexum* (Barrande, 1865)

Figures 9A–M, 12E

1865 *Trochoceras flexum* Barr.; pl. 44, figs 1–3.

1865 *Trochoceras distortum* Barr.; pl. 28, figs 11–14.

1867 *Trochoceras flexum* Barrande; p. 99.

1867 *Trochoceras distortum* Barrande; pp. 98, 99.

1894 *Ptenoceras flexum*. – Hyatt, p. 492.

1974 *T. flexum* Barrande. – Zhuravleva, p. 96.

1974 *T. distortum* Barrande. – Zhuravleva, p. 97.

*Type.* – Holotype by monotypy. An internal mould figured by Barrande (1865) as figs 1–3 on pl. 44, NM L 246.

*Type locality.* – Barrande’s locality “Tetin” in the Damil Hill area near Beroun, exact site unknown.

*Type horizon.* – Devonian, Early Devonian, Pragian (Barrande’s etage G, bande G-g<sub>1</sub>).

*Material.* – Holotype and eight additional specimens (NM L 197, NM L 8054, NM L 40502, NM L 40504, SM 324–327).

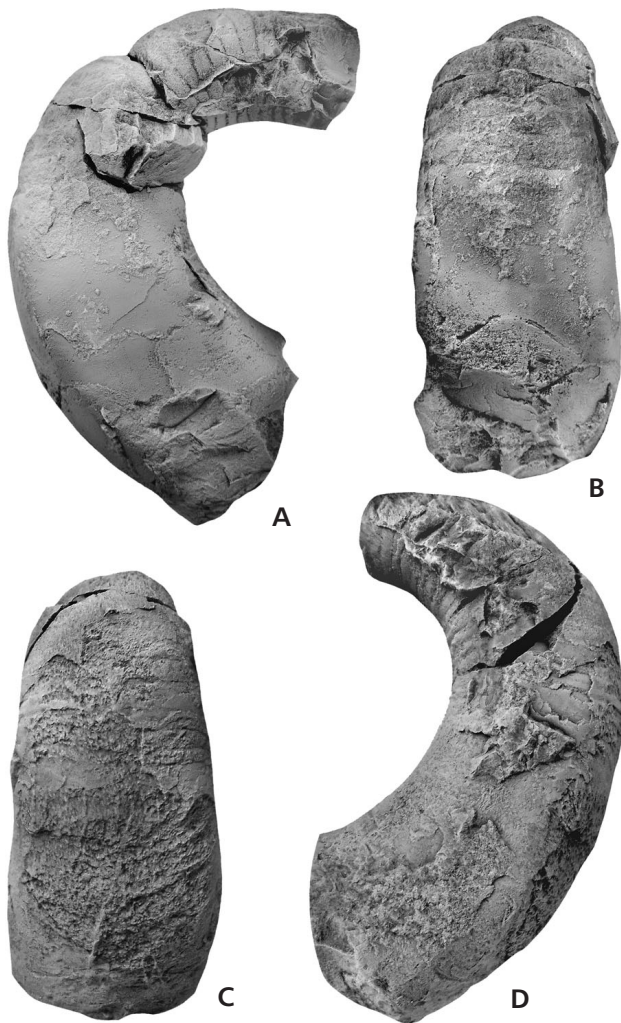
*Descriptions.* – Helicoid sinistrally coiled exogastric shell, perhaps with two whorls. Angle of expansion is about 10°. Cross-section of the whorl slightly asymmetrical, sub-trapezoidal; ratio of height/width decreases from 1.1 to 0.9 with growth. Siphuncle thin, ventral. Length of phragmocone chambers is variable; the ratio between shell height and length of phragmocone chamber varies between 4.5–8. Septa moderately vaulted with maximal depth in the shell axis. Suture oblique with shallow lateral saddles, ventral and dorsal lobes. Shell surface smooth or with fine and irregular growth lines. Recurrent growth ridges exhibit one ventral and two ventrolateral lobes, almost equal in dimension. The width of recurrent growth ridges in fully-grown shell is about 0.6 mm. Distance of adjacent ridges is approximately equal to half of the shell height. Hyponomic sinus is prominent and relatively broad. Length of the body chamber is approximately twice the shell height. The maximal adapertural shell height is 28 mm.

**Figure 9.** *Otomaroceras flexum* (Barrande, 1865). • A, J – lateral and ventral views; holotype NM L 246; × 0.9; Damil Hill near Tetin; late Pragian; Dvorce-Prokop Limestone. • B–D, I – lateral, dorsal and ventral views, cross section, × 1; CGS SM 325; Koněprusy, Houbův Quarry; Pragian; Koněprusy Limestone. • E – ventral view, × 1; NM L 40502; Koněprusy, Voskop Quarry; Koněprusy Limestone. • F–H – lateral (dextral), ventral and lateral (sinistral) views, × 0.9; CGS SM 324; Koněprusy, Houbův Quarry; Pragian; Koněprusy Limestone. K–M – dorsal, lateral and ventral views, × 0.7; NM L X; Damil Hill near Tetin; late Pragian; Dvorce-Prokop Limestone.









**Figure 10.** *Otomaroceras tardum* (Barrande, 1865). • A, B – lateral and ventral views; holotype NM L 40501; × 1; Damil Hill near Tetin; late Pragian; Dvorce-Prokop Limestone. • C, D – ventral and lateral views; CGS SM 390; Damil Hill near Tetin; late Pragian; Dvorce-Prokop Limestone.

**Discussion.** – The holotype of *Otomaroceras flexum* is a poorly preserved slightly corroded internal mould. Nevertheless, it exhibits distinct growth ridges with three lobes that may also be seen in better-preserved specimens in our repository; in addition, the mode of coiling is the same. Newly examined relatively complete shells of *O. flexum* suggest that “*Trochoceras distortum*” Barrande, 1865 (from the same locality as the holotype of *O. flexum*) is conspecific with *O. flexum* because it has a similar shell spire, cross-section, and length of body chamber. Both of the types of “*Trochoceras distortum*” are internal moulds, nevertheless the specimen figured by Barrande on pl. 28, figs 11, 12 shows imprints of growth ridges (see Fig 12E, note that the growth ridges is not visible in Barrande’s figure) with three lobes similar in shape with that at *O. flexum*, which further support the syno-

nymy of *O. flexum* with “*Trochoceras distortum*”. [The lectotype of “*Trochoceras distortum*” is selected herein as the specimen figured by Barrande (1865) on pl. 28 as figs 13, 14, type locality Tetin, *i.e.* Damil Hill, Pragian.]

**Occurrence.** – Early Devonian, Pragian; Bohemia, Prague Basin; Praha Formation. Koněprusy Limestone: Koněprusy, Zlatý Kůň Hill, Houbův Quarry; coarse crinoidal limestone (CGS SM 324, 326). Both specimens were collected by J. Bouška from the so-called “yellow beds”, *i.e.* strongly weathered limestones from which fossils are obtained by washing; for exact location and faunal list see Kodým *et al.* (1931). Koněprusy, Voskop Quarry, lower part of Koněprusy Limestone (NM L 40502). Road cut west of the Homolák Quarry at Měňany; coarse trilobite-brachiopod packstone (NM L 40502). Slivenec Limestone: Branžovy Quarry at Loděnice; coarse trilobite packstone, *Kolihapeltis* Community (CGS SM 325, 327). Dvorce-Prokop Limestone: Damil Hill at Beroun, exact site unknown; grey wackestones.

***Otomaroceras tardum* (Barrande, 1865)**

Figures 10 A–D, 11A–I

- 1865 *Trochoceras tardum* Barr.; Barrande, pl. 26, figs 9–12.
- 1867 *Trochoceras tardum* Barrande; Barrande, pp. 101, 102.
- 1894 *Ptenoceras tardum*. – Hyatt, p. 492.
- 1974 *T. tardum* Barrande. – Zhuravleva, p. 96.

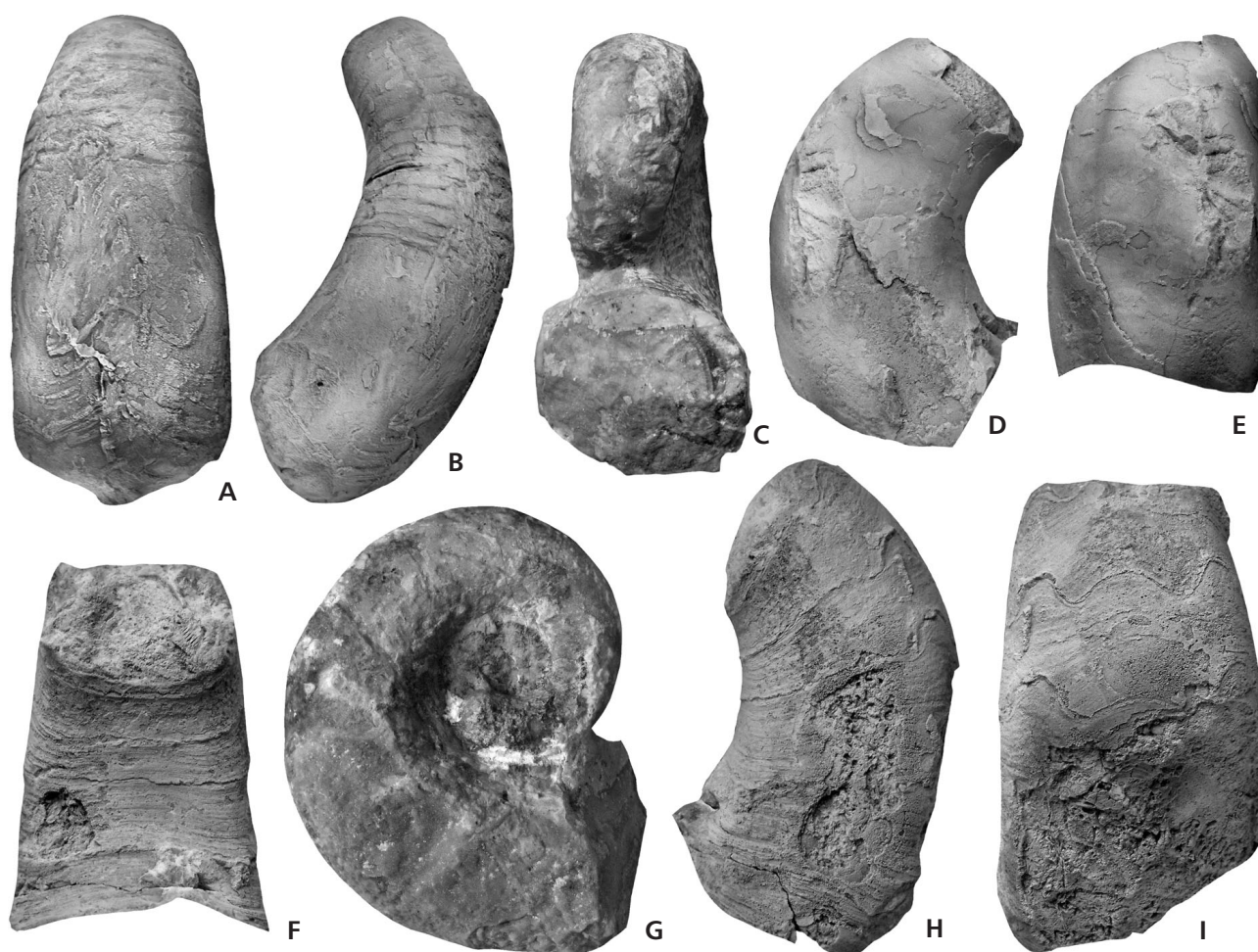
**Type.** – NM L 40501. Holotype by monotypy. Figured by Barrande (1865, pl. 26 as figs 9–12, see Fig. 10A, B).

**Type locality.** – Barrande’s locality “Tetin”, near the Damil Hill near Beroun, exact site unknown.

**Type horizon.** – Devonian, Early Devonian, late Pragian (Barrande’s etage G, bande G-g<sub>1</sub>).

**Other material.** – Four incomplete shells with broken-off apical portions (NM L40505, NM L 40506, CGS SM 330, MCZ 133261), one shell fragment (CGS SM 329), and two body chambers (CGS SM 328, CGS p824).

**Description.** – Gyroceraconic exogastric sinistrally coiled shell with two whorls. Angle of expansion is about 13°. Cross section sub-quadrate, slightly depressed; ratio of height/width is 0.9. Siphuncle relatively thin, marginal. Length of phragmocone chambers is variable, usually low. Septa moderately vaulted with maximal depth of the shell axis. Suture is oblique with shallow lateral and ventral lobes. Shell surface variable, either almost smooth or



**Figure 11.** *Otomaroceras tardum* (Barrande, 1865). • A, B – ventral and lateral views,  $\times 0.6$ ; MCZ 133261; Srbsko; late Pragian; Dvorce-Prokop Limestone. • C, G – dorsal and lateral views,  $\times 0.7$ ; NM L 40505; Koněprusy, exact site unknown; Pragian; Koněprusy Limestone. • D, E – lateral and ventral views,  $\times 0.8$ ; Koněprusy, Císařský Quarry; Pragian; Koněprusy Limestone. • F, H, I – lateral, ventral and dorsal views,  $\times 0.8$  (F),  $0.9$  (H, I); CGS SM 328; Koněprusy, Homolák Quarry; Pragian; Koněprusy Limestone.

with fine and irregularly arranged growth lines. Recurrent growth ridges with three lobes (ridges appear at a shell height of 25 mm), ventral lobe is shallower than ventrolateral lobes. Distance between ridges is variable. Hyponomic sinus relatively broad. Length of body chamber is about  $1/3$  of the whorl. Maximum shell height observed is 34 mm, width 45 mm. Maximal shell thickness is about 1.4 mm.

**Discussion.** – Comparison of the holotype with other specimens assigned to this species is complicated by the fact that the holotype consists of a poorly preserved internal mould. Five specimens from the old collections are similar to the holotype in their mode of coiling, cross-section, angle of expansion and length of body chamber. We consider all these specimens to be conspecific. Differences in shape of lobes at recurrent ridges (*i.e.* slightly narrower lateral lobes and shallower ventral lobe in holotype) may

be attributed to changes in lobe morphology during shell growth, as well as the mode of preservation. The holotype is an internal mould, and imprints of growth ridges on internal moulds differ slightly from their traces on the shell surface. *Otomaroceras tardum* differs from *Otomaroceras flexum* in having very shallow torticone shell, and the lateral lobes at recurrent ridges are deeper and shifted slightly ventrally.

**Occurrence.** – Devonian, Early Devonian, Pragian; Praha Formation. Koněprusy Limestone: Koněprusy, exact site unknown (NM L 40505, NM L 40506), Koněprusy, Zlatý Kůň Hill, Císařský Quarry (CGS p824); Měňany, Homolák Quarry, road cut approximately 50 m to the west from the quarry (CGS SM 328). Dvorce-Prokop Limestone: Tetín, Damil Hill (holotype, CGS SM 330). Srbsko, exact site unknown (MCZ 133261). Stydlé Vody Quarry near Svatý Jan pod Skalou (CGS SM 329).



Family Rutoceratidae Hyatt, 1884  
(syn. Ryticeratidae Hyatt, 1900, Halloceratidae Hyatt,  
1900, Adelphoceratidae Foerste, 1926)

*Diagnosis (emended).* – Oncocerids with exogastric cyrtocone to coiled shell, circular and sub-circular cross-section, growth lines transformed into undulated frills, periodic collar or annuli around whole shell.

*Genera included.* – *Adelphoceras* Barrande, 1870 (late Emsian); *Aphytoceras* Zhuravleva, 1974 (Pragian-Givetian); *Capricornites* Zhuravleva, 1974 (Emsian); *Casteroceras* Flower, 1936 (Middle Devonian); *Goldringia* Flower, 1945 (Pragian-Givetian); *Halloceras* Hyatt, 1884 (Emsian-Givetian); *Hindeoceras* Flower, 1945 (Middle Devonian); *Homoadelphoceras* Foerste, 1926 (Late Emsian); *Kophinoceras* Hyatt, 1884 (Middle Devonian); *Pseudorutoceras* gen. nov. (late Emsian); *Rutoceras* Hyatt, 1884 (Middle Devonian, ?Early Frasnian); *Tetranodoceras* Flower, 1936 (Middle Devonian).

#### ***Pseudorutoceras* gen. nov.**

*Type species.* – *Cyrtoceras bolli* Barrande, 1877. Lectotype – the specimen NM L 449 designated here, figured by Barrande in 1866 on pl. 119 as figs 5–9, type locality Praha-Hlubočepy, Early Devonian, late Emsian of Bohemia.

*Diagnosis.* – Oncocerid with slightly curved shell, circular or slightly depressed cross-section, sutures straight and oblique to shell axis, shell with distinct undulated frills (waves are almost equal in length and height) around whole shell; frills, except at the hyponomic lobe almost straight and oblique to shell axis.

*Name.* – Name is derived from Latin prefix *pseudo* and generic name *Rutoceras*.

*Discussion.* – *Pseudorutoceras* gen. nov. can be easily recognised by the presence of regularly undulated frills on the shell. Dark lines visible on the abraded surface of the lectotype in the adapical part of the shell were formerly interpreted as colour pattern (Foerste 1930b, Kobluk & Mapes 1989), an opinion later refuted by Turek (1990, in press).

Species assigned here to the *Pseudorutoceras* were previously placed in *Goldringia* Flower, 1945 and *Rutoceras* Hyatt, 1884 (e.g., Flower 1945, Zhuravleva 1974, Manda 2001). These genera differ from *Pseudorutoceras* in having distinct recurrent collars around the whole shell (e.g., Fig. 13A). The collar is formed from recurrent growth ridges developed during early growth stages (for example see early shell of *Goldringia gondola*; Fig. 12H–J). *Goldringia* and *Rutoceras* exhibit irregular undulation of

the growth lines, especially on the venter. These undulating growth lines sometimes form structures resembling longitudinal ribs because the lobes of these undulations are closer to each other than the saddles. It is probable that *Pseudorutoceras* shares a common ancestor with the *Goldringia-Rutoceras* group (Fig. 6).

*Pseudorutoceras* sp. from the Pragian of the Prague Basin represents the oldest known species of the new genus *Pseudorutoceras*. The two available specimens are poorly preserved, but the length of phragmocone chambers and the character of the undulating frills strongly resemble the younger species *Pseudorutoceras bolli* (Barrande, 1866) from the Třebotov Limestone, late Emsian. Both species probably represent a phyletic link from which all Middle Devonian species of *Pseudorutoceras* diverged.

*Species included.* – *Pseudorutoceras* sp., Pragian, Prague Basin. *Pseudorutoceras bolli* (Barrande, 1866), late Emsian, Prague Basin. *Pseudorutoceras citum* (Hall, 1879), Middle Devonian, New York. *Pseudorutoceras* cf. *citum* (Hall, 1879) *sensu* Fagerstrom (1961), Middle Devonian, SE Ontario. *Pseudorutoceras difficile* (Whidborne, 1890), Givetian, South England. *Pseudorutoceras fimbriatum* (Phillips, 1841), Givetian, South England. *Pseudorutoceras quindecimale* (Phillips, 1841), Givetian, South England.

#### ***Pseudorutoceras* sp.**

Figure 12A, F

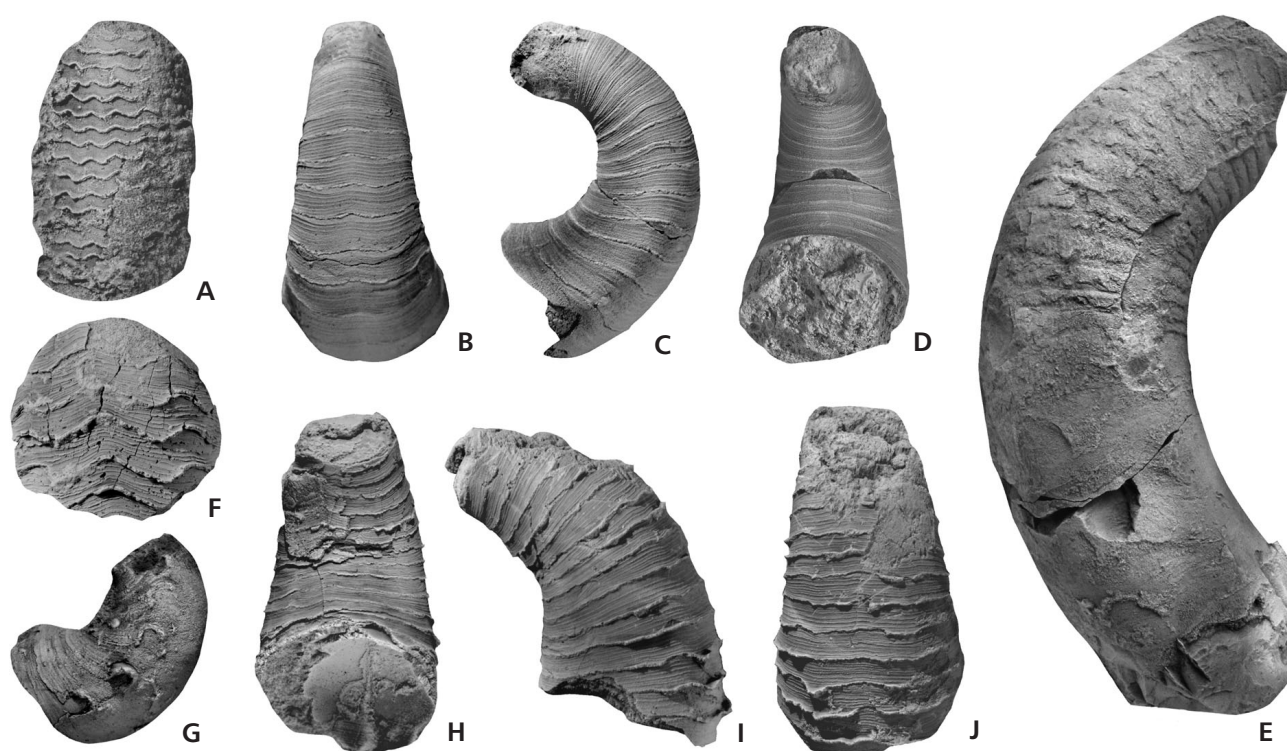
partim 2001 *Goldringia gondola* sp. nov.; Manda, pl. 1, fig. 12, p. 273.

*Material.* – Two shell fragments, NML 4050, CGS SM 5.

*Descriptions.* – Specimen CGS SM 5 is a fragment of the phragmocone and part of the body chamber, diameter 11 mm, length 21 mm. Shell is slightly curved with circular cross-section. Sculpture characterised by regularly undulated frills (1 mm apart). Length of the phragmocone chambers is 2 mm. Second available specimen (NML 4050) is a small fragment of a large shell, 17.5 × 18 mm. It shows well-developed undulated frills intercalated with parallel undulated growth lines. Distance of frills varies between 2–3.5 mm. Distance of growth lines varies slightly, 6 to 11 growth lines are visible between each pair of frills.

*Discussion.* – *Pseudorutoceras* sp. differs from all other species of the genus in the presence of growth lines between undulated frills; all other stratigraphically younger species share dense undulated frills similar to those seen in the juvenile shell of *Pseudorutoceras* sp. (Fig. 12A). Thus, the periodic growth structures were present in the ancestor of *Pseudorutoceras* and their reduction in all Emsian and





**Figure 12.** A – *Pseudorutoceras* sp.,  $\times 1.8$ ; CGS SM 5; Malá Chuchle; Pragian; Dvorce-Prokop Limestone. • B–D – *Ptenoceras alatum* (Barrande, 1865), ventral, lateral and dorsal views,  $\times 5.4$ ; CGS SM 331; Houbův Quarry; Pragian; Koněprusy Limestone. • E – *Otomaroceras flexum* (Barrande, 1865), lectotype of “*Trochoceras distortum*” Barrande, 1865, lateral view,  $\times 0.9$ ; NM L 197; Damil Hill near Tetin; late Pragian; Dvorce-Prokop Limestone. • F – *Pseudorutoceras* sp., lateral view,  $\times 1.7$ ; NM L 4050; Klukovice, Červený Quarry; late Pragian; Dvorce-Prokop or Loděnice Limestone. • G – *Hercoceras mirum* Barrande, 1865, lateral view,  $\times 1.8$ ; CGS SM 337; Holyně (see Bouček 1931), so-called “yellow beds”; latest Emsian. • H–J – *Goldringia gondola* Manda, 2001, dorsal, lateral and ventral view,  $\times 2$ ; CGS SM 323; Hlubočepy, Svätý Prokop Quarry; late Pragian, Dvorce-Prokop Limestone.

Middle Devonian species of *Pseudorutoceras* represents a derived character state.

**Occurrence.** – Early Devonian, Pragian, Praha Formation. Dvorce-Prokop Limestone, so-called “yellow beds”, i.e. weathered biomicritic limestones. Praha-Malá Chuchle, old quarry W of the Malá Chuchle and Malá Chuchle Valley (CGS SM 5); Praha-Klukovice, Červený Quarry.

### Genus *Aphytoceras* Zhuravleva, 1974

**Type species.** – *Rutoceras parvulum* Kuzmin, 1966. Middle Devonian, Eifelian. Novaya Zemlya.

**Discussion.** – This genus includes several species known from the Eifelian and Givetian strata of the Old World Realm, e.g., England, Germany, Morocco, Novaya Zemlya, Siberia and the Ural Mts. The single body chamber described by Barrande (1865, pl. 44, figs 4–7) as *Gyroceras annulatum* Barr. shows all diagnostic features of *Aphytoceras*. Thus, *Gyroceras annulatum* represents the oldest known species of *Aphytoceras*.

### *Aphytoceras annulatum* (Barrande, 1865)

Figure 13B–D

1865 *Gyroceras annulatum* Barr.; pl. 44, figs 4–7.

1867 *Gyroceras annulatum* Barr.; p. 163.

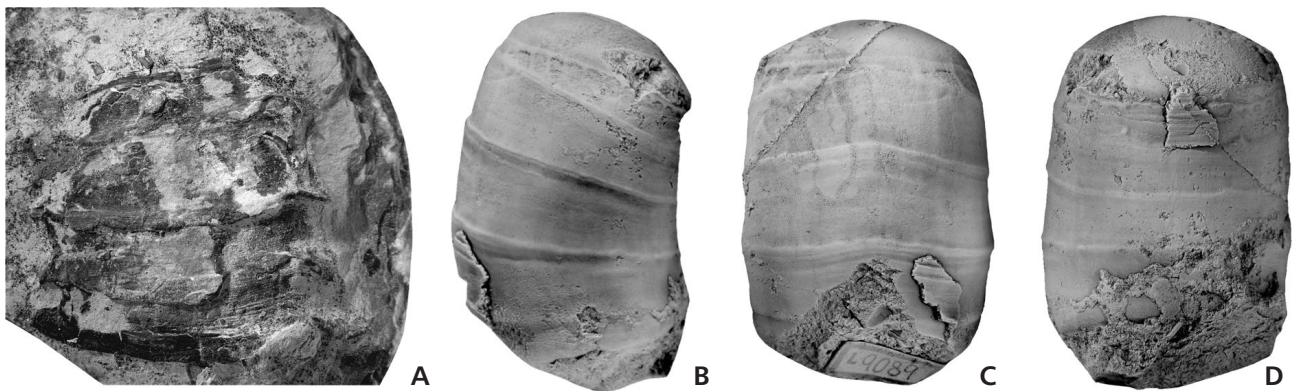
1957 *Ptenoceras(?) annulatum*. – Chlupáč, pp. 376, 436.

**Holotype.** – By monotypy, specimen figured by Barrande (1865) on pl. 44 as figs 4–7, NM L 9089.

**Type locality.** – After original designation Lochkov G-g<sub>1</sub>. Exact site unknown, Pragian strata crop out in the Černá Gorge and Radotín Valley SSE from the Praha-Lochkov Village.

**Type horizon.** – Early Devonian, Pragian, Dvorce-Prokop Limestone, grey muddy limestone.

**Description.** – Shell cyrtoceraconic and moderately expanding, slightly depressed (l/w ratio 0.9). Body chamber short; length of the body chamber exceeds 1.5 times the apertural width of the shell. Aperture slightly constricted. Surface with distinct, transverse, widely spaced annuli



**Figure 13.** A – *Goldringia gondola* Manda, 2001, ventrolateral view,  $\times 1$ ; Damil Hill at Tetín, Modrý Quarry; early Emsian (earlier Zlíchovian); Zlíchov Formation. • B–D – *Aphycoceras annulatum* (Barrande, 1865), holotype, lateral, ventral and dorsal views,  $\times 1$ ; NML 9089; Praha Lochov locality; early Pragian, Dvorce-Prokop Limestone.

forming a shallow, slightly acute ventral lobe. Longitudinal ribs are very weakly marked on the internal mould. Annular elevation with marked muscle imprints gradually enlarging laterally from both the ventral and dorsal sides.

*Occurrence.* – See the holotype.

## Conclusions

Previously unknown or newly examined material of rutoceratoids is described from the Pragian of the Prague Basin. This material enabled the evaluation of the classification of rutoceratoids as well as a revision of some previously published opinions concerning rutoceratoid systematics and the evolution of Devonian nautiloids.

1. Seven genera and eight species of rutoceratoids (Rutoceratoidea) are known from the Pragian of the Prague Basin. *Ptenoceras alatum* (Barrande, 1865) and *Ptyssoceras alienum* (Barrande, 1865) had already been placed in the rutoceratoids by Kummel (1964). *Goldringia gondola* was described by Manda (2001). In this paper, five additional taxa are added to the rutoceratoids: *Pseudorutoceras* sp., *Otomaroceras* gen. nov. [*C. flexum* (Barrande, 1865), *C. tardum* (Barrande, 1865)], *Aphycoceras* [*A. annulatum* (Barrande, 1865)], and *Parauloceras* gen. nov. [*P. pupus* (Barrande, 1877)].

2. The genera *Ptyssoceras* Hyatt, 1884, *Parauloceras* gen. nov. and *Otomaroceras* gen. nov. are at present known from the Prague Basin only. Currently, the earliest known representatives of the genera *Ptenoceras* Hyatt, 1894, *Aphycoceras* Zhuravleva, 1974, *Goldringia* Flower, 1945 and *Pseudorutoceras* gen. nov. are from the the Pragian of the Prague Basin.

3. Rapid diversification of the superfamily Rutoceratoidea took place in the early Pragian (*i.e.* just after “Basal Pragian Event”, Chlupáč & Kukul 1988). All major

clades of rutoceratoids originated during this radiation, *i.e.* Parauloceratidae fam. nov., Rutoceratidae Hyatt, 1884 and Hercoceratidae Hyatt, 1884 (Fig. 6). The palaeobiogeographical distribution of Pragian rutoceratoids seems to be limited to the Prague Basin area. Only *Goldringia valnevensis* Zhuravleva, 1996 is known from the Late Pragian of Novaya Zemlya. However, the major dispersion events of rutoceratoids happened later during the Emsian and Eifelian, when rutoceratoids became widespread within the faunas of the Old World (Rutoceratidae, Ptenoceratidae) and of Eastern American (Rutoceratidae) realms (Flower 1945).

4. The evolutionary success of the rutoceratoids reflects a high evolutionary plasticity of their shell form and sculpture, enabling adaptation to various environmental settings. Rutoceratoids rapidly occupied a variety of niches ranging from extremely shallow reef environments to deeper water settings below the storm wave base (Figs 2, 4). The radiation of ruthoceratids took place after the extinction event at the Silurian-Devonian boundary when many cephalopod clades became extinct (Manda 2001, 2007; Kröger 2008) and may correspond with the filling of vacant niches after this extinction. During the Pragian recovery of cephalopod faunas, rutoceratoids reached the highest diversity as well as the highest disparity among coeval nautiloid clades.

5. Rutoceratoids are considered as a monophyletic clade within the order Oncocerida (see Fig. 6). The superfamily Rutoceratoidea is divided into three families characterised by the presence of recurrent growth ridges and their modifications: Parauloceratidae fam. nov. (simple transversal ribs on adult shell), Hercoceratidae (recurrent raised growth ridges with three lobes transformed during ontogeny into ventrolateral outgrowths – auricles or hollow spines) and Rutoceratidae (growth ridges transformed into undulated frills or a recurrent collar around whole shell).

6. The origin of the *Rutoceratoidea* is unclear (see also Flower 1955, p. 254). The shell form and surface sculpture of the vast majority of *rutoceratoids* differs strongly from Silurian *oncocerids*. A possible ancestor may be indicated by the comparison of the juvenile shell of *Parauloceras* (Fig. 8), which in our opinion belongs to the basal clade of the *Rutoceratoidea* (Fig. 6). The juvenile shell of *Parauloceras pupus* is slightly curved, moderately depressed and smooth or with gentle growth lines. The siphuncle is marginal with cylindrical connecting rings and poorly developed intrasiphonal deposits resembling actinosiphonate deposits. Intrasiphonal deposits rapidly disappeared during the growth of the shell. Thus, the shell of *Parauloceras* resembles early shell of *Projovellania* Hyatt, 1900 (*sensu* Manda 2001) from the Ludlow–early Lochkovian strata. However, further investigations are needed in order to verify this.

7. The species of the newly established genus *Otomaroceras* share distinct recurrent low ridges with three lobes, but strongly differ in shell coiling; *O. tardum* has an almost planispirally coiled gyroceracone shell while *O. flexum* has a helicoid shell. These features suggest that differences in shell coiling might be rapidly fixed during evolution and, in fact, do not represent an important diagnostic feature among *rutoceratoids*. Similarly, Turek (2007) examined the distinct intraspecific variability of the shell form in *Ptenoceras* and *Hercoceras*.

8. The three dimensionally coiled shell is well known in heteromorph ammonoids. Among nautiloids, helicoid or high torticone shells are known only in Devonian *Lorieroceras* and perhaps in the Silurian *Foersteoceras*. An additional example is reported with the Pragian *Otomaroceras flexum*. The scarcity or absence of helicoid and high-torticone shells among nautiloids may be easily explained by an ontogenetic constraint. All nautiloids have planispiral shells after hatching. Consequently, shell transformation from a 2D to a 3D spire must have occurred during shell growth immediately after hatching; this transitional stage was most probably inconvenient with respect to drag and manoeuvrability.

9. An interesting feature of *rutoceratoid* diversity pattern is the change in diversity of the families *Hercoceratidae* and *Rutoceratidae*. If we summarise all available data, it is clear that the *Hercoceratidae* are more diverse during the Early Devonian, and *Rutoceratidae* during the Middle Devonian. The change in the diversity pattern coincides approximately with the Choteč extinction event (Chlupáč & Kukul 1988, House 2002). Since both families exhibit similar features (highly elaborated sculpture, shell outgrowths), the change in the diversity pattern is not easy to attribute to the acquisition of new characters and thus remains enigmatic.

10. The Pragian *rutoceratoids* appear to represent small, geographically restricted and isolated populations

within the Prague Basin (Figs 2, 3). They inhabited specific biotopes within carbonate platforms, namely mud-mounds and adjacent areas; settings close to reef cores, and a narrow zone along the lower slope (lower part of the Dvorce-Prokop Limestone overlying Loděnice Limestone during deepening). The mosaic distribution of *rutoceratoid* palaeo-populations accords well with their rapid radiation and diversity changes.

The maximum diversity of *rutoceratoids* coincides with the low stands and the subsequent initiation of deepening in the early and middle Pragian. It should be noted that in the Koněprusy area at least, late Pragian strata are missing due to emersion above sea level (Janoušek *et al.* 2001). The latest Pragian muddy limestones deposited during high stand conditions contain no *rutoceratids*. The base of the Zlíchovian (Emsian) again coincides with a shallowing and the reappearance of reefs. Although the brachiopod-bryozoan-coral fauna strongly resembles that in Koněprusy reef limestone (see Havlíček & Vaněk 1998, Chlupáč & Kolář 2001, Budil & Kolář 2004), the molluscan fauna is markedly reduced in diversity and abundance. *Goldringia gondola* is the only *rutoceratid* known from the earliest Zlíchovian (Zlíchov Limestone, grey fine-grained wackestone, Damil Hill; Fig. 13A). The muddy limestones of the middle to late Zlíchovian carbonate sequence were again deposited during deepening, and no *rutoceratoids* have been recorded from these strata. *Rutoceratoids* re-appeared again in the late Dalejan (latest Emsian) and the majority of them are considered as descendents of the Pragian *rutoceratoids* known from the Prague Basin (*e.g.*, *Ptenoceras alatum*-*P. proximum* and *Hercoceras mirum*; *Parauloceras pupus*-*P. sp. nov.*, *Pseudorutoceras sp.-P. bolli*).

11. From the palaeobiogeographical point of view the restriction of the Pragian *rutoceratoids* (as well as some other nautiloid taxa, *e.g.* *Cayugoceras*, *Gonatocyrtoceras*, *Nephriticerina*, *Sthenoceras*, *Zooceras*) to the Prague Basin is remarkable. Although many well-known terrains exhibit faunal affinities with the Prague Basin (*e.g.*, the Carnic Alps, Harz Mts, Linderer Mark at Giessen, Armorican Massif, Sardegna, Iberian Chain, Morocco, and the South Ural; see Zhuravleva 1972, 1974), no *rutoceratoids* have been reported from them. Palaeozoic nautiloids were more or less nectobenthic animals after hatching (for summary see Chirat & Rioult 1998, Manda 2008). As a consequence, their migration routes were restricted to shallow shelves and within shallow platforms. Migration across deep-water seas was possible, but represented rather long-term and multiphase processes (Manda 2008).

The Pragian rocks of the Prague Basin probably represent relict of a larger carbonate platform that was isolated from surrounding terrains by deep water, rather than forming part of a carbonate shelf. This conclusion further supports the concept of the Perunica microplate (Havlíček *et al.* 1994), which originated by rifting from the shelf of



Gondwana in the Ordovician. The Devonian history of Perunica is poorly known; nevertheless the onset of siliciclastic sedimentation in the Givetian documents its accretion to the Old Red Continent (e.g., Kukul & Jager 1988, Chlupáč 1998). The localised radiation of rutoceratoids during the Pragian suggests that the Perunica microplate was still separated from surrounding terrains by a deep sea at this time, which may have functioned as a barrier for some nectobenthic animals.

12. Signor & Brett (1984) suggested that highly elaborated shell sculptures in nautiloids (e.g., spines, wings, collars, distinct growth walls) functioned as protection against predators and they also pointed out that increasing diversity of well-sculptured nautiloids during the Devonian represents an adaptive reaction to the radiation of durophagous predators. Appearance and diversification of rutoceratoids in the Early–Middle Devonian seems to be in agreement with these suggestions. It is interesting that strongly sculptured nautiloids morphologically convergent with rutoceratoids had already appeared in the Ordovician and Silurian (e.g., *Zitteloceras* Hyatt, 1884, *Corbuloceras* Horný, 1965, *Torquatoceras* Stridsberg, 1988 and several others). Moreover, repaired injuries in shells of pre-Devonian nautiloids may suggest that there were some predators attacking cephalopods in this time. The relative high frequency of repaired injuries may further indicate that attacks by predators on nautiloids were a more than occasional event (and thus documents a relatively high predation pressure in the Ordovician and Silurian; for data see Barrande 1865–1877, Kröger 2004, Manda & Turek in press). If well-sculptured shells represented a predator resistant (defensive) feature, the question is then raised as to why Ordovician and Silurian nautiloids with such shell sculptures represent rare, palaeobiogeographically strongly limited and short-lived nautiloid taxa. We conclude, as did Signor & Brett (1984), that there does not appear to be any explanation for the scarcity of well-sculptured nautiloids in the Ordovician and Silurian and their rapid diversification in the Pragian (especially if such diversification was not coincident with the prominent radiation of durophagous predators in the Prague Basin).

It may be pointed out that rutoceratoids represent a single new Early Devonian cephalopod clade with highly sculptured shells and shell outgrowths. Remaining new Early Devonian clades exhibit clearly similar sculpture as analogous Ordovician and Devonian cephalopod morphotypes (e.g., Nephriticeratidae versus Lechritrochocerotidae, Spyroceratidae versus Kionoceratidae, Entimoceratidae versus Trimeroceratidae). Consequently, the radiation of rutoceratoids (i.e., highly sculptured cephalopods) in the Early Devonian probably represents an effect (fabricational noise) of cephalopod faunal recovery after the Silurian-Devonian boundary Event rather than a radiation of durophagous predators.

## Acknowledgments

David H. Evans (Natural England, Peterborough) and Christian Klug (Universität Zürich, Zürich) are deeply acknowledged for manuscript revision and valuable suggestions substantially improving this paper. Many thanks to Radvan Horný (National Museum, Prague) for critical reading of the manuscript and for language corrections. Petr Budil (Czech Geological Survey) kindly gave access to Bouška's collection. The authors thank Jessica Cundiff (Museum of Comparative Zoology, Harvard) for providing the material from Šárý's collection used in this study. The contribution was supported by the projects Kontakt (MEO8011), VaV DE08P04OMG002 (Š. Manda) and GACR 205/09/0260 (V. Turek).

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## Appendix: Classification of rutoceratoids

Only genera considered in this paper to be rutoceratoids are included.

Hyatt (1884, 1894)

Family Hercoceratidae Hyatt, 1884

*Ptyssoceras* Hyatt, 1884

*Hercoceras* Barrande, 1865

*Ptenoceras* Hyatt, 1894

Family Rutoceratidae Hyatt, 1884

*Halloceras* Hyatt, 1884

*Rutoceras* Hyatt, 1884

*Adelphoceras* Barrande, 1870

*Kophinoceras* Hyatt, 1884

Family Discoceratidae Hyatt, 1894

*Trochoceras* Barrande, 1848

Hyatt (1900)

Superfamily Ryticeratida Hyatt, 1900

Family Halloceratidae Hyatt, 1900

*Halloceras* Hyatt, 1884

Family Ryticeratidae Hyatt, 1900

*Ryticeras* Hyatt, 1900

(= *Rutoceras* Hyatt, 1884)

*Cophinoceras* Hyatt, 1884

(= *Kophinoceras* Hyatt, 1884)

Superfamily Hercoceratida Hyatt, 1900

Family Hercoceratidae Hyatt, 1884

*Hercoceras* Barrande, 1865

*Ptyssoceras* Hyatt, 1884

*Ptenoceras* Hyatt, 1894

Flower & Kummel (1950)

Order Rutoceratida Flower, 1950

Family Rutoceratidae Hyatt, 1884

*Rutoceras* Hyatt, 1884

*Adelphoceras* Barrande, 1870

*Casteroceras* Flower, 1936

*Centrolitoceras* Flower, 1945

*Diademoceras* Flower, 1945

*Goldringia* Flower, 1945

*Halloceras* Hyatt, 1884

*Hercoceras* Barrande, 1865

*Hindeoceras* Flower, 1945

*Homoadelphoceras* Foerste, 1926

*Ptenoceras* Hyatt, 1894

*Pleuronoceras* Flower, 1945

*Ptyssoceras* Hyatt, 1884

*Roussanoffoceras* Foerste, 1925

*Trochoceras* Barrande, 1848

Family Tetragonoceratidae Flower, 1945

*Nassauoceras* Miller, 1932

Ruzhencev *et al.* (1962)

Order Oncocerida Flower, 1950

Superfamily Ptenocerataceae Teichert, 1938

Family Ptenoceratidae Teichert, 1938

*Ptenoceras* Hyatt, 1894

*Adelphoceras* Barrande, 1870

*Homoadelphoceras* Foerste, 1926

Order Nautilida Agassiz, 1847

Suborder Rutoceratina Hyatt, 1884

Superfamily Rutocerataceae Hyatt, 1884

Family Rutoceratidae Hyatt, 1884

*Rutoceras* Hyatt, 1884

*Casteroceras* Flower, 1936

*Centrolitoceras* Flower, 1945

*Diademoceras* Flower, 1945

*Goldringia* Flower, 1945

*Halloceras* Hyatt, 1884

*Hercoceras* Barrande, 1865

*Hindeoceras* Flower, 1945

*Pleuronoceras* Flower, 1945

*Ptyssoceras* Hyatt, 1884

*Roussanoffoceras* Foerste, 1925

*Tetranodoceras* Flower, 1936

*Trochoceras* Barrande, 1848

Suborder Tainoceratina Hyatt, 1883

Superfamily Tainoceratidae Hyatt, 1883

Family Tetragonoceratidae Flower, 1945

*Nassauoceras* Miller, 1932

Kummel (1964)

Order Nautilida Agassiz, 1847

Superfamily Tainocerataceae Hyatt, 1883

Family Rutoceratidae Hyatt, 1884

*Rutoceras* Hyatt, 1884

*Adelphoceras* Barrande, 1870

*Casteroceras* Flower, 1936

*Centrolitoceras* Flower, 1945

*Diademoceras* Flower, 1945

*Goldringia* Flower, 1945

*Halloceras* Hyatt, 1884

*Hercoceras* Barrande, 1865

*Hindeoceras* Flower, 1945

*Homoadelphoceras* Foerste, 1926

*Ptenoceras* Hyatt, 1894

*Pleuronoceras* Flower, 1945

*Ptyssoceras* Hyatt, 1884

*Roussanoffoceras* Foerste, 1925

*Trochoceras* Barrande, 1848

Family Tetragonoceratidae Flower, 1945

*Nassauoceras* Miller, 1932

Zhuravleva (1974)

Order Oncocerida Flower, 1950

Family Ptenoceratidae Teichert, 1939

*Ptenoceras* Hyatt, 1894

*Adelphoceras* Barrande, 1870

*Doleroceras* Zhuravleva, 1972

*Homoadelphoceras* Foerste, 1926

*Megaloceras* Zhuravleva, 1974

*Ptyssoceras* Hyatt, 1884

*Spanioceras* Zhuravleva, 1974

*Trochoceras* Barrande, 1848

Order Nautilida Agassiz, 1847

Suborder Rutoceratina Hyatt, 1884

Superfamily Rutocerataceae Hyatt, 1884

Family Rutoceratidae Hyatt, 1884

*Rutoceras* Hyatt, 1884

*Adeloceras* Zhuravleva, 1974

*Alethynoceras* Zhuravleva, 1974

*Anepheloceras* Zhuravleva, 1974

*Aphytoceras* Zhuravleva, 1974

*Bastindoceras* Zhuravleva, 1974

*Casteroceras* Flower, 1936

*Capricornites* Zhuravleva, 1974

*Centrolitoceras* Flower, 1945

*Diademoceras* Flower, 1949

*Goldringia* Flower, 1945

*Halloceras* Hyatt, 1884

*Hercoceras* Barrande, 1866

*Hindeoceras* Flower, 1945

*Kophinoceras* Hyatt, 1884

*Piratoceras* Zhuravleva, 1974

*Pleuronoceras* Flower, 1950

*Uloceras* Zhuravleva, 1974

*Roussanoffoceras* Foerste, 1925

*Tetranodoceras* Flower, 1936

Family Tetragonoceratidae Flower, 1945

*Nassauoceras* Miller, 1932

Dzik (1984)

Order Oncocerida Flower, 1950

Family Rutoceratidae Hyatt, 1884

*Rutoceras* Hyatt, 1884 (= *Goldringia* Flower, 1945)

?*Ptenoceras* Hyatt, 1894 (= *Pleuronoceras* Flower, 1950)

*Aphytoceras* Zhuravleva, 1974

*Capricornites* Zhuravleva, 1974

*Casteroceras* Flower, 1936

?*Halloceras* Hyatt, 1884

*Hindeoceras* Flower, 1945

(= *Centrolitoceras* Flower, 1945)

Order Nautilida Agassiz, 1847

Suborder Centroceratina Flower, 1950

Family Trochoceratidae Zittel, 1884

*Trochoceras* Barrande, 1848

*Hercoceras* Barrande, 1865

(= *Adeloceras* Zhuravleva, 1974; *Spanioceras* Zhuravleva, 1974)

*Megaloceras* Zhuravleva, 1974)

*Nassauoceras* Miller, 1932

?*Doleroceras* Zhuravleva, 1972

?*Ptenoceras* Hyatt, 1894

?*Adelphoceras* Barrande, 1870

?*Anepheloceras* Zhuravleva, 1974

?*Halloceras* Hyatt, 1884

This paper

Order Oncocerida Flower, 1950

Superfamily Rutoceratoidea Hyatt, 1884

Family Parauloceratidae fam. nov.

*Parauloceras* gen. nov. (Pragian–Emsian)

*Uloceras* Zhuravleva, 1974 (Emsian)

Family Hercoceratidae Hyatt, 1884

(= Ptenoceratidae Teichert, 1939)

*Ptenoceras* Hyatt, 1894 (Pragian–Eifelian)

(= *Doleroceras* Zhuravleva, 1972)

*Adeloceras* Zhuravleva, 1974 (Emsian)

*Anepheloceras* Zhuravleva, 1974 (Emsian)

*Capricornites* Zhuravleva, 1974 (Emsian)

*Centrolitoceras* Flower, 1945 (Middle Devonian)

*Diademoceras* Flower, 12949 (Emsian)

*Hercoceras* Barrande, 1865 (Late Emsian–Eifelian)

(= *Bastindoceras* Zhuravleva, 1974; *Piratoceras* Zhuravleva, 1974; *Spanioceras* Zhuravleva, 1974; ?*Megaloceras* Zhuravleva, 1974; *Moneroceras* Zhuravleva, 1996;

?*Nassauoceras* Miller, 1932)

*Nozemoceras* Zhuravleva, 1996 (Emsian)

*Otomaroceras* gen. nov. (Pragian)

*Ptyssoceras* Hyatt, 1884 (Pragian)

*Pleuronoceras* Flower, 1950 (Middle Devonian)

New unnamed genus (based on *Rutoceras eospinosum* Zhuravleva, 1974, Emsian)

Family Rutoceratidae Hyatt, 1884

(= *Halloceratidae* Hyatt, 1900; *Ryticeratidae* Hyatt, 1900;

*Adelphoceratidae* Foerste, 1926)

*Adelphoceras* Barrande, 1870 (late Emsian)

*Aphytoceras* Zhuravleva, 1974 (Pragian–Givetian)

*Capricornites* Zhuravleva, 1974 (Emsian)

*Casteroceras* Flower, 1936 (Middle Devonian)

*Goldringia* Flower, 1945 (Pragian–Givetian)

*Halloceras* Hyatt, 1884 (Emsian–Givetian)

*Hindeoceras* Flower, 1945 (Eifelian–Frasnian)

*Homoadelphoceras* Foerste, 1926 (Late Emsian)

*Kophinoceras* Hyatt, 1884 (Middle Devonian)

*Pseudorutoceras* gen. nov. (Eifelian–Givetian)

*Rutoceras* Hyatt, 1884 (Pragian–Givetian, ?early Frasnian)

*Tetranodoceras* Flower, 1936 (Middle Devonian)

?Family Trochoceratidae Zittel, 1884

*Trochoceras* Barrande, 1848 (Pragian)