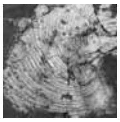
New Silurian nautiloids *Phragmoceras* Broderip, 1839, and *Tubiferoceras* Hedström, 1917, from the Prague Basin (Bohemia)

ŠTĚPÁN MANDA



The morphologically distinct nautiloid genera *Phragmoceras* and *Tubiferoceras* (Discosorida, Phragmoceratidae) with an endogastric brevicone shell and a contracted aperture are characteristic components of the Silurian tropical faunas of Baltica and Laurentia. Seven previously known species of *Phragmoceras* from the Prague Basin (Perunica) are mainly from cephalopod limestones of the Ludlow age. Amongst these, two species are recorded from beyond the Prague Basin. *Phragmoceras imbricatum* is recognised in Avalonia and Baltica and its geographic distribution suggests a palaeobiogeographical connection across the Rheic Ocean during the earlier Ludlow time. *Phragmoceras labiosum* was recorded in the Bohemian-type Ludfordian fauna of Sardinia (peri-Gondwana). This paper deals with several phragmocerids from the Prague Basin which have not been recorded before. They include *Phragmoceras munthei* from the latest Llandovery and earlier Wenlock, *Tubiferoceras proboscoideum* from the early Wenlock, *Phragmoceras acuminatum*, *Phragmoceras sigmoideum*, *Phragmoceras* cf. *undulatum,* and *Phragmoceras* cf. *ventricosum* from the late Wenlock. A new species *Phragmoceras koneprusensis* sp. nov. from the early Ludfordian (Ludlow) is established. These species are closely related or conspecific to those described from Gotland (Baltica), Ireland (Laurentia) or Wales (Avalonia) and indicate an open seaway between the Prague Basin (Perunica) and Baltica, Laurentia and Avalonia, respectively, since the latest Llandovery. In addition, occurrences of phragmocerids in the Prague Basin suggest that in contrast to the rest of peri-Gondwanan areas a relative temperate water environment was typical for Perunica since latest Llandovery. • Key words: Nautiloidea, Discosorida, new taxa, palaeobiogeography, Silurian, Prague Basin.

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Nautiloids of the genera *Phragmoceras* Broderip, 1839, and *Tubiferoceras* Hedström, 1917, form a characteristic component of Silurian nautiloid faunas, which inhabited mainly tropical carbonate platforms of the Baltica and Laurentia (*e.g.,* Flower & Teichert 1957, Holland & Stridsberg 2004). Barrande (1865–1877) described 33 species of *Phragmoceras* including cyrtocone brevicone shells with a contracted aperture from the Silurian and Devonian strata of the Prague Basin. The majority of these taxa were later recognised as new oncocerid genera (Hyatt 1883, Hedström 1917, Foerste 1926). Flower & Teichert (1957) emended the diagnosis of *Phragmoceras* and pointed out that, in fact, only six of Barrande's species in fact belong to the later genus, namely *Phragmoceras biimpresum* Barrande, 1865; *Phragmoceras broderipi broderipi* Barrande, 1865; *Phragmoceras broderipi sublaeve* Barrande, 1865; *Phragmoceras imbricatum* Barrande, 1865; *Phragmoceras labiosum* Barrande, 1865; and *Phragmoceras longum* Barrande, 1865. Dzik (1984) assigned the species *Cyrtoceras beaumonti* Barrande, 1866, to *Phragmoceras* suggesting that *C. beaumonti* is a junior synonym of *Phragmoceras broderipi*. Previously, Flower & Teichert (1957) had assigned this species to *Protophragmoceras* Hyatt, 1900.

Although phragmoceratids form rare elements of these faunal assemblages, examples of all of the species of *Phragmoceras* from the Prague Basin described by Barrande – with the single exception of *Phragmoceras biimpressum* – have been found during the last decades (Kříž 1998, Manda & Kříž 2006). Species assignable to *Phragmoceras* described by Barrande occur mostly in the cephalopod limestones of the Ludlow age; the oldest species of them, *Phragmoceras imbricatum*, appeared in the early Gorstian *N. nilsonni* Zone while the youngest, *Phragmoceras beaumonti*, occurred in the Ludfordian *N. kozlowskii* Zone (Fig. 2). In this paper, new phragmoceratid material from the latest Llandovery, Wenlock and

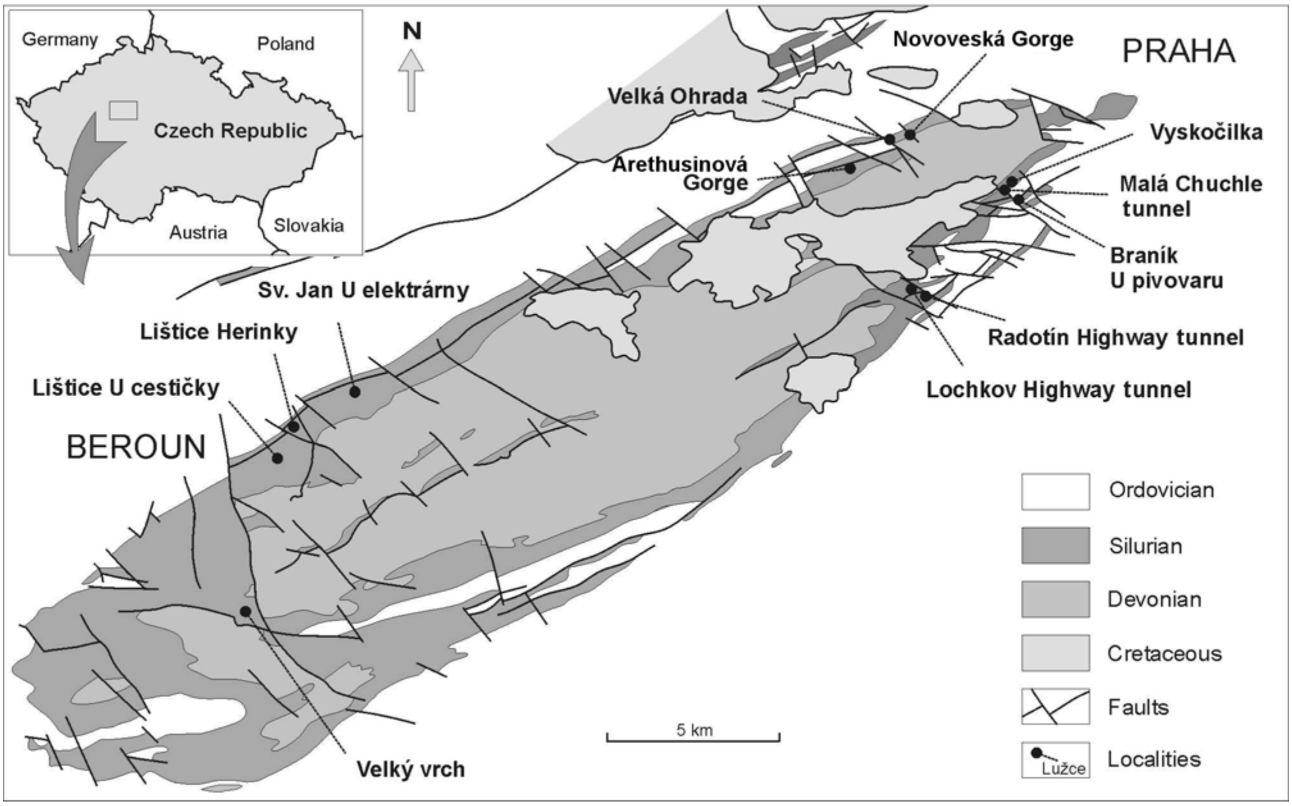

Figure 1. Distribution of Silurian rocks in the Prague Basin and position of the mentioned sections.

Ludlow series together with a revised stratigraphic range of the genus *Phragmoceras* in the Prague Basin are described.

Material and methods

The oldest phragmocerid in the Prague Basin was discovered by Bouček (1938) in a graptolite shale of the late Llandovery (Telychian) age exposed in the Novoveská Gorge at Malá Ohrada (Fig. 1). The material collected by B. Bouček is deposited in the collections of the Czech Geological Survey together with additional specimens collected later by M. Šnajdr in other sections. Štorch (1994) reported the occurrence of a mudstone bed with "surprisingly common phragmocerids" in the earlier Wenlock stage at Velká Ohrada Section (Fig. 1). Though, unfortunately, his material was lost, several years later a similar bed with *Phragmoceras munthei* Hedström, 1917, was found in dumps that originated from the highway tunnel construction at Lochkov Village in 2005 (Fig. 1). Study of *Phragmoceras sigmoideum* Hedström, 1917, and *Phragmoceras* cf. *undulatum* Hedström, 1917, was based on material from Barrande's collection. *Phragmoceras acuminatum* Hedström, 1917, and *Phragmoceras* cf. *ventricosum* Sowerby, 1928, were studied using newly obtained material from the Homerian limestone of the Motol Formation. A single new species *Phragmoceras koneprusensis* has been established, based on new material from the early Ludfordian limestone of the Kopanina Formation.

The description of *Tubiferoceras proboscoideum* (Hedström, 1917), is based on two specimens from the Sheinwoodian limestone of the Motol Formation exposed at U Elektrárny Section close to the village of Svatý Jan pod Skalou (Fig. 1). These specimens were noted as *Phragmoceras broderipi* by Barrande (1867) and Prantl (1952) and described as an indeterminable phragmocerid by Galle & Horný (1964).

Apart from their rarity, the mode of preservation of these fossils complicates their taxonomic determination. The state of phragmocerid preservation varies considerably in the early Silurian strata of the Prague Basin, although phragmocerids collected in the Ludlow limestone of the Kopanina Formation are usually well preserved. The description of *Phragmoceras munthei* Hedström, 1917, herein is based on complete but compressed shells collected from the calcareous shales of the lower Motol Formation. The other specimens were as usual found in the skeletal limestones of the upper Motol Formation, considered to have been deposited in relatively shallow, high-energy environments associated with submarine volcanic elevations (Kříž 1991). These shells are commonly disarticulated into body chambers and phragmocones in which the apical part and internal structures are usually broken. Only smaller phragmocerid shells are occasionally better preserved as the almost complete shell.

The terms describing morphology of the contracted aperture and shell dimensions are corresponding to Stridsberg (1985, pp. 8–10, figs 3, 4). Angle of shell expansion is measured in dorsoventral plane.

The described specimens are deposited in the author's collection of the Czech Geological Survey, Prague (SM), and in the collections of the Faculty of Natural Sciences, Charles University, Prague (FNS). Barrande's collection (L) is housed in the National Museum, Prague.

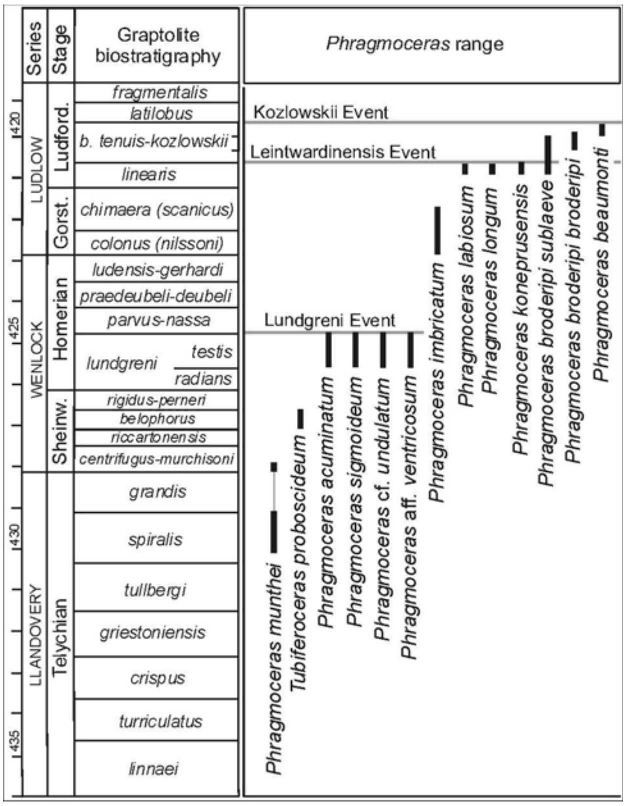

Figure 2. Range of phragmocerids in the Silurian of the Prague Basin. Graptolite biostratigraphy adopted from Kříž (1991), Manda & Kříž (2006), Štorch (2006).

Systematic palaeontology

Subclass Nautiloidea Agassiz, 1847
Order Discosorida Flower, 1950 (*in* Flower & Kummel 1950)
Family Phragmoceratidae Miller, 1877

Remarks. – Flower & Teichert (1957) and Teichert (1964) emended the diagnosis of the family Phragmoceratidae, which, in their opinion, included discosorids with a cyrtoconic, endogastric and compressed shell possessing a strongly contracted aperture "modified in various ways" and siphuncles with broadly expanded segments and thick connected rings. According to the authors, the family comprises seven Silurian and Devonian genera: *Phragmoceras* Broderip, 1839 (*in* Murchison 1839); *Protophragmoceras* Hyatt, 1900 (*in* Zittel 1900); *Endoplectoceras* Foerste, 1924; *Pristeroceras* Ruedemann, 1925; *Sthenoceras* Flower, 1957 (*in* Flower & Teichert 1957); *Tubiferoceras* Hedström, 1917; and *Phragmocerina* Flower, 1948. Two of them, namely *Phragmoceras* and *Tubiferoceras*, only clearly correspond to the emended family diagnosis.

Protophragmoceras and *Endoplectoceras* share a relatively thin siphonal tube and an open aperture and are probably closely related to the Late Ordovician *Strandoceras* Flower, 1946, Cyrtogomphoceratidae Flower, 1940 (see Dzik 1984). *Pristeroceras* possess a brevicone shell and a constricted aperture with six lobes resembling members of oncocerid family Hemiphragmoceratidae Foerste, 1926 (see Stridsberg 1985). *Sthenoceras* comprise several species having slightly curved shells with a relatively wide siphonal tube, circular cross section and an open aperture. The embryonic shell of the type species *Cyrtoceras aduncum* Barrande, 1868 (unpublished data) is markedly smaller than that of *Phragmoceras*. In addition, the embryonic shell of *Cyrtoceras aduncum* is only gently curved in contrast to that in species of the *Phragmoceras*. Thus, the *Sthenoceras* should be excluded from the family Phragmoceratidae. *Phragmocerina* is poorly known; nevertheless the straight brevicone shell and contracted aperture with almost circular apertural opening suggested position within family Mandaloceratidae Flower, 1957 (*in* Flower & Teichert 1957). As a consequence, Dzik (1984) considered just two genera, *Phragmoceras* and *Tubiferoceras,* as members of the Phragmoceratidae.

Dzik (1984) also added the late Emsian to Eifelian genus *Bolloceras* Foerste, 1926, to that family. However, although *Bolloceras* is similar in shape to *Phragmoceras*, it possesses actinosiphonate deposits, and it should be assigned to the Oncocerida (Zhuravleva 1974).

Thus, the family Phragmoceratidae consists of no more than Silurian genera: *Phragmoceras* and *Tubiferoceras*. The features they share are the contracted, more or less modified T-shaped apertures combined with siphuncles possessing broadly expanded segments and thick connected rings. *Phragmoceras* is probably derived from the Late Ordovician *Strandoceras* Flower, 1940 (Cyrtogomphoceratidae Flower, 1940) which possessed a cyrtoconic and endogastric shell with an open aperture (Flower & Teichert 1957). The current earliest records of *Phragmoceras* are found in the early Llandovery (*P. acuminatus* Zone, Siberia; Kiselev 1998, Bogolepova *et al.* 2000). Having reached its highest diversity during the Wenlock and early Ludlow, the genus became extinct during the late Ludlow. *Phragmoceras* is considered as including more than fifty species (*e.g.*, Flower & Teichert 1957). Besides the Prague Basin, *Phragmoceras* occurs in Gotland (Hedström 1917, Holland & Stridsberg 2004), Estonia (Kiselev *et al.* 1990), Podolia in Ukraine (Kiselev 1986, Kiselev *et al.* 1987), the North Ural (Kiselev 1984), Siberia (Kiselev 1998), Severnaya Zamlya (Bogolepova *et al.* 2000), Inner Mongolia (Zou Xi-Ping 1983), Tian Shan (Kiselev *et al.* 1993), Illinois, Indiana, New York, Ohio, Ontario, Quebec, Wisconsin (for summary see Flower & Teichert 1957), Scotland (Holland 2000), Wales and the Welsh Borderland (Murchison 1839, Blake 1882, Holland & Stridsberg 2004), Ireland (Evans 2002), and Sardinia (Stridsberg 1988a; Gnoli 1990, 1993).

The genus *Tubiferoceras* was derived from *Phragmoceras* and is characterized by a straight or only slightly curved brevicone shell and protruding apertural opening (Flower & Teichert 1957). The genus ranges from the Llandovery to the Wenlock and is known from Gotland (Hedström 1917), Scotland (Holland 2000), Indiana, Wisconsin (Flower & Teichert 1957) and Siberia (*Phragmoceras nikiforovae* sp. nov. *in* Kiselev 1998). *Tubiferoceras proboscoideum* from the Prague Basin represents the first genus recorded outside the tropical zone.

Genus *Phragmoceras* Broderip, 1839

Type species. – *Phragmoceras arcuatum* Sowerby, 1839 (*in* Murchison 1839). Gorstian. The Welsh Borderland, Ledbury.

Phragmoceras munthei Hedström, 1917
Figure 3A–G

- 1917 *Phragmoceras munthei* n.; Hedström; pp. 27, 28, pl. 25, figs 1–9.
- 1917 *Phragmoceras convolutum* n.; Hedström, p. 29, pl. 26, figs 1–14, pl. 8, figs 1–3.
- 1938 *Phragmoceras* sp. – Bouček, p. 172.
- ?1990 *Phragmoceras munthei* Hedström, 1917. – Kiselev *et al*., p. 50, pl. 11, fig. 2.
- 1994 *Phragmoceras* sp. – Štorch, p. 167.
- ?1994 *Protophragmoceras* ? sp. – Evans, p. 144, figs 16.2–4.
- ?2002 *Phragmoceras* sp. – Evans, p. 92, text-fig. 4b.
- 2004 *Phragmoceras munthei* Hedström, 1917. – Holland & Stridsberg, p. 309, fig. 4D, E.
- 2004 *Phragmoceras convolutum* Hedström, 1917. – Holland & Stridsberg, p. 309.

Lectotype. – Specimen designated by Holland & Stridsberg (2004) and figured by Hedström (1917) on pl. 25 as figs 1–3. Early Wenlock. Gotland. Visby Bed. Visby.

Material. – 14 specimens (SM 81–89, 93, 94, FNS 7754a, b, L 38728).

Description of the Bohemian material. – Coiled endogastric shell with medium angle of expansion. Aperture open up to a height of 50 mm (SM 85), contracted from a height of 65 mm, relatively wide apertural opening, moderately protruding hyponomic opening (SM 82). Hyponomic sinus deep and narrow. Prominent regular growth lines form dorsal parabolic lobe, small broad lateral saddle and narrow ventral lobe. Imbricate growth lines triangular in cross-section with ad-apical side longer than ab-apical side. Distance between the growth lines varies from dorsum to venter with the distance being about 2–2.5 times greater on the dorsum. Distance of growth lines generally increases with shell size; number of growth lines per 10 millimetres varies from 8 to 12. Maximum shell thickness is 0.5 mm. Maximum length of the shell is 95 mm, maximum height 65 mm.

Discussion. – Specimens from the Prague Basin are preserved as compressed shells with affected proportions, while shell size, mode of coiling, angle of expansion and sculpture are similar or identical to characters of *Phragmoceras munthei* from Gotland (Holland & Stridsberg 2004). Outside the island Gotland, *Phragmoceras munthei* is reported from the early Wenlock of Estonia (Kiselev *et al.* 1990). In addition, the specimens designated by Evans (1994, 2002) as *Protophragmoceras*? sp., *Phragmoceras* sp., respectively, from the latest Llandovery of Ireland and showing the same mode of preservation, shape of shell and sculpture as the Bohemian specimens could be placed in *Phragmoceras munthei*.

Occurrence. – Prague Basin (Bohemia): Silurian, latest Llandovery and earlier Wenlock. Motol Formation.

Latest Llandovery, Telychian, *O. spiralis* Zone: Braník, U Pivovaru Section (old quarry and sewerage system canal S7 beneath): shale with graptolites, pelagic orthocerids, cephalopod operculum *Aptychopsis prima* Barrande, 1872, rare bivalve *Slava norna* Kříž, 1985, brachiopod *Valdaria budili* Havlíček, 1990 (Kříž 1991) and Malá Chuchle, Tunnel Section: shale with graptolites and rare brachiopods, dendroids (Havlíček & Štorch 1990) and bivalve *Cardiola* sp. Novoveská Gorge Section: shale with graptolites, rare inarticulate and articulate brachiopods, dendroids, operculum *Aptychopsis* sp., and pelagic orthocerids (Bouček 1938). Radotín, highway tunnel: shale with common graptolites and rare brachiopods.

Earlier Wenlock, Sheinwoodian, *C. murchisoni* Zone: Malá Chuchle, Vyskočilka Section: mudstone and shale with graptolites, orthocerids and rare *Aptychopsis prima*. Lochkov, highway tunnel: mudstone bed within shale containing brachiopod *Valdaria budili*, orthocerids, dendroids and fragments of eurypterids. Velká Ohrada Section: mudstone bed

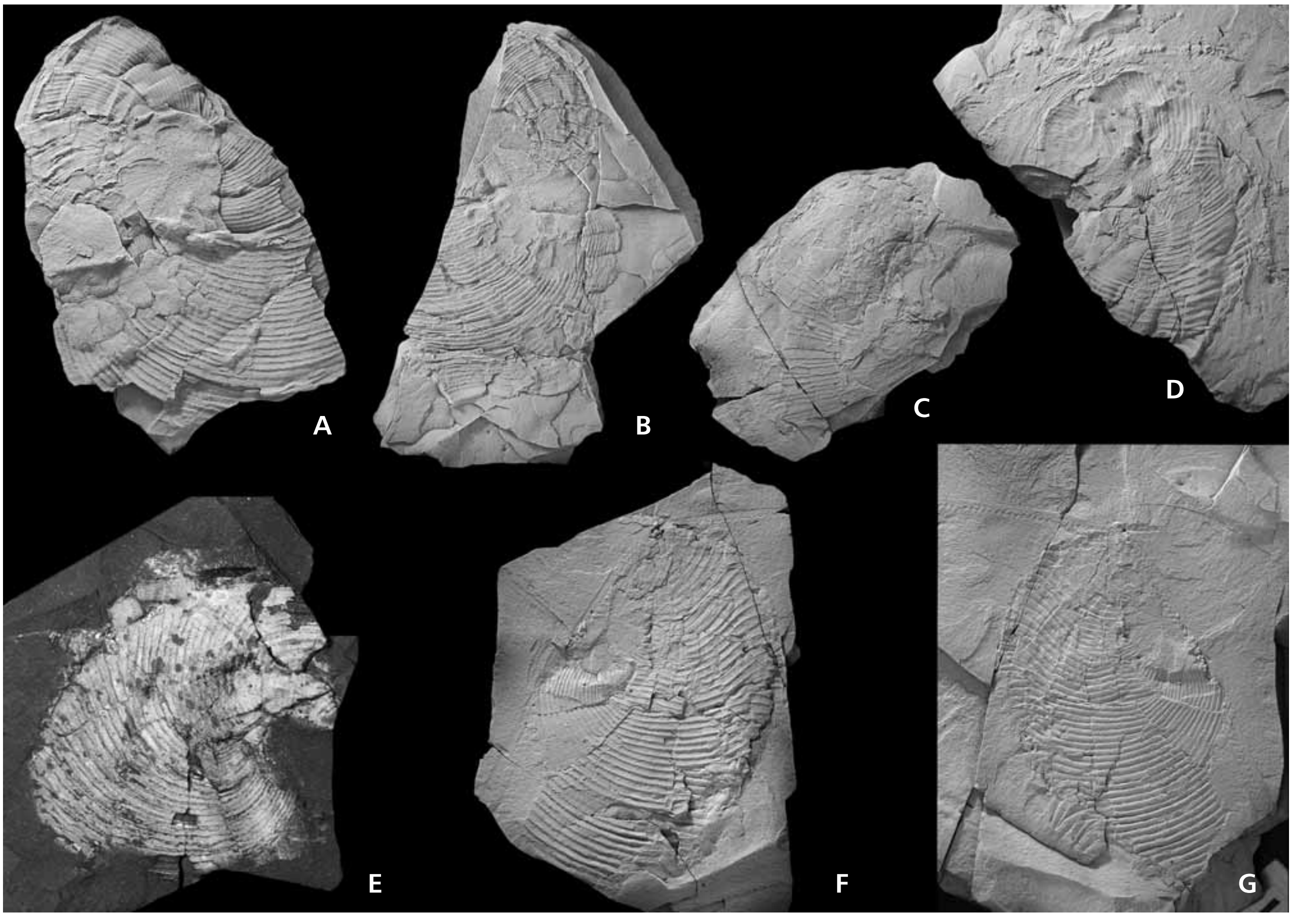

Figure 3. *Phragmoceras munthei* Hedström, 1917, from the latest Llandovery and earlier Wenlock of the Prague Basin, all specimens come from the Motol Formation. • A, B – lateral views, part and counterpart, specimen SM 82a, b; Nová Ves Section; Llandovery, Telychian, *O. spiralis* Zone. • C – lateral view, specimen FNS 7754b; Malá Chuchle, Vyskočilka Section; Wenlock, Sheinwoodian, *C. murchisoni* Zone; × 2.2. • D – lateral view, specimen SM 86; Braník U pivovaru Section, sewerage system canal S7 beneath; Llandovery, Telychian, *O. spiralis* Zone; × 2. • E – lateral view, specimen SM 87; Braník U pivovaru Section; Llandovery, Telychian, *O. spiralis* Zone; × 1. • F, G – lateral views, part and counterpart, specimen SM 81a, b; Nová Ves Section; Llandovery, Telychian, *O. spiralis* Zone; × 1.3.

within shale, the mudstone contains except common phragmocerids also graptolites, orthocerids, *Aptychopsis* sp., brachiopod *Valdaria budili* and dendroids (Štorch 1994).

Gotland: Late Llandovery and early Wenlock. Visby Beds (Hedström 1917, Holland & Stridsberg 2003). ?Estonia: Early Wenlock. Janis Horizon (Kiselev *et al.* 1990). ?Ireland: Latest Llandovery. Kilbride Formation. Kilbride (Evans 1994, 2002).

Phragmoceras acuminatum Hedström, 1917

Figure 4A–D

1917 *Phragmoceras acuminatum* n.; Hedström, p. 17, pl. 10, figs 2–7.
1957 *Phragmoceras acuminatum* Hedström. – Flower & Teichert, p. 120.
?1986 *Phragmoceras acuminatum* Hedström. – Kiselev, pp. 88, 89, pl. 1, fig. 1.
?1987 *Phragmoceras acuminatum* Hedström. – Kiselev *et al.*, p. 88, pl. 15, figs 1, 2.
2004 *Phragmoceras acuminatum*. – Holland & Stridsberg, p. 302.

Lectotype. – Specimen designated by Kiselev (1986) and figured by Hedström (1917) on pl. 10 and figs 5, 6. Wenlock. Visby Bed. Gotland, Larbo.

Material. – Four specimens; SM 58, 78, 90, 91.

Description of the Bohemian material. – Endogastric, breviconic cyrtocone with sub-triangular ventrally flattened cross-section, the ratio between dorsoventral and lateral diameter is about 1.4. Ventral, rather thin siphonal tube of sub-circular cross-section. Angle of shell expansion is about 25°. Septa very shallow. Suture straight, oblique. Camerae relatively shallow. Distance between septa ventrally side is approximately half that of the dorsal side. The body chamber (SM 58) is 42 mm long and 39 mm high with almost straight, ventral and moderately curved dorsal side. Hyponomic sinus is shallow and narrow. Aperture opened yet at height of 33 mm and contracted still at height of 40 mm. Aperture opening moderate elliptical, laterally elongated and oblique to the hyponomic sinus. Shell smooth or with fine irregular growth lines. Traces of growth lines follow hyponomic sinus, close to the ventral side growth lines form small lobe extended to the shallow broad saddle at dorsal side. The distance between growth lines varies between 0.25 and 1 mm. The shell thickness is about 1 mm. Maximum length of the shell is ca 80 mm and height 40 mm.

A neanic shell with open aperture from the Velká Ohrada, Arethusina Gorge Section (SM 78), probably belongs to *Phragmoceras acuminatum*. The body chamber is 15 mm wide and 19 mm high; length is 17 mm. Aperture opened with shallow and broad hyponomic sinus and very shallow and broad dorsal lobe. Septa very shallow. Sutures straight, oblique with small dorsal saddle. Camerae shallow, about 1 mm in length. Shell thickness is 0.2 mm.

Discussion. – Specimens from the Prague Basin differ from those of Gotland in less frequent irregular growth lines suggesting intra-specific variation.

Occurrence. – Prague Basin (Bohemia): Silurian, Wenlock, Homerian, *C. lungreni* Zone, *T. testis* Subzone. Motol Formation. Herinky Hill near Lištice, Barrande's pit: grainstone with *Plicocyrtia* Community (Havlíček & Štorch 1990) and overlaying cephalopod-trilobite packstone (Manda 1996). Velká Ohrada (Prague): Arethusinová Gorge, cephalopod limestone, *Cardiola agna* Community (Kříž 1998).

Gotland: Wenlock. Silte Beds (Hedström 1917). ? Podoli in Ukraine: Early Wenlock. Sokolovsk and Grinchevsk formations (Kiselev *et al.* 1987).

***Phragmoceras sigmoideum* Hedström, 1917**
Figure 5A–D

1917 *Phragmoceras sigmoideum* n.; Hedström, pp. 22, 23, pl. 17, figs 1–5, pl. 18, figs 1–7.
1957 *Phragmoceras sigmoideum* Hedström. – Flower & Teichert, p. 120.
1984 *Phragmoceras sigmoideum* Hedström, 1917. – Kiselev, p. 42, pl. 4, fig. 2, pl. 5, fig. 1, pl. 9, fig. 1.
non 2004 *Phragmoceras undulatum*. – Holland & Stridsberg, p. 302.

Lectotype. – Specimen designated by Kiselev (1984) and figured by Hedström (1917) on pl. 17, fig. 1. Wenlock. Visby Bed. Gotland, Larbro, Storugns.

Material. – Single specimen L 38727.

Description of the Bohemian material. – The only known specimen is represented by body chamber, 69 mm long, 74 mm high and 46 mm wide, ventral and dorsal sides are equally moderately curved. Cross-section elliptical, the ratio between dorsoventral and lateral diameter is about 1.4. Subventral siphonal tube with dorsoventrally elongated elliptical cross-section, 10 mm high and 6.5 mm wide, the distance of the siphuncle from the ventral side is 2 mm. Suture oblique with very shallow ventral lobe, angle between suture and line of hyponomic sinus is approximately 16°. Septa are moderately deep. An aperture opening is as wide as body chamber, approximately elliptical, laterally elongated with a symmetrical pair of lobes directed ventrolaterally: its height is 35 mm and width is 22 mm. Hyponomic sinus narrow with minimum width of 2.5 mm. Hyponomic opening slightly protruding, but its end is not preserved. Shell smooth with one preserved distinctive growth line forming a broad lateral lobe. Maximum shell thickness is 3 mm at apertural opening, but as usual about 0.5 mm.

Discussion. – The single specimen from the Prague Basin shows the same morphological features as specimens from Gotland. *Phragmoceras sigmoideum* exhibits a slightly curved shell, medium compressed cross-section and shape of aperture with downward directed apertural opening and smooth shell with some narrow and irregular growth lines. Holland & Stridsberg (2004) considered *Phragmoceras sigmoideum* as conspecific with *Phragmoceras undulatum* Hedström, 1917; ascribing the prominent regular annulation and more compressed cross-section of *P. undulatum* to sexual dimorphism. Nevertheless, as no Palaeozoic nautiloid is documented to have prominent sexual dimorphism of the shell surface; *i.e.* smooth shell with gently irregular annulae *versus* regular prominent annulation. No phragmocerid population of shells (up to 25 shells) from a single bed and locality, collected during this study of the Prague Basin assemblages, exhibited a similar variation in shell surface and cross-section. Thus, both taxa are probably closely related, but represent rather distinctive species.

Occurrence. – Prague Basin (Bohemia): Silurian, Wenlock, Homerian, *C. lungreni* Zone, *T. testis* Subzone. Motol Formation. Malá Chuchle, Vyskočilka. The single specimen of *Phragmoceras sigmoideum* exhibits unusual preservation. The body chamber is filled by grey micrite and coarse milky sparite, the shell is substituted by medium crystals of dark grey calcite. This mode of preservation is found at the Vyskočilka locality in a single bed of shale with limestone nodules and several cephalopods preserved as nodules. The bed corresponds with the latest *T. testis* Subzone and occurs about 80–160 cm bellow the *Monograptus dubius parvus* Zone (unpublished data).

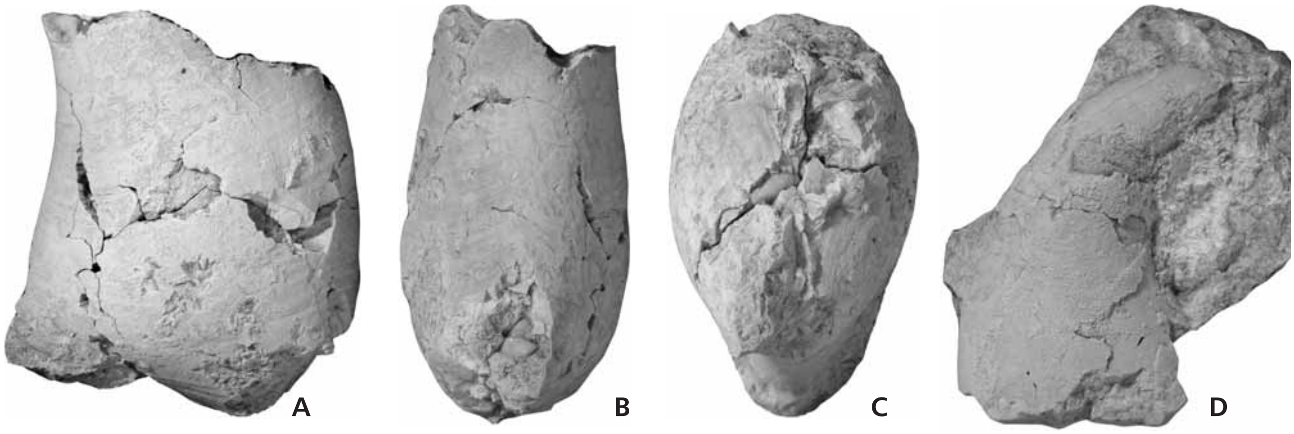

Figure 4. *Phragmoceras acuminatum* Hedström, 1917; Lištice, Herinky Hill, Barrande's pit; Wenlock, Homerian, *C. lundgreni* Zone, *T. testis* Subzone; Motol Formation; A–C (SM 58), D (SM 91). • A – lateral view. • B – ventral view. • C – apertural view. × 1. • D – lateral view; × 1.

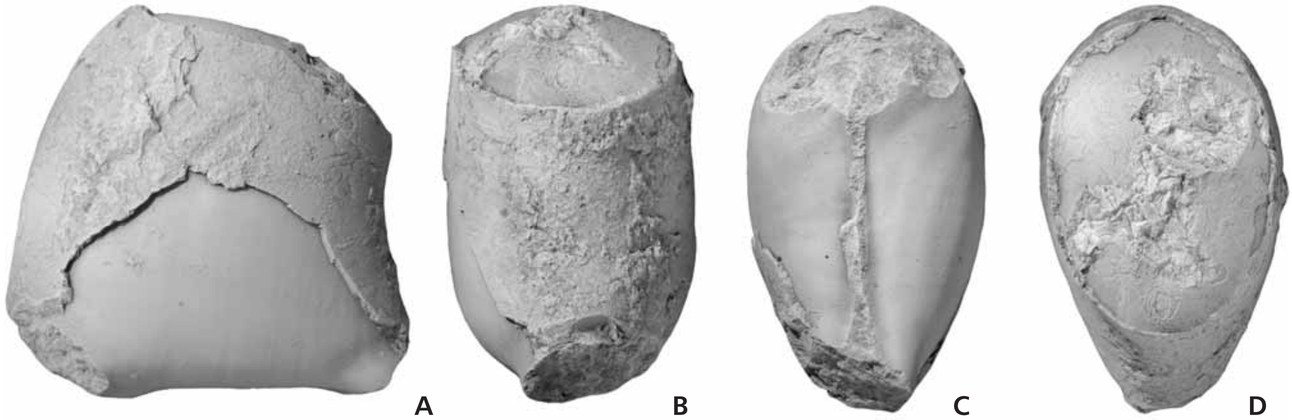

Figure 5. *Phragmoceras sigmoideum* Hedström, 1917; Malá Chuchle, Vyskočilka; Wenlock, Homerian, *C. lundgreni* Zone, latest *T. testis* Subzone; Motol Formation; L 38727. • A – lateral view. • B – ventral view. • C – apertural view. • D – cross section of the body chamber. × 1.4.

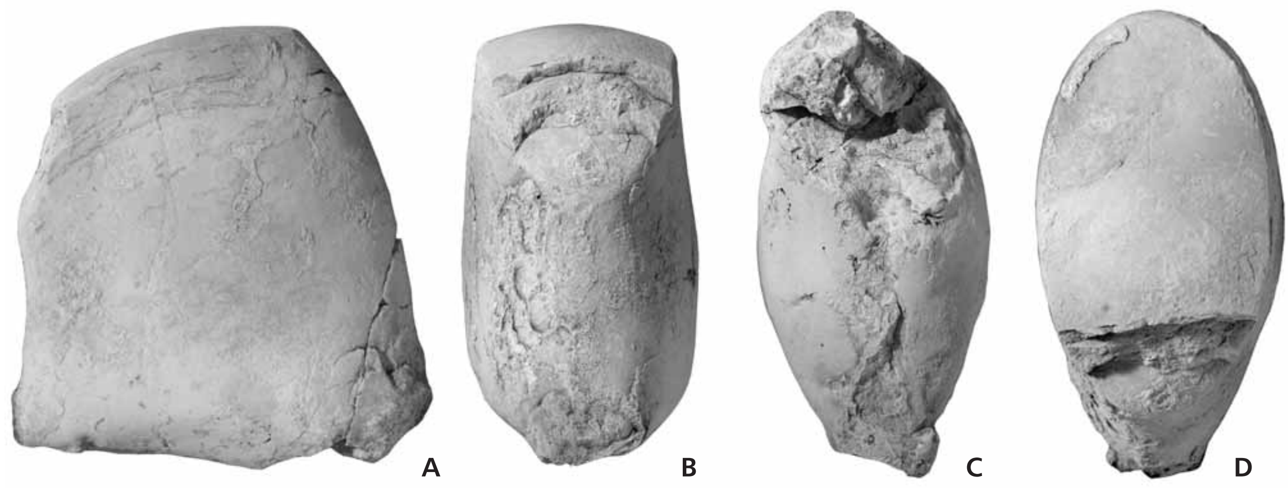

Figure 6. *Phragmoceras* cf. *undulatum* Hedström, 1917; Lištice, exact site unknown; Wenlock, Homerian, *C. lundgreni* Zone, *T. testis* Subzone; L 38729. • A – lateral view. • B – ventral view. • C – apertural view. • D – cross section of the body chamber. × 1.2.

Figure 7. *Phragmoceras* cf. *ventricosum* Sowerby, 1839; Lištice U cestičky Section 759; Wenlock, Homerian, *C. lundgreni* Zone, *T. testis* Subzone; SM 76. Lateral view, × 1.5.

Gotland: Wenlock. Hemse Beds (Hedström 1917). North Ural, Bolshezemskaya Tundra: Early Ludlow. Gerdbyusk Formation (Kiselev 1984).

***Phragmoceras* cf. *undulatum* Hedström, 1917**
Figure 6A–D

Material. – Single specimen L 38 729.

Description. – The single known specimen consists of a body chamber and two camerae. The body chamber is 59 mm long, 64 mm high and 38 mm wide; its ventral and dorsal sides are moderately curved in the same way. Cross-section approximately elliptical, strongly laterally compressed, more flattened at ventral side; the ratio between dorsoventral and lateral diameter is about 1.8. The oldest septum is 56 mm high, 32 mm wide, and moderately deep. Distance between septa is 5 and 2.5 mm respectively. The second shallowest camera is probably gerontic. Suture oblique with prominent broad lateral lobe. Angle between hyponomic sinus and suture approximately 15°. The apertural opening is as wide as the body chamber and directed downward although its margin is slightly oblique to the dorsal side. Detailed shape of apertural opening is not visible. Hyponomic sinus is narrow, minimum width 1 mm. Hyponomic opening is slightly protruding, its end not preserved.

Discussion. – In the shape of its body chamber, cross-section and shape of an aperture, the single specimen from the Prague Basin is similar to *Phragmoceras undulatum* Hedström, 1917 (for description see Holland & Stridsberg 2004). However, the specimen from the Prague Basin is slightly smaller in size. The exact determination is complicated by the absence of the shell surface and most of the phragmocone in the specimen under study.

Occurrence. – Prague Basin (Bohemia): Silurian, Wenlock, Homerian, *C. lungreni* Zone, *T. testis* Subzone. Motol Formation. Lištice, exact site unknown. The specimen is preserved as internal mould with a dark rusty and glossy surface. The body chamber is filled (as visible on apertural opening) with pyroclastic material containing calcite chambers and crinoidal particles. This mode of preservation is characteristic for most distal parts of basalt flows, where pyroclastic and lava fragments are mixed with shells and mud from the bottom. Such facies occurred in the Lištice area in the late Wenlock *T. testis* Subzone, for instance at the Lištice U Cestičky Section 759 (Kříž *et al.* 1993).

***Phragmoceras* cf. *ventricosum* Sowerby, 1839 (*in* Murchison 1839)**
Figure 7

Material. – Three specimens SM 74, 76, 77.

Description. – Endogastric breviconic cyrtocone with an elliptical laterally compressed cross section, the ratio between dorsoventral and lateral diameter is about 1.5. Ventral siphonal tube with elliptical cross-section. Angle of expansion is approximately 25°. Suture is straight and oblique with a shallow broad lateral lobe, dorsolateral saddle and shallow narrow dorsal lobe. Septa are moderately deep, depth of the septum is ca 5/4 of the cameral depth. Camerae relatively deep, around 5 mm at ventral side despite shell diameter. Last camera at height of 62 mm is twice shorter than other camerae. Body chamber size: 78 mm high, 56 mm wide and 84 mm long. Annular elevation is 4 mm wide with poorly developed serial sagitally elongated elliptical muscle scars. Aperture contracted; apertural opening is shorter than body chamber width. Sculpture is not preserved. The shell thickness reaches its maximum, about 3 mm, on ventral side of phragmocone. Total length of the shell is ca 120 mm and height is 80 mm.

Juvenile specimen SM 74 probably belongs to the same species as it comes from the same locality as the adult specimens. It consists of an embryonic chamber, three camerae and a part of a body chamber. Embryonic chamber is slightly curved and 5.5 mm long, 9 mm high, and 8 mm wide. Camerae are 1, 1.4 and 2 mm deep (on dorsal side). Septa almost flat. Suture straight and oblique with a shal-

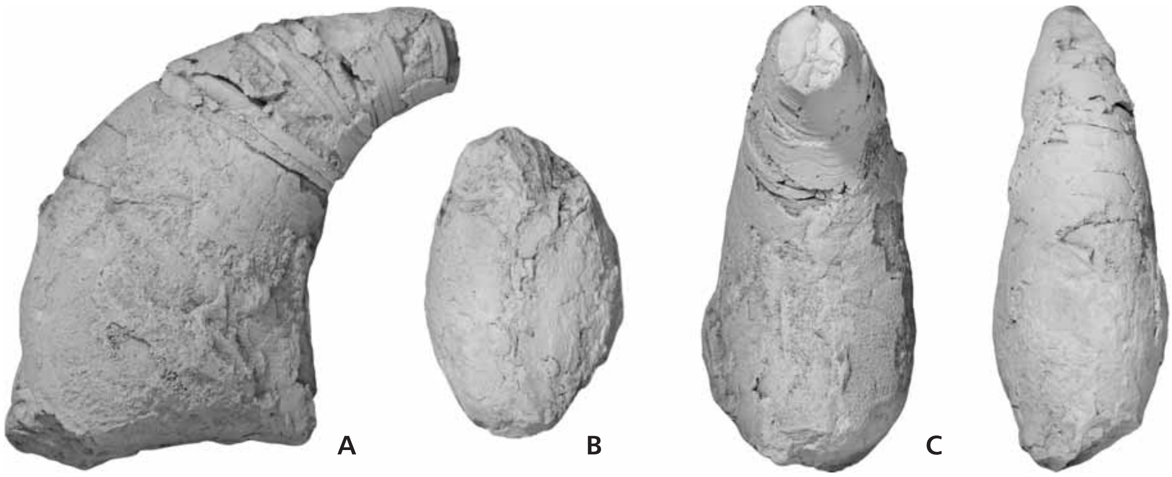

Figure 8. *Phragmoceras koneprusensis* sp. nov.; Koněprusy, Velký vrch Hill; Ludlow, Ludfordian, upper *S. linearis* Zone; SM 75. • A – lateral view. • B – apertural view. • C – ventral view. • D – dorsal view. × 0.7.

low dorsal lobe. Gentle growth lines appear around smooth apical part of the shell with cicatrix already at embryonic chamber. Prominent growth lines developed at the margin of embryonic chamber. The shell is about 0.3 mm thick. The body chamber is 9 mm long, 11 mm wide and ca 15 mm high.

Discussion. – Blake (1882) reported *Phragmoceras ventricosum* from the late Llandovery, the Wenlock and early Ludlow of Wales the Welsh Borderland. Holland & Stridsberg (2004) indicated that the early Ludlow Series was the indisputable age of its occurrence. The poorly preserved Bohemian specimens cannot be determined to the species level with certainty because the shape of the contracted aperture and the sculpture of the shell are not preserved.

Occurrence. – Prague Basin (Bohemia): Silurian, Wenlock, Homerian, *C. lungreni* Zone, *T. testis* Subzone. Motol Formation. Lištice U Cestičky Section 759: brachiopod packstone with *Buceqia obolina* Community (Kříž *et al.* 1993, Manda 1996).

***Phragmoceras koneprusensis* sp. nov.**
Figure 8A–D

Holotype. – Specimen figured here on Fig. 8A–D (SM 75).

Name. – Specific name is derived from Koněprusy Village in the proximity of which type locality occurs.

Type locality. – Velký vrch Hill at Koněprusy (Fig. 1).

Type horizon. – Ludlow, Ludfordian, upper *S. linearis* Zone. Kopanina Formation.

Material. – Holotype only.

Diagnosis. – Small species of *Phragmoceras* with a strongly compressed cross-section, downward oriented U-shaped apertural opening with coupled dorsally expanded lobes.

Description. – The holotype represents an almost complete endogastric cyrtocone with the most apical part missing. The preserved length of the shell is 43 mm in total. The body chamber is 33 mm long; 28 mm high and 19 mm wide. Cross-section is elliptical, laterally compressed, the ratio between dorsoventral and lateral diameter is about 1.5. Septa very shallow. Suture almost straight and oblique; the angle between hyponomic sinus of contracted aperture and suture is about 45°. Camerae are very shallow; distance of septa increase adorally continually from 0.6 mm to 1.1 mm. The distance of two last chambers is about 2.2 mm. The siphuncle is ventral in position and sub-circular in cross-section. Growth lines are fine and regular with very shallow lateral saddles and ventral lobes. Relatively deep and narrow hyponomic sinus is present on the evidence of the growth lines. The growth lines on the body chambers become slightly irregular and are poorly developed. The aperture is contracted with a narrow hyponomic sinus *ca* 1 mm wide. The hyponomic opening is incompletely preserved. The laterally elongated apertural opening is oriented downward, dorsally placed, and U-shaped, with coupled dorsally expanding lobes.

Discussion. – *Phragmoceras koneprusensis* sp. nov. is similar to *Phragmoceras labiosum* Barrande, 1865 (for description see Gnoli 1993), and occurs at the same horizon in the Prague Basin as the former species (Fig. 2). *Phragmoceras koneprusensis* sp. nov. differs from *Phragmoceras* *labiosum* in a more compressed cross-section, slightly more curved shell, smaller size, shallower camerae, and a downward oriented apertural opening with prominent coupled lobes.

Another close related species, *Phragmoceras parvulum* Hedström, 1917 (holotype by monotypy, specimen figured by later author on pl. 14 as figs 3–5), was described from the Middle Silurian of Gotland. *Phragmoceras koneprusensis* differs in possessing a slightly more compressed and curved shell; and although the apertural opening is similar in shape, it is directed downward.

Phragmoceras parvulum, Phragmoceras koneprusensis and *Phragmoceras labiosum* are considered as closely related species and represent a clade within the genus *Phragmoceras*. *Phragmoceras* may include more than sixty species and the phyletic relationships between the majority of them remain unclear. Later species are distinctive in the small size of the shell, the elliptical cross section and the U-shaped apertural opening with coupled lobes; *P. koneprusensis* and *P. labiosum* represent the smallest phragmocerids known from the Prague Basin at the present time, which should also be noted for *P. parvulum* with respect to Gotland. The decrease in the shell size was accompanied by decreasing the spacing of the apertural opening, which became extremely narrow, although the ratio between the spacing of the aperture opening and cross-section area is similar to that of phragmocerids of average size. The narrow width of the aperture opening probably limited food-capture and led to dietary specialization.

The trend toward decreasing shell size is not restricted to later lineages. A small-sized species was described from the Silurian of Ohio as *Phragmoceras parvum* Hall & Whitfield, 1875 (pp. 151, 152, pl. 8, fig. 10). The maximum diameter of its shell is 23 mm, but in contrast to the allied species, *P. parvulum*, *P. parvum* exhibited a relatively wide apertural opening.

Remarks. – Holotype comes from Velký vrch locality at Koněprusy. It was collected in 0.5 m-thick bank of light-grey cephalopod grainstone corresponding to the uppermost part of the *S. linearis* Zone. The cephalopod grainstone contains a rich cephalopod assemblage (including, among others, *Phragmoceras broderipi sublaeve* Barrande, 1865) and a benthic fauna suggesting the high-energy, well-ventilated and thus relatively shallow water environment.

Tubiferoceras Hedström, 1917

Type species. – Phragmoceras proboscoideum Hedström, 1917. Early Silurian. Gotland.

Tubiferoceras proboscoideum (Hedström, 1917)

Figure 9A–D

1917 *Phragmoceras proboscoideum* n.; Hedström, pp. 8, 9, pl. 1, figs 1–10.
1926 *Tubiferoceras proboscoideum* (Hedström). – Foerste, p. 352, pl. 48, figs 2a–c.
1957 *Tubiferoceras proboscoideum* (Hedström). – Flower & Teichert, p. 123.
1964 Phragmoceratid cephalopod. – Galle & Horný, p. 126, figs 1, 2.

Lectotype. – Specimen designated by Foerste (1926) and figured by Hedström (1917) on pl. 1 as figs 4, 5-2. Early Silurian of Gotland.

Material. – Two specimens (FNS 15.493 and L 16/64).

Description of the Bohemian material. – The specimen FNS 15.493, representing the body chamber, is preserved as an internal mould with remains of the shell. Its length reaches 74 mm, width 58 mm and height 96 mm. The ventral side of the body chamber is straight, and the dorsal moderately curved. Aperture contracted; dorsally placed protruding apertural opening with elliptical cross-section is 39 mm long and 24 mm wide (no collar around apertural opening has been preserved). Hyponomic sinus is very narrow. Hyponomic opening is slightly protruding, its end is no longer preserved. Cross-section is rather elliptical on the ventral side and slightly compressed, 68 mm high and 52 mm wide, the ratio between dorsoventral and lateral diameters is about 1.3. Septa moderately deep. Suture straight and oblique, declined to the ventral side. Ventral laterally compressed siphonal tube. Remnants of the shell at the aperture show fine growth lines. Annular elevation is relatively high, 4–5 mm wide with poorly developed serial sub-circular muscle scars.

The specimen L 16/64 is covered by a coral colony grown inside of the body chamber and thus keeping its shape. It shows the same features as the specimen FNS 15.493 mentioned above (for detailed description see Galle & Horný 1964).

Discussion. – All the preserved features of the specimens described here are identical with those of *Tubiferoceras proboscoideum* from the early Silurian of Gotland.

Occurrence. – Prague Basin (Bohemia): Silurian, Wenlock, Sheinwoodian. Motol Formation. *M. belophorus* Zone: U elektrárny Section, Svatý Jan pod Skalou, trilobite-brachiopod packstone-wackestone, *Leptaena rugalita* Community (Havlíček & Štorch 1990).

Gotland: Early Silurian (for detail see Hedström 1917).

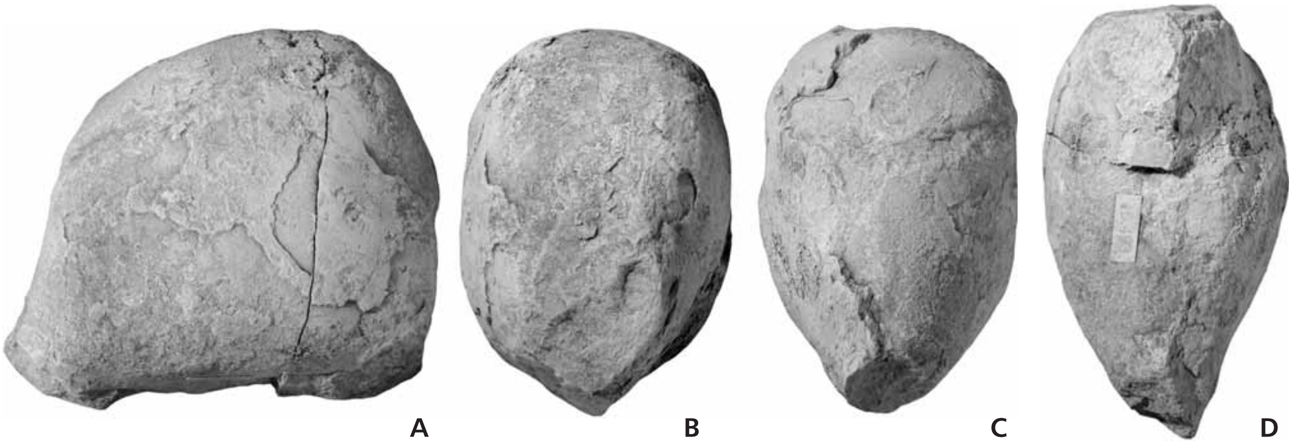

Figure 9. *Tubiferoceras proboscoideum* (Hedström, 1917); Svatý Jan pod Skalou, U Elektrárny Section; Wenlock, Sheinwoodian, *M. belophorus* Zone; FNS 15.493. • A – lateral view. • B – dorsal view. • C – ventral view. • D – apertural view. × 1.6.

Discussion

The nautiloids belonging to the genera *Phragmoceras* and *Tubiferoceras* are characteristic component of the Silurian nautiloid faunas, which had been inhabiting mainly tropical carbonate platforms of Baltica and Laurentia. Phragmocerids and other nautiloids represent K-selected cephalopods with their slow growth rate, long life-span, large embryonic shell, great weight, lack of pelagic stage, and very low juvenile mortality (for summary see Chirat & Rioult 1998). Their relatively warm water, well-oxygenated and stable life environment (*e.g*., Baltica platform) corresponds with their K-strategy. The absence of a planktic stage in phragmocerids is considered to be a cause of their gradual dispersion in the shallow seas of tropical platforms during the earliest Silurian (*e.g*., Baltica and Laurentia) and followed by further immigrations to more distant areas (*e.g*., Inner Mongolia) or even outside the tropical zone (*e.g*., Prague Basin).

Outside the Prague Basin, only two species of *Phragmoceras* occur of six previously known ones described by J. Barrande from the Ludlow (Fig. 2). The early Ludlow *Phragmoceras imbricatum* was recognised by Blake (1882) and Holland & Stridsberg (2004) in Avalonia and Baltica. Its geographical range suggests similar conditions suitable for habitation by these taxa combined with an occasionally open migration route between the Prague Basin (Perunica) and Baltica-Avalonia during the earlier Ludlow time. The joint occurrences of some oncocerids with the contracted aperture also suggest a close relationship between the nautiloid faunas of Gotland and the Prague Basin during the Ludlow series (Stridsberg 1985, 1988b). The revision of species of the coiled tarphycerid *Ophioceras*, described under different names from Perunica, Baltica, Avalonia and Laurentia (Stridsberg & Turek 1997), lead to the similar conclusion.

On the other hand, *P. labiosum* occurs in the early Ludfordian strata of the Prague Basin and Sardinia (Gnoli 1993). In Sardinia, orthocone cephalopods generally dominate the cephalopod faunas while nautiloids are extremely rare. Most of these nautiloids show close affinity to taxa from the Prague Basin (Gnoli 1993). Stridsberg (1988a) concludes that *P. labiosum* from Sardinia represents a stray immigrant to the cooler peri-Gondwanan sea rather than *in situ* population.

Until now, no joint occurrence of nautiloid species has been reported from the Llandovery or Wenlock of the Prague Basin, Baltica, and Laurentia. *Phragmoceras munthei* appears in the Prague Basin within narrow intervals in the latest Llandovery and earlier Wenlock shale. *P. munthei* occurs in coeval strata of the carbonate platform at Gotland and probably terrigenous shelf of Ireland. Thus the occurrence of *P. munthei* in shale with a pioneer community is unusual and may reflect an environmental event accompanied by phragmocerid immigration into the deeper water and a less ventilated environment.

The second reported phragmocerid *Tubiferoceras proboscoideum* occurs in the middle Sheinwoodian shallow-water limestones on the Svatý Jan Volcanic submarine elevation. *T. proboscoideum* is also known from the Wenlock of Gotland. In addition, *T. proboscoideum* from the Prague Basin represents the first report of the genus outside the tropical waters of Laurentia, Avalonia and Baltica.

The following four species, *Phragmoceras sigmoideum, P. acuminatum, P*. cf. *undulatum* and *P*. cf. *ventricosum*, are described from the *T. testis* Subzone (early Homerian). The first three of them are conspecific or closely related to the forms from Gotland (Baltica) whilst the fourth species is closely related to *Phragmoceras ventricosum* from Wales as well as the Welsh Borderland.

The newly established *Phragmoceras koneprusensis* sp. nov. is closely related to *P. labiosum*. They are both very rare within the limestone strata of the late *S. linearis* Zone of the early Ludfordian, of the Prague Basin. Later species may represent the only known example of a phragmocerid immigrant to the Prague Basin that then gave rise to several species within the Prague Basin. The closely related *Phragmoceras parvulum* was described from the middle Silurian of Gotland. All the mentioned species are exceptional for *Phragmoceras* by virtue of their small shells and relatively narrow apertural opening.

Conclusion

The seven phragmocerid taxa described herein considerably increases the number of species from the Prague Basin. The 13 species of phragmocerid known from the Prague Basin represent the second most diverse phragmocerid fauna hitherto known. The highest diversity of its kind may be typical for Gotland where 25 taxa have been described (Holland & Stridsberg 2004). Perhaps six of these are common to both regions. This fact supports a faunal connection from the latest Llandovery up to the early Ludlow. In contrast to that the late Ludlow phragmocerids of the Prague Basin are mostly "endemic" species (only the single species, *Phragmoceras labiosum*, is reported from Sardinia and interpreted as stray immigrant). Nevertheless, these "endemic" are closely related species to those described from Gotland (*e.g., Phragmoceras koneprusensis* and *Phragmoceras labiosum* are close related to *Phragmoceras parvulum*). The shift of Perunica microplate towards the equator (Havlíček *et al.* 1994) linked with changes in the environment as the warming allowed further evolution of phragmocerid immigrants there. In addition, the occurrence of phragmocerids in the Prague Basin indicates, in contrast to the rest of the peri-Gondwanan areas, a relatively temperate water environment for Perunica since latest Llandovery.

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