

New cephalopod limestone horizon in the Ludlow (Gorstian, lower *L. scanicus* Biozone) of the Prague Basin (Bohemia, Perunica)

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KEY WORDS - Silurian, Ludlow, Cephalopod limestones, Bivalvia, Cephalopoda, Palaeoecology.

ABSTRACT - A new cephalopod limestone horizon is described from the lower *L. scanicus* Biozone (Gorstian, Ludlow, late Silurian) at Vyskočilka Section near Praha-Malá Chuchle (Prague Basin, Bohemia, Perunica). It contains the new Bivalvia dominated benthic *Cardiola donigala*-*Slava sathon* Community and the new water column cephalopod fauna of the *Pseudocycloceras duponti*-*Kionoceras doricum* Assemblage. The discovered horizon complements the record of the recurrent cephalopod limestone biofacies in the Silurian. Generally, the Silurian cephalopod limestone biofacies originate in relatively shallow environment where surface currents ventilate the sea bottom just below the storm wave base. Shallow water conditions are caused by the global lowstands or by the local bottom rising due to volcanic or tectonic activity. In the Gorstian, the cephalopod limestone horizons are known in the lower *N. nilssoni* Biozone, the lower and upper *L. scanicus* Biozone. The *N. nilssoni* Biozone and the upper *L. scanicus* Biozone cephalopod limestone horizons occur besides the Prague Basin also in other parts of peri-Gondwana (Sardinia and Montagne Noire) and their origin is related to the sea level lowstand and regression. Described lower *L. scanicus* Biozone cephalopod horizon originated in the relatively shallow water environment of the local rising zone due to volcanic activity in the Prague Basin and document distinct faunal change in lower *L. scanicus* Biozone corresponding to the Gorstian highstand coeval with restricting occurrence of the cephalopod limestone biofacies in other peri-Gondwana.

RIASSUNTO - [Nuovo livello di calcari a cefalopodi dal Ludlow (Gorstiano, Biozona a *L. scanicus* inferiore) del Bacino di Praga (Boemia, Perunica)] - Dalla sezione di Vyskočilka, vicino a Praga-Malá Chuchle (Bacino di Praga, Boemia, Perunica), viene descritto un nuovo livello di calcari a cefalopodi nella prima parte della biozona a graptoliti *L. scanicus* (Gorstiano, Ludlow, tardo Siluriano). Il sito, dal quale furono descritti da Barrande i bivalvi e cefalopodi (tra i quali *Slava sathon*, *Kionoceras doricum*, *Ophioceras tener* e *Peismoceras asperum*) del Gorstiano inferiore (Ludlow), è stato a lungo dimenticato ed è stato riscoperto durante una dettagliata analisi degli affioramenti realizzata dagli autori nel 2004 e 2005 nelle vicinanze di Černá Gorge, sopra Vyskočilka Rocks. Questo livello contiene la nuova Comunità a bivalvi *Cardiola donigala*-*Slava sathon* ed una nuova fauna a cefalopodi pelagici dell'associazione *Pseudocycloceras duponti*-*Kionoceras doricum*. Questo orizzonte ben s'inserisce nella ricorrente biofacies dei calcari a cefalopodi del Siluriano. Essi rappresentano una facies caratteristica ampiamente diffusa nel peri-Gondwana (Montagne Noire, Spagna, Sardegna, Alpi Carniche, Marocco, Algeria, Bolivia, ecc.) dal tardo Wenlock fino al Lochkoviano inferiore, sviluppato in 14 livelli stratigrafici e caratterizzato da comunità bentoniche con dominanza di bivalvi. Di solito la biofacies dei calcari a cefalopodi del Siluriano si sviluppava in ambienti di mare poco profondo, dove le correnti superficiali rimescolavano ed ossigenavano il fondo appena sotto il livello di base delle onde di tempesta. Le condizioni di mare sottile erano probabilmente dovute a condizioni di lowstand globale, oppure a locali sollevamenti del fondo dovuti ad attività vulcanica o tettonica. Nel Gorstiano, i livelli dei calcari a cefalopodi si trovano nella prima parte della Biozona a *N. nilssoni* e nella prima ed ultima parte di quella a *L. scanicus*. I livelli a cefalopodi della biozona a *N. nilssoni* e della parte alta di quella a *L. scanicus* sono presenti sia nel Bacino di Praga sia in altre parti del peri-Gondwana (Sardegna e Montagne Noire), originati da lowstand e fenomeni regressivi. L'orizzonte a cefalopodi descritto nella prima parte della biozona a *L. scanicus* si formò in un ambiente marino poco profondo in un'area del Bacino di Praga rilevata a causa dell'attività vulcanica e documenta un distinto cambiamento faunistico nella parte inferiore della Biozona a *L. scanicus*, corrispondente all'highstand Gorstiano e contemporaneo alla minore diffusione della biofacies dei calcari a cefalopodi in altre parti del peri-Gondwana. La massima espansione della biofacies dei calcari a cefalopodi nel peri-Gondwana fu raggiunta durante il Ludfordiano (Ludlow). La stabilità del sistema di correnti marine superficiali era favorevole allo sviluppo delle associazioni a cefalopodi entro la colonna d'acqua, mentre sul fondo le comunità erano dominate da bivalvi con alta diversità ed alta densità di popolazione. Alla base del Přídolí la sedimentazione dei calcari a cefalopodi fu bruscamente interrotta da un innalzamento eustatico globale. La biofacies dei calcari a cefalopodi del tardo Přídolí conteneva comunità a bivalvi omologhe (ma non analoghe) alle precedenti, con cardiolidi fossatori dominanti. Le comunità a bivalvi dei calcari a cefalopodi del Lochkoviano (Bacino di Praga, Massiccio Armorico e Marocco) non erano omologhe (né analoghe) alle precedenti, essendo dominate da bivalvi antipleuridi infaunali.

INTRODUCTION

The cephalopod limestones represent a distinctive and widely spread peri-Gondwanan recurrent facies (the Montagne Noire, Spain, Sardinia, the Carnic Alps, Morocco, Algeria, Bolivia etc.) from the late Wenlock up to the early Lochkovian. They developed at 14 stratigraphical levels and are characterized by the Bivalvia dominated benthic communities (Ferretti, 1988; Kríž, 1991, 1998; Kríž et al., 2003; Gnoli, 2003, and this paper). In the Prague Basin, thin beds of the

cephalopod limestone occur in the Homerian and Gorstian shallow water limestone-volcanic products sequences on the volcanic and tectonic elevations grading to the deeper water hemi-pelagic shale with tuffitic admixture. Ludfordian sequences include thick shallow water brachiopod, crinoidal and cephalopod limestones above the volcanic and tectonic elevations, grading basinward to the calcareous shales (Bouček, 1934, Horný, 1955, Kríž, 1991), see Fig. 1.

Fauna of the Silurian cephalopod limestone biofacies contains mainly bivalves and cephalopods adapted to

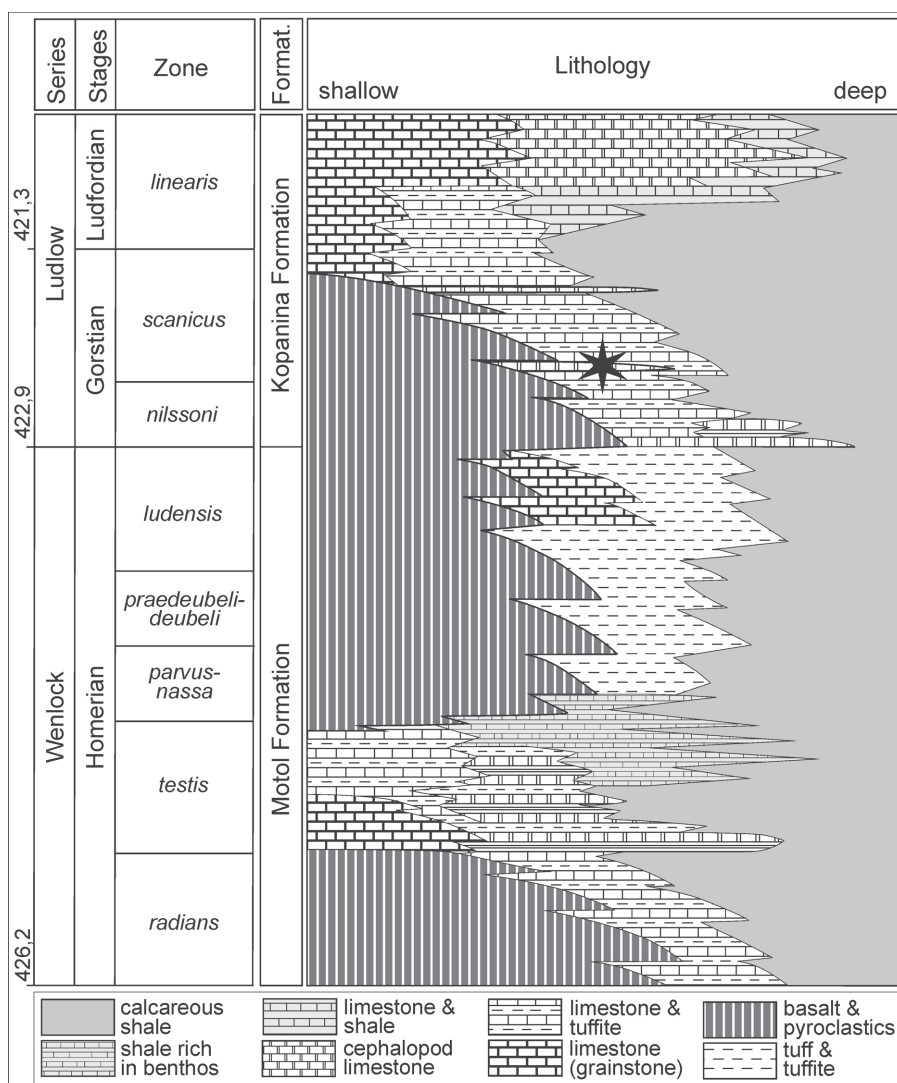


Fig. 1 - Homerian, Gorstian and early Ludfordian stratigraphy and lithostratigraphy of the Prague Basin (after Kříž, 1991, modified). Asterisk shows position of the studied section. Timescale after Gradstein et al. (2004).

this biofacies (Kříž, 1984, 1999a). Progressive changes in the cephalopod limestone biofacies extension, and in the communities and assemblages composition, reflect eustatic and climatic changes (Kříž, 1998). Each of recurrent horizons of the cephalopod limestone contains distinct bivalve dominated community and cephalopod assemblage (Kříž, 1998, 1999a, b).

The early Gorstian (Ludlow) cephalopod limestone horizon with the *Cardiola gibbosa* Community occurs during eustatic lowstand in the *N. nilssoni* Biozone. Following thick Gorstian, predominantly shale sequence contains only isolated beds of the cephalopod limestone. The new cephalopod limestone horizon in the lower *L. scanicus* Biozone is described here from the Vyskočilka Section and located in SW part of Prague (Fig. 2) and the upper *L. scanicus* Biozone horizon with the *Cardiola donigala-Slava cubicula* and *Cardiola donigala* communities (Kříž, 1998, 1999c). The cephalopod assemblages were not yet described from the upper *L. scanicus* Biozone but similarly to the benthic Bivalvia dominated communities each horizon carry distinct cephalopod assemblage (Manda in Kříž, 1998). Higher levels of the cephalopod limestone with the *Cardiola signata* and *Cardiola docens* communities occur in the early Ludfordian, upper *S. linearis* Biozone (Kříž, 1998).

VYSKOČILKA LOCALITY: HISTORICAL OVERVIEW

The classic Barrande's locality Vyskočilka E (Wyskočilka, Wiskočilka, Viskočilka) includes several fossil sites in the famous Silurian-Devonian section below Barrandov District, between Malá Chuchle Village and Rothe Mill in the Hlubočepy-Valley (Chlupáč, 1983; Kříž, 1999d). J. Barrande draw the sketch of the Vyskočilka Section in his notebook (1865) deposited in the National Museum, Prague (Chlupáč, 1999, pl. 2, fig. 1). Barrande distinguished two "bandes" of "etage E" (e1 and e2) at the locality. Vyskočilka e1 includes graptolite shale and limestone sequence from the late Llandovery up to the early Ludlow. The graptolite shale is exposed between railway cut near tunnel in Malá Chuchle Village and Vyskočilka Rocks (Fig. 1) and was described by many authors (e.g. Počta, 1897; Liebus, 1911; Přibyl, 1938; Bouček, 1941, 1953; Kříž, 1999d). Barrande (1865-1874, 1881) used the locality name Vyskočilka e2 for the late Ludlow, Přídolí and early Lochkovian parts of the Vyskočilka Section. The Ludfordian cephalopod limestone horizon was by Barrande collectors quarried in the test pits close to the Filmařská Street (Kříž, 1999d). Late Přídolí and early Lochkovian fossils come

from the old “Herget” Quarries close to the Barrandev’s Rock (Bouček 1941; Kříž, 1999d; Frýda & Manda, 1997). The early Lochkovian bivalves were marked Vyskočilka e2 - Černá rokle (Barrande, 1881). The site from where the early Gorstian (Ludlow) bivalves and cephalopods were described by Barrande (e.g. *Slava sathon*, *Kionoceras doricum*, *Ophioceras tener*, and *Peismoceras asperum*) has been forgotten for long time, and has been rediscovered during detailed sectioning of the natural outcrop realised by authors in 2004 and 2005 near the Černá Gorge above Vyskočilka Rocks (Fig. 1).

SEDIMENTARY SEQUENCE

Studied part of the Vyskočilka Section (Fig. 3) starts with grey calcareous shale without fossils. Higher up, the tuffitic shale and platy grey laminated limestone occur. The limestone contains thin levels of unsorted cephalopod-graptolite packstone above the erosive base. The overlying hyaloclastite metamorphosed the

uppermost level of the limestone and false mud-cracks with calcite and pyrite fillings are developed here (for comparison see Kříž & Štěpánek, 1979). Shale and limestone contain common graptolites of the *N. nilssoni* Biozone: *Colonograptus colonus*, *C. roemeri*, *Lobograptus progenitor*, *Neodiversograptus nilssoni*, *Bohemograptus bohemicus*, *Pristiograptus ex gr. dubius*, and *Monograptus uncinatus*. Cephalopods are represented by pelagic orthocerids *Michelinoceras michelini*, *Kopaninoceras amoenum*, *Arionoceras* sp., *Parakionoceras originale*, *Caliceras capillosum*, and single nautiloid *Oonoceras* sp. Juvenile cephalopods are also abundant. The cephalopod shells are relatively complete, mostly flattened. Small Bivalvia shells, juvenile cephalopods or parts of adult shells (septa, internal moulds) are sometimes pyritised. Cephalopods and graptolites are usually well current oriented. Low diversity benthic fauna includes common ostracods *Entomozoe?* sp. and rare bivalves *Cardiola gibbosa*, *Slava bohémica*, and *Manulicula manulia*.

The section continues by 150 cm thick grey-green hyaloclastite (bed no. 1) overlain by 10-25 cm thick

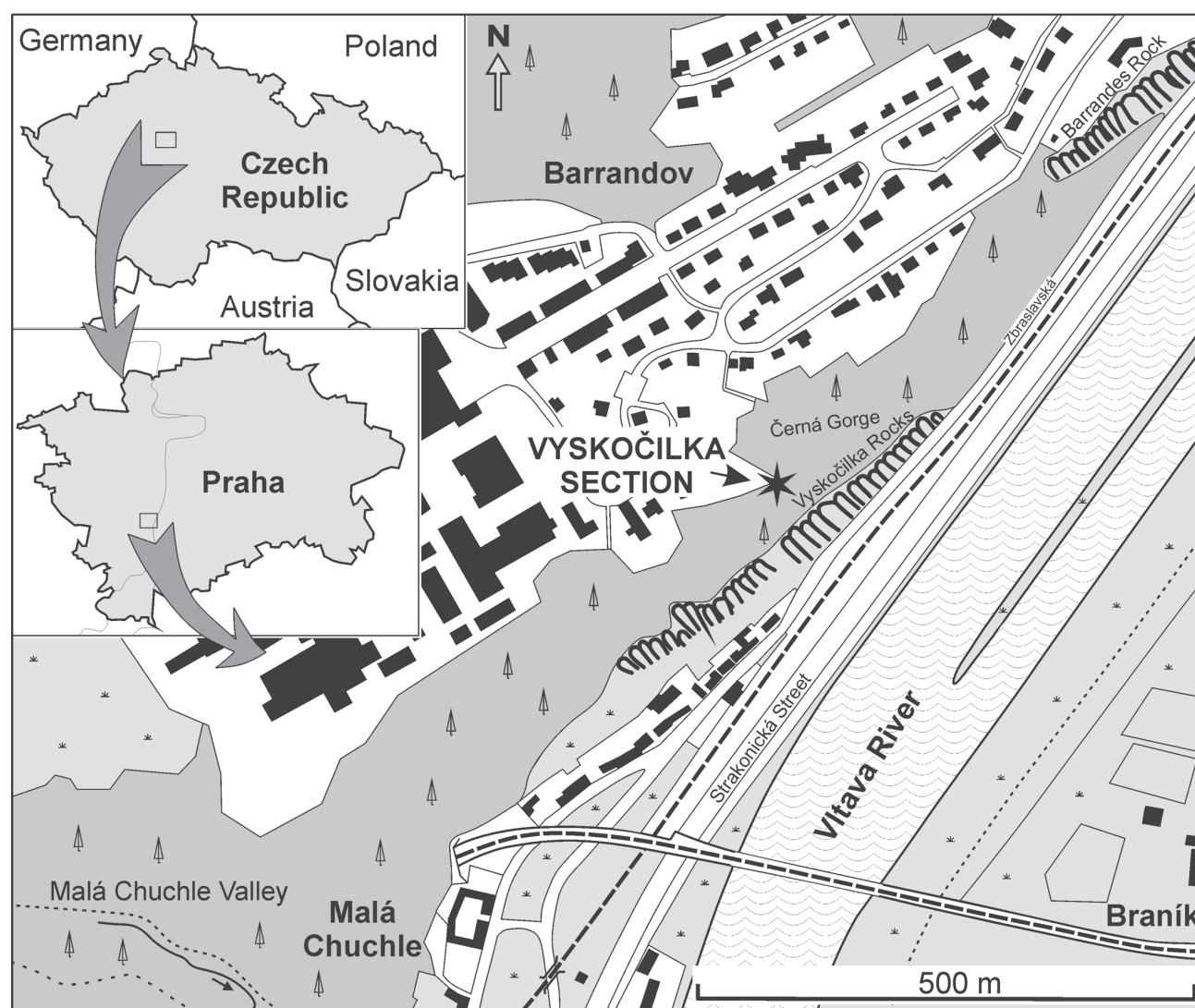


Fig. 2 - Position of the Vyskočilka Section.

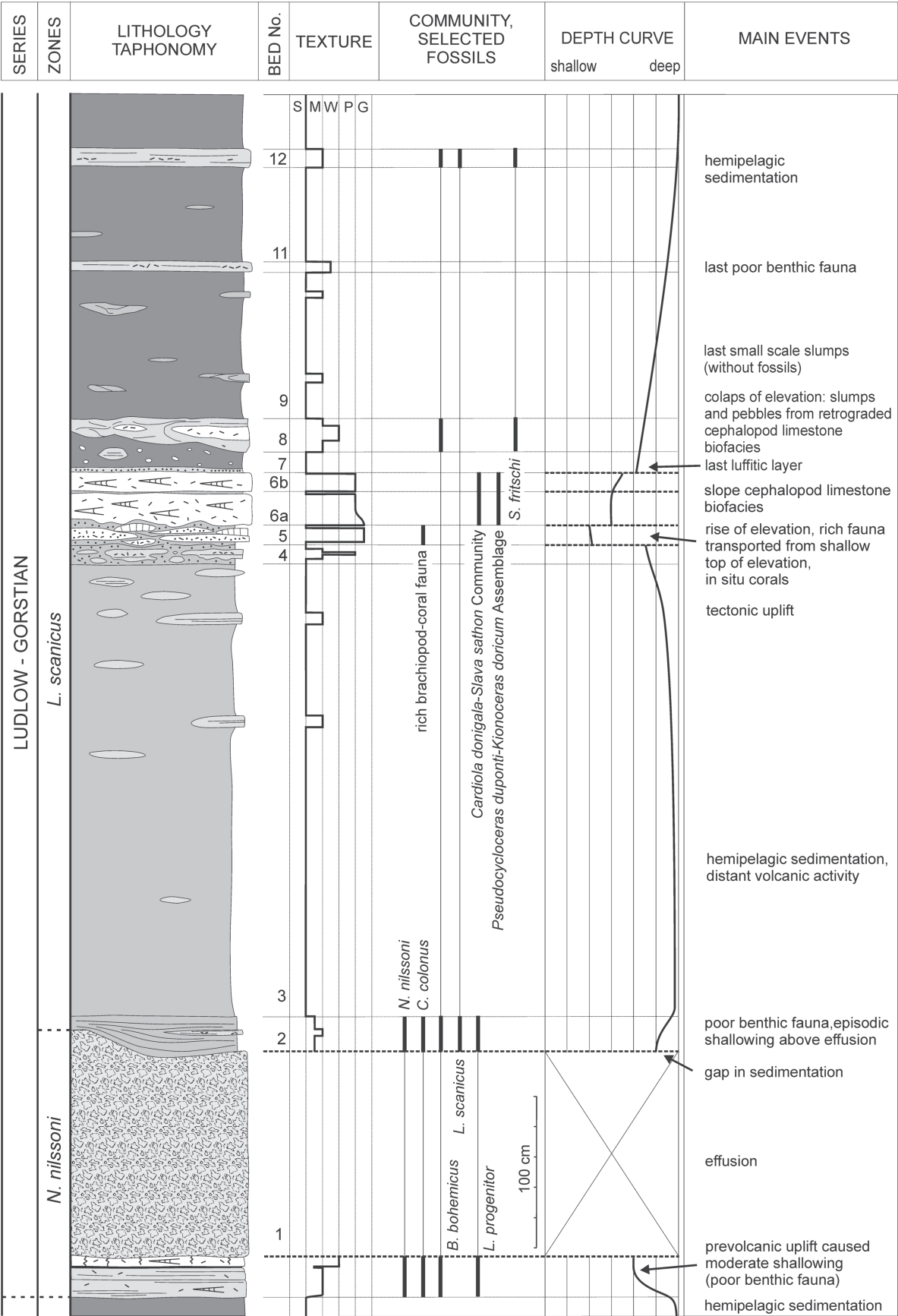


Fig. 3 - Vyskočilka Section showing lithologies, ranges of selected fossils, bivalve community, cephalopod assemblage and summary of main depositional events in the measured section. The colours used for lithology expression are stepped from white for limestone to dark grey for calcareous shale. Simple dots mean tuffite. See text for detail description. Abbreviations using in column "Texture": S - shale. Carbonate lithology followed Dunham's classification (1962): M - mudstone, W - wackestone, P - packstone, G - grainstone.

compact, grey finely laminated calcareous shale (bed no. 2) filling depressions in the upper surface of hyaloclastite. The shale includes common well-preserved graptolites of the lower *Lobograptus scanicus* Biozone: *Colonograptus colonus*, *C. varians*, *C. aff. roemeri*, *Lobograptus progenitor*, *L. scanicus*, *Neodiverso-graptus nilssoni*, *Saetograptus chimaera*, *Bohemograptus bohemicus*, and *Pristiograptus ex gr. dubius*. Some bedding planes are covered with current-oriented graptolites. In other beds graptolites occur rarely, not so well oriented, but better preserved. Fragments of trilobites (Proetida), smooth ostracods, bivalves (Cardiolidae) and small shells of pelagic orthocerids (mostly fossilised by pyrite) are confined in a few thin levels. Mudstone intercalations contain smooth ostracods, graptolite fragments and fragments of the phyllocarid *Ceratiocaris* sp.

Section continues by 300 cm thick weathered ash-grey thinly laminated calcareous shale with nodules (max. 15x20 cm) of laminated muddy limestone in upper part (bed no. 3). The contact with underlying consolidated shale is sharp, sometimes with rusty crust. Only rare fragments of graptolite *Pristiograptus ex gr. dubius* have been collected.

Following bed of 12 cm thick rusty-yellow tuffitic shale contains common or associated nodules formed by laminated mudstone with thin cephalopod wackestone (bed no. 4).

Bed no. 5 (12 cm thick) consists of weathered yellow tuffite with levels of upward fining, cross-laminated tuffitic packstone-grainstone of the well-sorted fine fragments of brachiopods (mostly minute orthids and strophomenids), rounded crinoids, fragments of trilobites (mostly odontopleurids and proetids), ostracods and gastropods (totally over 15 species). In the uppermost part of the bed thin and local accumulations of coarse cephalopod packstone, composed of cephalopod fragments and disarticulated brachiopods *Gypidula* cf. *vestita*, rhynchonellids and strophomenids, occur. *Favosites* aff. *tachlowitzensis*, the corals with maximum dimension 13x5 cm, were observed in living position.

The tuffite is overlain by 27 cm thick bank of blue-grey cephalopod limestone (bed no. 6) with erosive base with relief up to 3 cm. The cephalopod limestone consists of grainstone-packstone-wackestone beds separated by flat erosive surfaces affected by stylolites with clay residuum. The fine pyrite occurs especially close to the erosive surfaces. Packstone (locally grainstone) deposited just above erosive surfaces is composed of large fragments of cephalopods mostly with umbrella effect. Above erosive surfaces are sometime developed thin micrite-rich beds terminated by mineralised hardgrounds. Thickness of individual limestone beds or depositional cycles varies from 2 cm to 11 cm. Some thicker beds show upward decreasing shell size (packstone-wackestone transition).

Bivalves are disarticulated; large valves (< 2 cm) are commonly fragmented (*Slava*, *Maminka*). Cephalopod phragmocones with preserved septa and broken apical part are common while body chambers are rare. Only smaller (up to 10 cm long) longicone, brevicone and coiled shells are sometimes complete. Gas chambers are mostly filled with calcite, body

chambers with micrite and subordinately with geopetal structures with prevailing micritic part. Currents of SW-NE direction oriented the cephalopod shells. The cephalopod limestone contains benthic *Cardiola donigala-Slava sathon* Community and cephalopod *Pseudocycloceras duponti-Kionoceras doricum* Assemblage.

The cephalopod limestone is capped by 4 cm thick bed of laminated tuffite (bed no. 7a). Above, the ash-grey 20 cm thick calcareous laminated shale with tuffitic admixture is developed (bed no. 7b). The shale contains rare nodules of laminated argillite to mudstone with small orthocerids *Parakionoceras originale*, *Michelinoceras michelini* (commonly juvenile), graptolite fragments and local accumulations of trilobite fragments. In addition, shale contains common decalcified and mostly sub-angular intraclasts of cephalopod limestone up to four centimetres in diameter.

The section continues with limestone lenses with flat upper surface (bed no. 8: 100 x 20 cm). The core of the lenses is composed by grey wackestone with unsorted fragments of cephalopods, brachiopods (articulated *Septatrypa* aff. *caprilupa*, disarticulated *Cyrtia* aff. *bedya bedya*), trilobites (*Cromus* sp.) and bivalves (*Cardiola* sp., *Maminka arachne*). Lower part of lenses consists of mudstone and the upper part is laminated mudstone with more common graptolites. Outside of mudstone core the argillite contains flattened fossils, although some small shells, parts of large shells (siphonal tube of cephalopods) and proximal graptolite rhabdosomes are 3D preserved by pyrite. The graptolites *Saetograptus fritchi*, *Bohemograptus bohemicus*, and *Pristiograptus ex gr. dubius* occur here. Orthocerids *Arionoceras* sp., *Kopaninoceras* sp., and *Kentronites transiens* are also common. Local accumulations of minute and disarticulated brachiopods occur on some bedding planes (*Bleshidium* aff. *patellinum*, juvenile *Cyrtia* sp.).

Overlying calcareous shale, 70 cm thick, (bed no. 9) contains rare small nodules of mudstone with juvenile cephalopods. Some small lenses are similar to that in the bed no. 8.

Higher, the 6 cm thick laminated mudstone with fragments of trilobites and ostracods is developed (bed no. 10).

Above 63 cm thick shale without nodules (bed no. 11) the grey laminated mudstone 11 cm thick occurs (bed no. 12). It contains few laminas with common graptolites of the *L. scanicus* Biozone: *Saetograptus fritchi*, *S. chimaera*, *Lobograptus scanicus*, *Pristiograptus dubius*, *Bohemograptus bohemicus*, few juvenile brachiopods, and pyritised cephalopods.

Above the measured section, approximately 10 meters thick shale of the *L. scanicus* Biozone is exposed with a few up to 15 cm thick beds of the irregularly laminated mudstone containing flattened and usually articulated brachiopod *Septatrypa* aff. *caprilupa*.

DEPOSITIONAL ENVIRONMENT

The calcareous shale that separates the lower Homerian and Gorstian strata in the Vyskočilka Section

suggests that relatively deeper-water hemi-pelagic sedimentation took place in this part of the Prague Basin. Mudstone-wackestone with cephalopods and low-diversified benthic fauna has been deposited since the early Gorstian *N. nilssoni* Biozone at the shallowing bottom which became better oxygenated by surface currents. Discrete cephalopod packstone reflects short-term high-energy events. The shallowing corresponds to the early Gorstian local rise of sea bottom (Kříž, 1991, 1998) controlled by volcanic activity. The volcanic activity culminated in this part of the basin with the overlying basalt effusion. The basalt effusion corresponds most probably to the latest *N. nilssoni* Biozone. It might be contemporary with the effusion developed above cephalopod limestones at the Na břekvici Section in Praha-Butovice (Kříž, 1991).

The shale-mudstone with poor benthic fauna above the basalt effusion corresponds to moderate shallowing in the early *L. scanicus* Biozone. The shale above and below basalt effusion contains rich graptolite assemblages with common index taxa. The graptolite fauna is similar to that from the relatively shallow water sediments of the Butovice and Konvářka sections (Bouček, 1937, Přibyl, 1944). The deeper water shale contain less diverse assemblages usually with missing index taxa (Jaeger, 1964).

The following thick shale sequence corresponds to the hemi-pelagic sedimentation. Upward increasing portion of mudstone nodules with carbonate and tuffitic admixture suggests slow shallowing and distant source of volcanic clastics. In the uppermost part of the shale the nodules merge in nodular beds containing thin layers of cephalopod wackestone-packstone deposited by the short-term surface currents ("initial stage of the cephalopod limestone biofacies"). Higher up, the tuffitic shale passes in the tuffite containing thin well-sorted packstone-grainstone with benthic fauna transported from relatively shallow environment. In addition, the occurrence of a tabulate corals in living position and some pentamerid brachiopods point up the shallowing peak. Until now the similar shallow-water fauna of the lower *L. scanicus* Biozone (Havlíček, 1995) has not been known from the eastern part of the Central Segment of the Prague Basin (Kříž, 1991, text-fig. 2).

The overlying cephalopod limestone indicates surface current overflowing slope of the elevation in the SW-NE direction. Sediments that bracketed the cephalopod limestone bank reflect rapid changes in the current activity. The truncated erosive surfaces correlate with the maximum current activity and erosion. Individual beds of the cephalopod limestone deposited on erosive surfaces correlate with continual deposition. The packed large shell-fragments close to erosive surfaces pass to packstone and later to wackestone containing numerous cephalopod shells reflecting decrease in the current activity. Usually only part of the cycle is preserved due to erosion at the base of following cycle. In the middle part of the cephalopod bank the truncated erosive surfaces are the most densely packed and suggests maximal current activity and erosion. Where only base of the cycle with packed shell fragments is preserved, the minimum distance between succeeding unconformities is 2 cm. Above some erosive surfaces a few millimetres thick

mudstone terminate with flat mineralised hardground showing abrupt break in sedimentation.

The cephalopod limestone is covered by thin bed of tuffite passing to the shale with upward decreasing tuffitic admixture. The shale contains intraclasts derived from the retrograded cephalopod limestone. Slightly higher the last limestone bed with benthic fauna occurs. The following sequence with graptolite fauna suggests that hemi-pelagic conditions returned (Fig. 3).

Studied section documents elevation with shallow water sedimentation located outside main volcanic centres with long-term shallow water setting (Svatý Jan Volcanic Centre: Wenlock-Lochkovian; Nová Ves Volcanic Centre: Ludlow; Kosov Volcanic Centre: Ludlow; Horný, 1955 and Kříž, 1991). The Vyskočilka Section has been presumably situated on the slope of this elevation, although not far from the central part. The transported intraclasts in shale above the cephalopod limestone suggests that skeletal sands were replaced by cephalopod limestone in shallower part of the elevation.

In the Vyskočilka Section the early Gorstian tuffites with shallow water brachiopods, and cephalopod limestone correspond to the short-term local shallowing most probably caused by syn-sedimentary uplift due to the local volcanic activity. The shallow water sequence is only about 50 cm thick.

FAUNA OF CEPHALOPOD LIMESTONES

The most diverse fauna dominated by benthic bivalves and nectobenthic cephalopods occurs in the cephalopod limestone together with pelagic cephalopods and relatively rare graptolites of the water column fauna. Benthic fauna represented by bivalve dominated *Cardiola donigala-Slava sathon* Community is analogous and homologous (Boucot & Kříž, 1999) with other communities of the *Cardiola* Community Group (Kříž, 1999a) of the late Wenlock and Ludlow age.

Benthic fauna

Cardiola donigala-Slava sathon Community

Name - Used here for the first time.

Assemblage group assignment - *Cardiola* Community Group (Kříž, 1999a).

Age - Ludlow, Gorstian, early *L. scanicus* Biozone.

Type locality - Vyskočilka Section, bed no. 6.

Geographic distribution - Type locality only.

Community and environment interpretation, ecogeny - Besides abundant cephalopods, described below as the assemblage of the water column fauna, the Bivalvia dominated benthic community is accompanied by very rare low-spired and high-spired gastropods (two species). The single specimen of the monoplacophor *Drahomira kriziana* was found for the first time in the *L. scanicus* Biozone (see Horný 2005). The worm

“*Spirorbis*” sp. overgrows rarely cephalopod shells. Non-vascular plants *Prototaxites* sp. and *Pachythea* sp. are present.

Bivalvia shells occur disarticulated and commonly fragmented. All bivalves are filtrators, 52.4% of which are epibyssate, 10.5% semi-infaunal and 47.8% endobyssate-reclining. The community is homologous and analogous to other *Cardiola* Community Group communities from the late Wenlock and Ludlow. The *Cardiola donigala*-*Slava sathon* Community member species are the same (e.g. *Butovicella migrans*, *Slavinka acuta*, *Cardiola agna agna*, *Dualina longiuscula*, *Mila* sp., and *Patrocardia* sp.), or the closely related (e.g. *Maminka arachne*, *Cardiola donigala*, *Slava sathon*, *Slavinka* sp., *Cardiola signata*, *C. aff. pectinata*, and *Spanila* sp.) to the ancestral species of the *Cardiola gibbosa* Community from the *N. nilssoni* Biozone described from the Na Břekvíci Section (Kříž, 1999a). Very common fragments of cephalopods formed substrate for prevailing epibyssate bivalves. On the other hand the packstone-wackestone micrite rich limestone was also suitable for the semi-infaunal and endobyssate reclining bivalves (47.8%). The community existed in relatively very shallow environment, sometimes probably within the reach of fair-weather waves as documents common fragments of the larger shells (*Slava* and *Maminka*). The surface current mostly well ventilated the bottom except short periods documented by the mass mortalities of the relatively common juvenile bivalves. In comparison the *Cardiola donigala*-*Slava sathon* Community is less diversified than the *Cardiola gibbosa* Community and also population density is lower. Lower diversity corresponds most probably to the short duration of the cephalopod limestone biofacies on the local elevation and to the higher energy of the environment time to time within the reach of waves.

The *Cardiola donigala*-*Slava sathon* Community may be considered to be ancestral to the late *L. scanicus* *Cardiola donigala*-*Slava cubicula* Community from the locality Sedlec (Kříž, 1999c). The diversity and population density of the both communities are very

similar. In both communities *Maminka arachne*, *Cardiola donigala* and evolutionary very closely related *Slava sathon* and *S. cubicula* represent most prominent and dominant species.

In general the Gorstian may be characterized by the eustatic sea-level lowstand in the lower part of the *N. nilssoni* Biozone. Most probably in higher parts of the biozone started global rise of sea level that persisted to the upper *L. scanicus* Biozone. The highstand is characterized by sedimentation of hemipelagic sediments in most of the basins and marginal seas. The cephalopod limestones occurred only in the shallower environments mostly below the wave base within the reach of the surface currents on the local tectonic or volcanic elevations and probably close to shorelines. The bivalve fauna of the lower *N. nilssoni* Biozone reduced in diversity due to highstand settings and new species occurred in the lower *L. scanicus* Biozone (e.g. *Cardiola signata* and *Cardiola donigala* as descendants of *Cardiola gibbosa* and *Maminka arachne* as descendant of *Maminka comata*).

Water column fauna

Pseudocycloceras duponti-*Kionoceras doricum* Assemblage

Name - Used here for the first time.

Assemblage group assignment - Not established yet.

Age - Ludlow, Gorstian, lower *L. scanicus* Biozone.

Type locality - Vyskočilka Section, bed no. 6.

Geographic distribution - Type locality only.

Composition - The assemblage includes 25 species of cephalopods and represents rather highly diversified cephalopod assemblage. All basic morphotypes and life strategies are presented except very specialised asconic shell (Fig. 5). The nectobenthic cephalopods are represented by 12 species (46.63% of the cephalopod shells). The nectobenthic pseudorthocerids with longicone shell are the most characteristic, namely *Pseudocycloceras* with horizontal biologic orientation and *Kionoceras* with vertical biologic orientation. Among nectobenthic nautiloids the *Oonoceras* with cyrticone and *Peismoceras* with coiled shells are common. Both are rather mobile forms among nectobenthic cephalopods. Less mobile brevicone forms with open aperture are very rare. The brevicone cephalopods with contracted aperture and thus microphage habit are also very rare (1.13%). Nektonic palliocerids (*Plagiostomoceras* and *Sphooceras*) represent 15.41% of collected cephalopods, which is average value among the Silurian cephalopod assemblages.

The pelagic orthocerids of the genera *Kopaninoceras*, *Arionoceras*, *Michelinoceras* and *Parakionoceras* represent 31.20% of collected cephalopods, but their original frequency was higher. Underrate of the pelagic cephalopods reflects high post-mortem destruction of their shells. Thin and smooth

Species	Life habits	R+L	A	RA	AA	R
<i>Maminka arachne</i>	reclining	24	-	27.9	-	1
<i>Butovicella migrans</i>	epibyssate	19	-	22.1	-	2
<i>Cardiola donigala</i>	epibyssate	15	-	17.4	-	3
<i>Slava sathon</i>	reclining	6	-	7.0	-	4
<i>Slavinka acuta</i>	semi-infaunal	6	-	7.0	-	4
<i>Cardiola agna agna</i>	epibyssate	6	-	7.0	-	4
<i>Slavinka</i> sp.	semi-infaunal	2	-	2.3	-	5
<i>Actinopteria</i> sp.	epibyssate	2	-	2.3	-	5
<i>Cardiola signata</i>	epibyssate	1	-	1.2	-	6
<i>Cardiola</i> aff. <i>pectinata</i>	epibyssate	1	-	1.2	-	6
<i>Dualina longiuscula</i>	reclining	1	-	1.2	-	6
<i>Mila</i> sp.	reclining	1	-	1.2	-	6
<i>Patrocardia</i> sp.	epibyssate	1	-	1.2	-	6
<i>Spanila</i> sp.	semi-infaunal	1	-	1.2	-	6
Totals		86	-	100.2	-	

Fig. 4 - Numerical and ranked abundance of bivalves in the *Cardiola donigala*-*Slava sathon* Community, Ludlow, Gorstian, lower *L. scanicus* Biozone. Vyskočilka Section, bed no. 6. Abbreviations: R+L = right and left valves; A = articulated shells; RA = percentage relative abundance; AA = percentage relative abundance of articulated shells, R = rank..

Species	S	P	Morphotype	BO	Life habits	R
<i>Pseudocycloceras duponti</i>	66	24.81	long orthocone longicone, an., d.	EN-v	nectobenthic	1
<i>Arionoceras-Kopaninoceras</i> sp.	42	15.79	short orthocone longicone, d.	v	pelagic	2
<i>Plagiostomoceras</i> sp.	25	9.40	long orthocone longicone, d.	h	nektonic	3
<i>Michelinoceras michelini</i>	22	8.27	long orthocone longicone	v	pelagic-passive	4
<i>Oonoceras</i> sp.	19	7.14	cyrtocone longicone	EX-v	nectobenthic	5
<i>Kionoceras doricum</i>	18	6.77	slightly cyrthocone-longicone	EN-v	nectobenthic	6
<i>Cyrtocycloceras</i> sp.	15	5.64	cyrtocone longicone, an.	EN-v	nectobenthic	7
<i>Sphooceras truncatum</i>	12	4.51	short orthocone longicone, tr., d.	h	nektonic	8
<i>Parakionoceras originale</i>	7	2.63	short orthocone longicone	v	pelagic	9
<i>Peismoceras asperum</i>	7	2.63	free coiled, an.	Ex-v	nectobenthic	9
<i>Kopaninoceras</i> aff. <i>timidum</i>	6	2.26	short orthocone longicone	v	pelagic	10
<i>Kopaninoceras spiculum</i>	4	1.50	orthocone longicone	v	pelagic	11
<i>Sphooceras sacculus</i>	4	1.50	short orthocone longicone, tr., d.	h	nektonic	11
<i>Oonoceras</i> aff. <i>imperiale</i> n.sp.	3	1.13	cyrtocone longicone	EX-v	nectobenthic	12
<i>Sactoceras</i> sp.	3	1.13	slightly cyrthocone-longicone	EX-v	nectobenthic	12
<i>Calorthoceras butovitzense</i>	2	0.75	orthocone longicone, an.	-	pelagic	13
<i>Lycoceras</i> sp.	2	0.75	orthocone longicone	EX-v	nectobenthic	13
<i>Jeppssonoceras</i> sp.	2	0.75	brevicone, ca.	EX-v	microphage	13
<i>Kentronites transiens</i>	2	0.75	short slightly cyrtocone longicone	EX-v	nectobenthic	13
<i>Dawsonoceras</i> sp.	1	0.38	orthocone longicone, an., d.	v	nectobenthic	14
<i>Mandaloceras</i> sp.	1	0.38	brevicone, ca.	EX-v	microphage	14
<i>Ophioceras rudens</i>	1	0.38	involute, an.	EX-v	nectobenthic	14
<i>Ophioceras simplex</i>	1	0.38	involute, an.	EX-v	nectobenthic	14
<i>Rizoceras</i> sp.	1	0.38	slightly cyrthocone brevicone	EN-v	nectobenthic	14
Total	266	100.01				

Fig. 5 - Numerical and ranked abundance of cephalopods in the *Pseudocycloceras duponti*-*Kionoceras doricum* Assemblage, Ludlow, Gorstian, lower *L. scanicus* Biozone. Vyskočilka Section, bed no. 6. Abbreviations: S = number of collected specimens; P = percentage relative abundance; BO = biologic orientation of the shell (EX - exogastric curved shell, EN - endogastric curved shell, v - vertical respectively sub-vertical biologic orientation of the shell, h - horizontal respectively sub-horizontal biologic orientation of the shell); R = rank; Life habits - nectobenthic mode of life sometimes separates to the two categories, *nectobenthic* - prevail rather benthic mode of life, *nectobenthic* - prevail rather nektonic mode of life, pelagic - active respectively passive mean pelagic life of passive floating within current respective active correction with jet propulsion. Morphotypes after Flower (1964) and Teichert (1964), an. - annulations, ca. - contracted aperture, d. - cameral deposits, tr. - truncation (for explanation see Flower 1964).

shells of pelagic orthocerids produced the majority of free cephalopod bioclasts comprising the cephalopod limestone. Due to difficult identification of the pelagic taxa with longicone smooth shells the most common convergent genera *Kopaninoceras* and *Arionoceras* are grouped on Fig. 5 despite the fact that they belong to different families (see Dzik, 1984).

In addition, some graptolites occur in cephalopod limestones; *Pristiograptus* ex gr. *dubius* occur rather commonly in micrite rich inter-beds while proximal parts of *Colonograptus roemeri* are rare in bioclast-rich beds.

Comparison - The *Pseudocycloceras duponti*-*Kionoceras doricum* Assemblage is closely related with cephalopod assemblage of the lower *N. nilssoni* Biozone known from the Praha-Butovice, Na břekvíci Section. Eighteen species occur in both homological and analogical assemblages characterised by ancestor-descendent lineages *Peismoceras amicum*-*P. asperum* and *Kionoceras electum*-*K. doricum*. The *Pseudocycloceras duponti*-*Kionoceras doricum* Assemblage is less diversified than the assemblage of the lower *N. nilssoni* Biozone and two new genera-

species "*Oonoceras*" aff. *imperiale* (gen. nov.) and *Jeppssonoceras* sp. appear in the later assemblage.

Younger cephalopod assemblage - that of the upper *L. scanicus* Biozone, Sedlec Section (Kříž, 1999c) - is closely linked to the *Pseudocycloceras duponti*-*Kionoceras doricum* Assemblage by twenty common species. The cephalopod assemblage from the Sedlec Section contains some distinct, rare new taxa. In the Sedlec Section pelagic orthocerids are more common and *Kionoceras doricum* is less abundant. Pelagic orthocerids were most probably destructed to indeterminable fragments in higher environment energy in the Vyskočilka Section.

Remarks - Vyskočilka Section represents the type locality of *Kionoceras doricum* and of *Ophioceras tener* (Stridsberg & Turek, 1997). *Kionoceras doricum* is the type species of world-wide distributed genus *Kionoceras* (Hyatt, 1884) ranging from the late Ordovician to the late Carboniferous (Sweet, 1964). *Ophioceras tener* is a junior synonym of *Ophioceras rudens* (Stridsberg & Turek, 1997).

Discussion - The high disparity of the cephalopod assemblage indicates relatively stable surface currents to offer optimal condition for cephalopods with different biologic position and morphotype. Similarly, absence of cephalopod pelagic larvae in the sediment shows that they were carried out by stable surface current. The highly diversified nectobenthic cephalopods document rather shallow environment of well-ventilated bottom. Rare less mobile nectobenthic cephalopods and absence of trilobites and brachiopods nevertheless indicate instability in the bottom ventilation.

DEPOSITIONAL ENVIRONMENT AND ECOGENY OF THE WENLOCK (EARLY HOMERIAN) AND LUDLOW (GORSTIAN) CEPHALOPOD LIMESTONE BIOFACIES

Activation of the current system after early Silurian anoxia caused the development of the cephalopod limestone biofacies at the depths ventilated by the surface current below the storm base since the late Sheinwoodian (Kříž, 1998). During the early Homerician

(Wenlock) and especially in the Ludfordian (Ludlow) carbonate sedimentation extended as well as did the cephalopod limestone sedimentation and spread all around northern Gondwana basins at the same stratigraphic horizons as shown by the analysis of Bivalvia dominated communities, nectobenthic and pelagic cephalopods assemblages, by occurrence of conodonts and rare graptolites (Kříž, 1991, 1998, 1999a; Ferretti & Kříž, 1995; Gnoli, 2003).

The sedimentation of cephalopod limestones is characterized by the cycles consisting in general of (1) mudstone with erosive surface and (2) 3 to 10 cm thick cephalopod wackestone-packstone followed by the mudstone. The erosive surface in upper level of the basal mudstone corresponds to the start of the surface current activity and erosion of the bottom. It followed development of the cephalopod limestone biofacies during slow deepening of the environment up to the anoxic water conditions and pelagic mudstones sedimentation covering the cephalopod limestone.

In the Prague Basin the Wenlock and early Ludlow (Gorstian) cephalopod limestones are developed mostly as separate beds within the shale sequence usually deposited in either the single cycle or a few depositional

Series	Stages	Zone	Cephalopod limestone horizons	Bivalvia dominated communities	Cephalopod assemblages	
Ludlow	Ludfordian	<i>linearis</i>				

Fig. 6 - Distribution of bivalve communities (Kříž, 1999a, c) and cephalopod assemblages (Manda, 2003) in the Prague Basin during late Wenlock and early Ludlow.

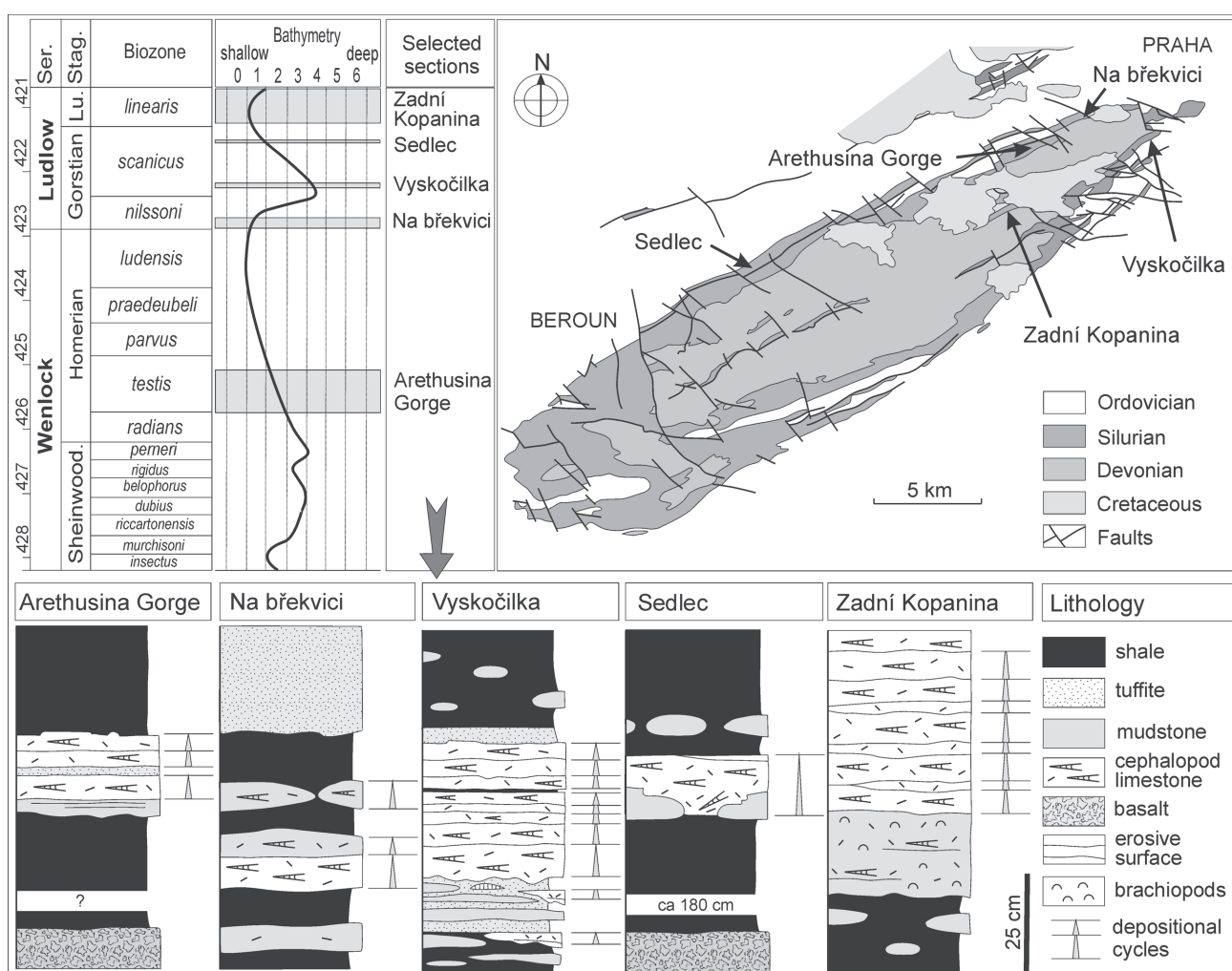


Fig. 7 - Position of the cephalopod limestone horizons (indicated by grey colour) plotted against global eustatic curve of Johnson et al. (1996) and selected sections showing changes in the cephalopod limestone framework during the late Wenlock (Homerian) and the Ludlow (Gorstian-early Ludfordian). The position of selected section is giving in right upper part. Arethusina Gorge Section after unpublished data of Kříž (1966), Na břekvici Section after Kříž (1992), Sedlec Section after Kříž (1999c) and Zadní Kopanina Section after Manda (2003).

cycles (Arethusinová Gorege Section, Na břekvici Section, Vyskočilka Section and Sedlec Section). They correspond to the relatively short-term existence of the surface current above the locally shallow and then rapidly subsiding bottom. A few depositional cycles represent another evidence of the local elevations subsidence due to general subsidence of the Central Segment in the Wenlock (Kříž, 1991) and to general uplift of the Central Segment compensating the sea-level rise in early Ludlow (Gorstian) (Johnson et al., 1998, Text-fig. 7).

The Ludfordian (Ludlow) cephalopod limestones developed in the Central and Pankrác segments of the Prague Basin (Kříž, 1991) are more complex and the resulting beds or banks (up to 380 cm thick) are composed of numerous alternating relatively thin micritic layers with dominant pelagic organisms with the beds of varying thickness of coarse bioclasts composed of cephalopod shells and benthic organisms (Ferretti & Kříž, 1995). They represent depositional cycles separated by erosive surfaces (e.g. Praha-Pankrác sections, Praha-Řeporyje, Mušlovka Section; Praha-

Zadní Kopanina sections, Praha-Lochkov, Cephalopod Quarry and Marble Quarry sections, and Kosov near Beroun sections). They represent longer history of the cephalopod limestone biofacies at the depths below wave base influenced by more stable surface current system with minimal lateral shifts for longer periods of time. These numerous depositional cycles represent another evidence of generally lowstand and contemporary oscillating uplift combined with slow subsidence of the Central and Pankrác segments during the Ludlow (Ludfordian) (Kříž, 1991).

Rediscovered cephalopod limestone of the lower *L. scanicus* Biozone from the Vyskočilka Section contains new *Cardiola donigala-Slava sathon* Community and *Pseudocycloceras duponti-Kionoceras doricum* Assemblage homologous and analogous with older (lower *N. nilssoni* Biozone) *Cardiola gibbosa* Community (Kříž, 1999a) and cephalopod assemblage (Manda in Kříž, 1998) as well as with younger (upper *L. scanicus* Biozone) *Cardiola donigala-Slava cubacula* Community (Kříž, 1999c) and cephalopod assemblage (Manda in Kříž, 1999c). Lower *L. scanicus* Biozone cephalopod

limestone fauna from the Vyskočilka Section is closely related to that of the upper *L. scanicus* Biozone than to the *N. nilssoni* Biozone cephalopod limestone from the Butovice Section. Higher fragmentation-disarticulation at the Vyskočilka Section reflects higher environment energy during cephalopod limestone sedimentation.

In the early Ludlow cephalopod limestones occur during eustatic lowstands in the early Gorstian *N. nilssoni* Biozone and in the early Ludfordian *S. linearis* Biozone. The later Gorstian highstand (Johnson et al., 1998) caused global retrogradation of the cephalopod limestone biofacies and the cephalopod limestone biofacies persisted only on the local rising zones due to volcanic or tectonic activity and probably close to shorelines. Upper *L. scanicus* Biozone cephalopod limestone horizon was described from SW Sardinia (Kříž & Serpagli, 1993), Tajmyr, Russia (Kříž & Bogolepova, 1995), Montagne Noire (Kříž, 1996) and the Prague Basin (Kříž, 1998).

The maximum expansion of the cephalopod limestone biofacies was reached in peri-Gondwana in the Ludfordian (Ludlow) (Kříž, 1998). The more stable surface current system was favourable for the development of water column cephalopod assemblages and of the Bivalvia dominated communities with high diversity and population density. During very early Přídolí the sedimentation of the cephalopod limestones was abruptly interrupted by the global sea-level rise (Kříž, 1998). The cephalopod limestone biofacies of the late Přídolí contained homological but not analogical Bivalvia dominated communities where shallow burrowing cardioids were dominant (Kříž, 1999a). The Bivalvia dominated communities of the Lochkovian cephalopod limestones (Prague Basin, Massif Armoricain and Morocco) were neither homological nor analogical and were dominated by the infaunal antipleurid bivalves (Kříž, 1999a).

ACKNOWLEDGEMENTS

Our special thanks are extended to the Czech Geological Survey of Prague for permitting and supporting this study. The research was also founded by GA ČR (Czech Science Foundation) project 205/06/1367. We are indebted to Petr Štorch and Arnošt Galle, Institute of Geology, Czech Academy of Science, Praha, for identification of graptolites and corals. Finally, thanks to Petr Štorch for critical reading of the manuscript.

INDEX OF FOSSILS

The species mentioned in the text are listed below with the author and publication date.

“Vermes”

“*Spirorbis*” sp.

Tabulata (determined by A. Galle)

Favosites aff. *tachlowitzensis* Pošta, 1902

Monoplacophora (determined by J. Kříž)

Drahomira kriziana Horný, 2005

Bivalvia (determined by J. Kříž)

Actinopteria sp.

Butovicella migrans (Barrande, 1881)

Cardiola agna agna Kříž, 1979

C. donigala Kříž, 1993

C. docens Barrande, 1881

C. gibbosa Barrande, 1881

C. aff. pectinata Barrande, 1881

C. signata Barrande, 1881

Cardiola sp.

Dualina longiuscula Barrande, 1881

Maminka arachne Barrande, 1881

M. comata Barrande, 1881

Manulicula manulia (Barrande, 1879)

Mila sp.

Patrocardia sp.

Slava cubacula Kříž, 1985

S. sathon Kříž, 1985

Slavinka acuta (Barrande, 1881)

Slava bohémica Barrande, 1881

Slavinka sp.

Spanila sp.

Cephalopoda (determined by Š. Manda)

Arionoceras sp.

Caliceras capillosum (Barrande, 1868)

Calorthoceras butovitzense Chen, 1981

Cyrtocycloceras sp.

Dawsonoceras sp.

Jeppssonoceras sp.

Kentronites transiens (Barrande, 1866)

Kionoceras doricum (Barrande, 1868)

K. electum (Barrande, 1866)

Kopaninoceras amoenum (Barrande, 1866)

K. spiculum (Barrande, 1868)

K. aff. timidum (Barrande, 1866)

Kopaninoceras sp.

Lycoceras sp.

Mandaloceras sp.

Michelinoceras michelini (Barrande, 1866)

Oonoceras aff. *imperiale* (Barrande, 1866) n. sp.

Oonoceras sp.

Ophioceras rudens Barrande, 1865

O. simplex (Barrande, 1855)

Parakionoceras originale (Barrande, 1868)

Peismoceras amicum (Barrande, 1865)

P. asperum (Barrande, 1865)

Plagiostomoceras sp.

Pseudocycloceras duponti (Barrande, 1866)

P. nereidum (Barrande, 1868)

Rizoceras sp.

Sactoceras sp.

Sphooceras sacculus (Barrande, 1860)

S. truncatum (Barrande, 1860)

Brachiopoda (determined by Š. Manda)

Bleshidium aff. *patellinum* (Barrande, 1879)

Cyrtia aff. *bedya bedya* Havlíček, 1990

Cyrtia sp.

Gypidula cf. *vestita* (Barrande, 1879)

Septatrypa aff. *caprilupa* Havlíček, 1990

Trilobita

Cromus sp.

Phyllocarida

Ceratiocaris sp.

Ostracoda

Entomozoe? sp.

Graptoloidea (determined by P. Štorch)

Bohemograptus bohemicus (Barrande, 1850)

Colonograptus colonus (Barrande, 1850)

C. varians (Wood, 1900)

C. roemeri (Barrande, 1850)
Lobograptus progenitor Urbanek, 1966
L. scanicus (Tullberg, 1883)
Monograptus uncinatus Tullberg, 1883
Neodiversograptus nilssoni (Lapworth, 1876)
Pristiograptus dubius (Suess, 1851)
P. ex gr. dubius (Suess, 1851)
Saetograptus fritchi (Perner, 1899)
S. chimaera (Barrande, 1850)

Non-vascular plants
Prototaxites sp.
Pachythea sp.

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Manuscript received 31 October 2005

Revised manuscript accepted 10 January 2007

