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DISERTAČNÍ PRÁCE

VÝVOJ PROSTŘEDÍ A SPOLEČENSTEV VE SVRCHNÍM SILURU A NEJNIŽŠÍM DEVONU

ŠTĚPÁN MANDA

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Mark Twain

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OBSAH

SEZNAM PŘÍLOH

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1. ÚVOD

Evoluce života a mořských ekosystémů v geologické minulosti je bezesporu jedním z nejzajímavějších témat věd o Zemi. Výzkum globálních změn přírodních ekosystémů vede k porozumění zákonitostí vývoje organismů a charakteru jejich reakce na změny prostředí. Lidská civilizace podstatně ovlivňuje nejen terestrická prostředí, ale i relativně stabilnější, přesto však velmi citlivé mořské prostředí, které hraje v planetárním ekosystému hlavní roli. Je zneklidňující na jedné straně vidět dlouhodobý a složitý vývoj života na Zemi trvající stovky milionů let, růst diverzity a rozmanitosti života, jeho postupnou stabilizaci v různých ekosystémech a na druhé straně rychlou destrukci většiny ekosystémů a vymírání všech forem organismů v průběhu rozvoje moderní civilizace a našich krátkých životů. Většinu existence Země se život vyskytoval pouze v moři a kontinenty byly pusté a neobydlené, a někdy se zdá, že se tento stav může v budoucnu zopakovat. Studium minulosti nejen odpovídá na otázku, proč svět je takový, jaký je, ale umožňuje také pochopit zákonitosti a mechanismy jeho vývoje. Vědecké poznatky samy o sobě ale nejsou ničím samospasitelným. To podstatné, co by nám mělo studium minulosti ukázat, se nachází v myšlení a přístupu společnosti k přírodnímu dědictví a tedy i k sobě samé. Léčit obezitu někoho, kdo se neustále přežírá, je totiž možné, ale zbytečné. Stejně tak se lidé potřebují naučit jinak přemýšlet, ale kategorie jako zdrženlivost a respekt nejsou věcí vědy. Snad návratu k těmto hodnotám narůstající vědění přispěje. Jinou možnost totiž lidstvo ani nemá. Vědy o Zemi a živé přírodě se postupně stávají součásti kultury, obecného povědomí a vzdělání a společně spoluutvářejí náš pohled na přírodu.

Žádný živočišný ani rostlinný druh žijící v paleozoiku či mezozoiku nepřežil do současnosti. Více než 99 % druhů, které kdy na Zemi žily, vymřelo (Stanley 2007). Mnoho skupin obývající v minulosti mořské prostředí ve velké druhové i početní četnosti nemá dnes žijící příbuzné nebo patří do kategorie tzv. žijících fosilií, zatímco jiné skupiny se rozvíjejí i dnes. Lidstvo potřebuje porozumět evoluci a její dynamice, aby bylo schopné je v budoucnosti ovlivňovat anebo z nich vyvodit důsledky pro své směřování. Narůstající a stále přesnější studia vývoje života nám dávají unikátní příležitost přemýšlet o životě na Zemi a rozpoznat obecné zákony řídící vývoj organismů přerušovaný globálními krizemi a rozsáhlými změnami. Klíčovou otázkou je, jak a proč se ekosystémy v minulosti měnily, a tuto otázku nelze zodpovědět bez studia fosilního záznamu.

Jedním ze základních obecných makroevolučních problémů je otázka vztahu mezi vývojem organismů a prostředí a mezi organismy navzájem. Dlouhou dobu se lidé ukolébávali myšlenkou stability a pomalé kontinuální evoluce vedoucí k adaptační dokonalosti. Není bez zajímavosti, že i když fosilní záznam je s tím v přímém rozporu, našlo se dost vysvětlení, jak tuto nejasnost zbagatelizovat. Chlácholivá jednota moderní syntézy byla nahrazena celou řadou makroevolučních teorií akcentujících různé rysy evolučních procesů jako morfologická a konstrukční omezení, význam parazitů, náhodné neutrální změny a podobně. Zdá se ale, že přírodní procesy nelze vysvětlit jednostranným tvrzením. E. Hobswam ve své známé knize „Věk extrémů/Krátké století" uvádí, že jedním z klíčových momentů, kdy se začal měnit náš pohled na pomalou evoluci zdánlivě směřující k dokonalosti, bylo formulování teorie přerušovaných rovnováh Eldridgem a Gouldem (1972) a že tato změna pohledu (někdo by řekl paradigmatu) není omezena jen na přírodní vědy, společnost začala nazírat na svět i sebe samu se značnou dávkou nejistoty. Na teorii přerušovaných rovnováh navázala řada autorů, Vrba a Gould (1986) postulovali hierarchickou teorii evoluce, o možné evoluci společenstev uvažoval i Boucot (1990) a jako o koordinované stázi i Brett a Baird (1995) a tak dále. Důsledkem je zmíněná řada přístupů, v nichž se orientuje jen málo specialistů; jejich společným rysem je vědomí komplexnosti a kauzality evolučních procesů, ale také akceptování jisté náhodnosti.

Jiná skupina často řešených otázek je spojená se studiem globálních krizí ekosystémů – jak společenstva reagují na změny prostředí? jaké jsou příčiny těchto změn? jak dochází ke vzniku nových společenstvech po takových krizích? (Walliser ed. 1996, Hart ed. 1996). Výzkum posledních let se zaměřil na to, zda rychlé změny ekosystému v minulosti opravdu probíhaly, do jaké míry jsou skutečně rychlé (geologický čas je poněkud specifické povahy), jak časté takové krize byly, a na řadu podobných otázek. Co se ukázalo zřejmým, je, že makroevoluční procesy hrají důležitou roli v období krizí a utváření nových společenstev. Stanley (2007) dokládá, že globální krize jsou jediným mechanismem, který omezuje exponencionální růst biodiverzity v obou hlavních ekosystémech. Nicméně se zdá, že odpovědi na tyto otázky a testování stávajících modelů vyžadují precizně sebraná a nově zhodnocená data (například

Boucot 1990 a Bonuso et al. 2002). Zdá se, že pro mnoho badatelů je přemýšlení u kávy a klávesnice pohodlnější než pobyt v terénu.

Obecné modely a hypotézy evolučních procesů a vývoje ekosystémů jsou testovány-falzifikovány na konkrétních studiích. Jednotlivé útvary, oddělení a stupně v geologické minulosti umožnují takové studie s různou přesností, a to vzhledem k preciznosti časového dělení i rozsahu změn v dané době. Nemusí nutně platit tvrzení, že čím starší období, tím horší možnosti pro studium poskytuje. Mezi neustále znovu a znovu studovaná období patří objevení prvních metazoí ve svrchním proterozoiku, radiace mořských organismů s pevným skeletem ve spodním kambriu, spodnoordovická radiace a podobně (přehled podávají kompendia Zhuravlev a Riding 2000, Webby et al. 2004). Také silur a spodní devon, kterých se týká tato dizertační práce, jsou pozoruhodná období v minulosti Země. Svrchnoordovické zalednění způsobilo rozsáhlé vymírání, jedno z pěti největších v geologické minulosti, které postihlo řadu vývojových linií. Rozlišit ordovické a silurské fauny je možné na první pohled. Rychlý ústup ledovců vyvolal vzestup hladiny oceánů a vedl k rozšíření anoxických podmínek v období spodního siluru (v podobném rozsahu se nikdy něco podobného v historii Země neopakovalo). Přežívající fauny na mělkovodních plošinách postupně diverzifikovaly a expandovaly směrem k pólům s postupným zlepšením ventilace všech světových oceánů (např. Kaljo et al. 1995, Luning et al. 2000). Nicméně diverzifikaci přerušovala řada větších či menších vymírání. V devonu došlo k další významné změně rozšířením řady predátorů. Zejména radiace rybovitých obratlovců je významná, do té doby tvořili nejvyšší predátory hlavonožci. To změnilo celé ekosystémy i vytvořilo adaptační tlaky na mnoho skupin (antipredační znaky, raná ontogeneze, tlak na přechod k nektonnímu způsobu života, viz souhrn Signor a Brett 1984, Klug et al. 2010). Od svrchního siluru také probíhala expanze rostlin na souš. Pobřeží pustých kontinentů se začínalo pokrývat vegetací, která postupovala dále do vnitrozemí. Rostliny následovali i živočichové. V nejvyšším siluru na pobřeží moří rostly malé rostliny bylinného vzhledu, ale po středním devonu už existovaly ve vnitrozemí lesy (souhrn např. McGhee 2005). Tato změna vyvolala i změnu v chemismu atmosféry a oceánů, rychlosti a typu zvětrávání hornin, poklesl i podíl suspenze splavované do moří, protože vegetace stabilizuje reliéf (například Simon et al. 2007). V devonu vzniklo i mnoho nových kladů, mezi něž patří amoniti a coleoidi. Přelom siluru a devonu je tak kritickým bodem ve vývoji marinních i kontinentálních ekosystémů plně srovnatelným s raně ordovickou radiací. Někteří autoři milující slogany hovoří o paleozoické marinní revoluci, „precursor" mezozoické revoluce, střednopaleozoické revoluci a devonské nektonní revoluci.

Jak je uvedeno výše, ne všechna období v minulosti Země jsou stejně vhodná pro testování různých hypotéz a něco podobného platí i pro oblasti. Pro studium současných ekosystémů jsou některé oblasti důležitější než jiné, protože je zde možné pozorovat něco, co jinde není možné nebo by to bylo obtížnější. Pověstnou „Mekkou" biologů jsou například Galapágy. Podobně pro studium fosilního záznamu existují klasické oblasti, kde je v nějakém ohledu zachováno něco, co jinde není, nejznámější jsou patrně burgeské břidlice v Kanadě, ale takových míst různého významu je mnohem více. Střední Čechy jsou takovým mezinárodně klasickým regionem pro výzkum období spodního paleozoika s dlouhodobou tradicí výzkumu. Již Charles Darwin (1809–1882) ve své knize „O původu druhů" považoval data shromážděná Joachimem Barrandem (1799–1883) z této oblasti jako nejlepší dostupnou paleontologickou evidenci své teorie evoluci druhů v geologické historii. Bohužel musel konstatovat, že tento záznam jeho teorii nepotvrzuje, druhy se objevují rychle, poté se minimálně mění a nakonec zanikají. Byl to jeden z důvodů, proč formuloval svojí tezi o neúplnosti geologického záznamu (Haubelt 1984). J. Barrande byl přívržencem Cuvierova katastrofismu, tedy teorie vycházející spíše z biblické potopy než racionality. Barrandovy sběry nepocházely proto z celých vrstevních sledů, ale vybraných bohatých vrstev, a tedy nějakou kontinuální změnu ani ukázat nemohly. Od Barrandových dob výzkum pokračoval s různou intenzitou až dodnes. Z tohoto malého území byly popsány stovky druhů, část z nich byla později objevena v ostatních paleozoických regionech Evropy, severní Afriky, Asie a jinde a přispěly k rozvoji paleobiogeografie. Výzkum fosilních faun a jejich evoluce, biostratigrafie a korelace tak závisely na výzkumu v Čechách, ne jenom vzhledem k správné taxonomické identifikaci vycházející ze srovnání s typy, ale následně i v návazných studiích obecného charakteru. Střední Čechy jsou také klasický region chronostratigrafie, jak dokumentují tři stratotypy GSSP (Chlupáč et al. 1972, Kříž et al. 1986, Chlupáč a Oliver 1989) a typové lokality pro řadu extinkčních krizí (souhrn House 1985, 2002; Chlupáč a Kukal 1986, Walliser 1996).

2. CÍLE PRÁCE, JEJÍ STRUKTURA A METODIKA

Z přechozího stručného přehledu je zřejmé, že dosavadní představy o stavu a vývoji mořského ekosystému jsou v mnohých aspektech protichůdné a bude ještě dlouho trvat, než naše poznatky vyústí v obecně akceptovaný model. Jedním z možných přístupů, jak rozšířit naše poznání, je detailní studium sedimentárních sledů, pečlivější sběr dat než dosud a studium nových a doposud opomíjených modelových skupin organismů; pokus o takový přístup je záměrem této disertace.

Cílem této práce nebylo a není komplexně studovat vývoj ekosystémů v siluru a devonu, tedy období dlouhém mnoho milionů let, to ostatně není ani možné. Jednotlivé publikace řeší dílčí témata, která v nějakém smyslu doplňují stávající data anebo korigují či zpřesňují stávající modely/představy a mají obecný dopad na naše vnímání vývoje ekosystémů v siluru a spodním devonu. Cílem této disertační práce je prohloubit znalosti o klíčových otázkách, které zakládají naše současné představy o vývoji prostředí v období siluru a spodního devonu, a to studiem klíčových globálních krizí či nových modelových skupin organismů. Dílčí témata, jejich sumarizace a diskuse nově zjištěných poznatků následuje v dalších odstavcích. Úplný citační aparát a metodiku k jednotlivým tématům je možné najít v publikovaných pracích, zde jsou uváděny jen práce klíčové a klasické, popřípadě obecnější studie.

2.1. STUDIUM EXTINKČNÍCH EVENTŮ: STŘEDNOLUDFORDIANSKÁ KRIZE

Krizová vymírání jsou v pražské pánvi intenzivně studovaná, bylo nalezeno a více či méně zhodnoceno mnoho takových událostí nebo byl v rámci studia chronostratigrafických hranic publikován dostatek dat, které takovou interpretaci umožňují. Jedním z posledních významných rozhraní, které nebylo detailně studováno, je svrchnoludfordianské vymírání doprovázené největší změnou globálního cyklu uhlíku (pozitivní výchylka $\delta^{13}C$) ve světových oceánech v průběhu fanerozoika. Toto vymírání bylo popsáno jako Kozlowskii a Lau event.

Dílčím cílem disertace byla detailní korelace sekvencí kolem tohoto vymírání, zejména analýza, zda jsou Kozlowskii event a Lau event totožné události, jak se *předpokládalo, jaký byl vývoj eustáze a zda je tento event(y) spojen s vymíráním u jiných skupin než graptolitů a konodontů, zda se projevuje v různých mořských prostředích a zda je možná jeho korelace pomocí sekvenčních hranic a graptolitových faun.*

Tohoto tématu se týkají publikace:

Manda, Š., Kříž, J. 2006. Environmental and biotic changes of the subtropical isolated carbonate platforms during Kozlowskii and Lau events (Prague Basin, Silurian, Ludlow). GFF 128, 161–168.

Manda, Š., Štorch, P. Slavík, L., Frýda, J., Kříž, J., Tasáryová, Z. Přijato. The graptolite, conodont and sedimentary record through the late Ludlow Kozlowskii Event (Silurian) in the shale-dominated succession of Bohemia. Geological Magazine.

2.2. HLAVONOŽCI JAKO MODELOVÁ SKUPINA PRO STUDIUM MAKROEVOLUČNÍCH TRENDŮ, MORFOLOGICKÝCH ZMĚN A CHARAKTERU VYMÍRÁNÍ

Druhá skupina prací zahrnutá do disertace se týká použití hlavonožců jako modelové skupiny pro studium evolučních změn a ekosystémů. Tato skupina měkkýšů byla doposud ve starším paleozoiku opomíjena. Hlavonožci s vnější schránkou jsou přitom tradiční modelovou skupinou pro studium ekologických a evolučních změn v období svrchního paleozoika a zejména mezozoika. Tradičními skupinami pro studium morfologických trendů a vymírání v siluru a spodním devonu jsou graptoliti a konodonti, tedy skupiny bez žijících potomků, jejichž způsob života je dosti nejistý. Není však jasné, zda studia těchto skupin poskytují obecně platné výsledky aplikovatelné na jiné skupiny. Cílem bylo odpovědět na následující dílčí otázky:

(1) Vymírání versus strategie. Jaké byly ontogenetické strategie u silurskodevonských hlavonožců? Existují důkazy o vztahu ontogenetických strategií hlavonožců a dynamiky jejich evoluce, jak naznačují žijící skupiny hlavonožců a svrchnopaleozoičtí a mezozoičtí amoniti?

(2) Jaký byl migrační potenciál silurských hlavonožců a jak se utvářela společenstva biofacie hlavonožcových vápenců v temperovaných a chladných vodách po odeznění spodnosilurské anoxické periody? Jaké byly zákonitosti a fáze této kolonizace a jaký mají potenciál pro rekonstrukce vývoje klimatu a migračních cest ve vztahu k dlouhodobým paleogeografickým změnám a oscilacím mořské hladiny (eustázi)?

(3) Mají paleozoičtí hlavonožci, jako například amoniti, význam pro paleogeografické rekonstrukce? Pokud ano, jaké informace mohou poskytnout? Proč je v oblasti pražské pánve tak vysoká biodiverzita hlavonožců (větší než v tropech) a mnoho enedemických forem a jaký to má význam pro paleobiogeografii a evoluci paleozoických hlavonožcových faun?

(4) Jaká je dynamika morfologických změn schránek hlavonožců a co ji řídí? Jsou patrné nějaké dlouhodobé morfologické trendy? (a) Jsou posílené skulptury schránky důsledkem radiace predátorů schopných schránky destruovat, jak bylo předpokládáno? (b) Existuje vztah mezi zbarvením schránky a prostředím nebo morfotypem, tak jako u moderních hlavonožců? Je zbarvení schránky řízené jako adaptační znak? Jaká byla embryogeneze silurských a devonských nautiloidů? Lišila se od recentního Nautila, pokud ano, proč, a jaký to mělo vztah k vývoji společenstev a dispersi nautiloidů?

Těchto otázek se týkají publikace:

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Manda, Š. 2008a. Palaeoecology and palaeogeographic relations of the Silurian phragmoceratids (Nautiloidea, Cephalopoda) of the Prague Basin (Bohemia). Bulletin of Geosciences 83, 39–62.

Manda, Š. 2008b. Trocholites Conrad, 1838 (Nautiloidea, Tarphycerida) in the Middle Ordovician of the Prague Basin and its palaeobiogeographical significance. Bulletin of Geosciences 83, 327–334.

Manda, Š., Kříž, J. 2007. New cephalopod limestone horizon in the Ludlow (Gorstian, early L. scanicus Zone) of the Prague Basin (Bohemia, Perunica). Bollettino della Societá Paleontologica Italiana 46, 33–45.

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Manda, Š., Turek, V. 2009c. Minute Silurian oncocerid nautiloids with unusual colour patterns. Acta Palaeontologica Polonica 54, 503–512.

Turek, V., **Manda, Š**. 2010. Variability of colour pattern and shell malformations in Silurian nautiloid Peismoceras Hyatt, 1884. Journal of the National Museum, Natural History 179, 171–178.

Manda, Š., Frýda, J. 2010. Silurian–Devonian boundary events and their influence on cephalopod evolution: a comparison of faunal and carbon isotopic records from GSSP area (Barrandian). Bulletin of Geosciences 85, 513–540.

Turek, V., **Manda, Š**. 2011. Colour pattern polymorphism in Silurian nautiloid Phragmoceras Broderip, 1839. Bulletin of Geosciences 86, 91–105.

Manda, Š., Turek, V. In press. Late Emsian Rutoceratoidea (Nautiloidea) from the Prague Basin, Czech Republic: morphology, diversity and palaeoecology. Palaeontology.

Budil, P., Collette, J., **Manda, Š.** 2010. An unusual occurrence of the Laurentian phyllocarid crustacean Ceratiocaris papilio Salter in the lower Ludfordian (Silurian) of Bohemia (peri-Gondwana). Bulletin of Geosciences 85, 551–564.

3. DÍLČÍ TÉMA „EXTINKČNÍ EVENTY – KRIZOVÉ UDÁLOSTI"

3.1. CHARAKTERISTIKA PROBLEMATIKY

Vymírání druhů a vývojových linií neprobíhalo v geologické minulosti vždy stejnou rychlostí. Existují časově krátké úseky, kdy z nějakého důvodu dochází ke zvýšenému vymírání. Takové události se nazývají eventy (z anglického event – událost) nebo krize (z řeckého krinó, což znamená něco ve smyslu vybírat mezi opačnými variantami, odvozené krisis má pak význam rozhodné chvíle). I když v geologickém záznamu jsou takováto období zřejmá, studium extinkčních eventů začalo ve větší míře až v 80. letech minulého století. Část těchto eventů pro svou nápadnost v sedimentárním záznamu nicméně sloužila již dříve jako lito/chronostratigrafické hranice v historické geologii. Patrně nejznámějším příkladem je event na hranici křída-terciér, který byl dán do souvislosti s pádem kosmického tělesa na Zemi. Postupně byla popsána celá řada eventů různé intenzity a geografického rozsahu. Narůstající diskuse o příčinách eventů a jejich časovém rozsahu přinesla celou řadu často protichůdných vysvětlení (pád mimozemského tělesa, eustatické pohyby a zalednění, vulkanická činnost, klimatické cykly apod.). A tento stav trvá dosud. Zřetelná je přitom snaha o nalezení jednotného modelu, který krize vysvětlí. Mají ale všechny krize stejnou příčinu? Zdá se, že touha po jednotném vysvětlení je zřejmá, například Raup a Sepkoski (1984) se zabývali periodicitou vymírání a dali ji do souvislosti s pády kosmických těles na Zemi, tato teorie dostala poněkud zavádějící název podle řecké bohyně odplaty Nemesis. Nicméně pravděpodobnější se zdá, že vymírání mají specifický průběh a patrně různou příčinu.

Extinkční eventy nejsou jen pouhým vymíráním, ale mají zásadní význam pro vývoj ekosystémů. Souvislost s evolučními procesy a speciací se postupně stala zřejmou. Dokud v evoluční biologii převládala myšlenka postupného přizpůsobovaní, gradualismu, zdály se eventy poněkud zavádějící a zbytečnou myšlenkou, když ale Eldridge s Gouldem (1972) přišli s teorií přerušovaných rovnováh, pohled se změnil. Po vymírání totiž dochází k obnově ekosystémů, jsou k dispozici uprázdněné niky a potravní zdroje. Obnova je tak spojená se vznikem nových druhů, adaptivní radiací, rozsáhlými migracemi a změnou trofických vztahů v ekosystémech. Důležité přitom je, že během krizí může přežití vývojových linií být spíš náhodné (prostředí je jiné, než jaké druh obýval před krizí) a existující například morfologické prvky mohou získat novou funkci. V malých populacích přežívajících po krizích může nepochybně docházet k fixování nových znaků (souhrn např. Flegr 2009).

Pochopení významu eventů v makroevoluci vyžaduje především přesnější sběr dat než dříve. Paradoxně možná existuje více teoretických článků a úvah než kvalitních dat s vysokým stratigrafickým rozlišením. Stávající databáze biodiverzity jsou často sporné kvality (Boucot 1990) a umožňují spíše pochopení obecných evolučních trendů než jednotlivých detailů. Patrně nejjasnějším je vzrůst diverzity od spodního triasu (Stanley 2007). Mnoho dalších tvrzení je naopak často zpochybňováno, jako například prodlužování průměrné doby trvání druhu (Bornholdt et al. 2009).

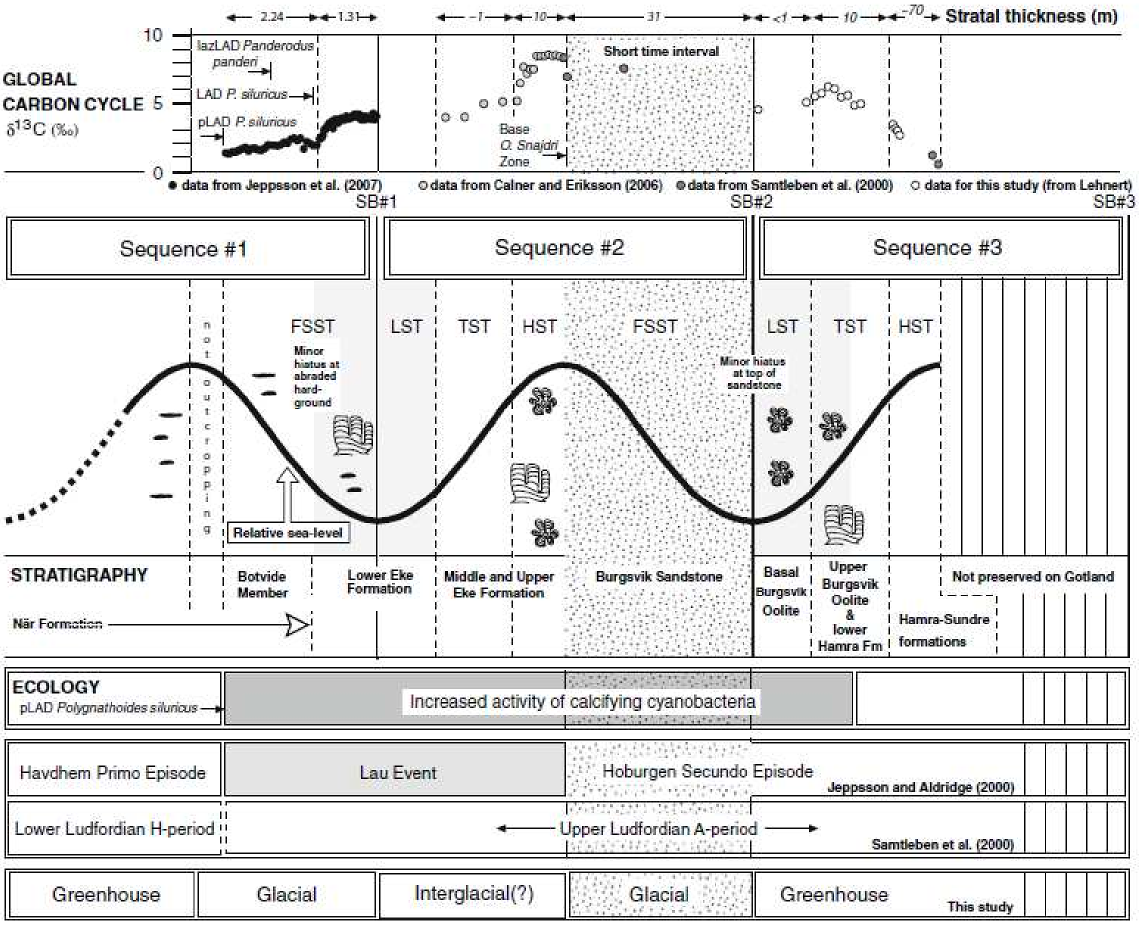
Období siluru je dobrým příkladem výše popsaného vývoje. Dlouhou dobu převládal názor, že se jednalo o relativně stabilní období s teplým klimatem bez ledovců (souhrn Holland 1991). V osmdesátých letech byly nicméně publikovány práce o významných vymíráních u graptolitů a konodontů. Vymírání graptolitů bylo vysvětlováno eustatickými pohyby a anoxiemi (Jaeger 1991, Urbanek 1993, Koren' 1993, Štorch 1995a, Melchin et al. 1998), vymírání konodontů oceánskými cykly a stratifikací vody v oceánech (Jeppsson 1990, 1998). Později byla tato vymírání dána do souvislosti s uhlíkovým cyklem v oceánech, vymírání odpovídají obdobím s nástupem zvýšeného ukládání organického uhlíku v sedimentech, a tedy zvýšenou produkcí planktonu (Munnecke et al. 2003). Studium izotopů kyslíku v konodontech umožňující odhadnout teplotu vody odhalilo několik období s výrazným rozšířením ledovců (Joachimski et al. 2009). Představa idylického silurského období se tak postupně změnila v pravý opak (přehled viz Calner 2008).

V současnosti je v siluru popsáno tolik extinkčních eventů různé intenzity, například Kaljo et al. (1995) jich uvádí 15, že období stáze mezi nimi se pohybují mezi 1 až 5 miliony let. Nepřehlédnutelný je i zmatek v názvosloví eventů – různá jména u extinkcí definovaných konodonty (12 eventů, Jeppsson 1998), graptolity (10 eventů, Melchin et al. 1998) nebo geochemicky (osm období se zvýšenou $\delta^{13}C$ v sedimentech, Munnecke et al. 2010). Nejasné též zůstává, zda se jedná o kauzální události, tedy jestli se jedná o následek jedné události či nikoliv.

3.2. SVRCHNOLUDLOWSKÁ KRIZE: KOZLOWSKII EVENT

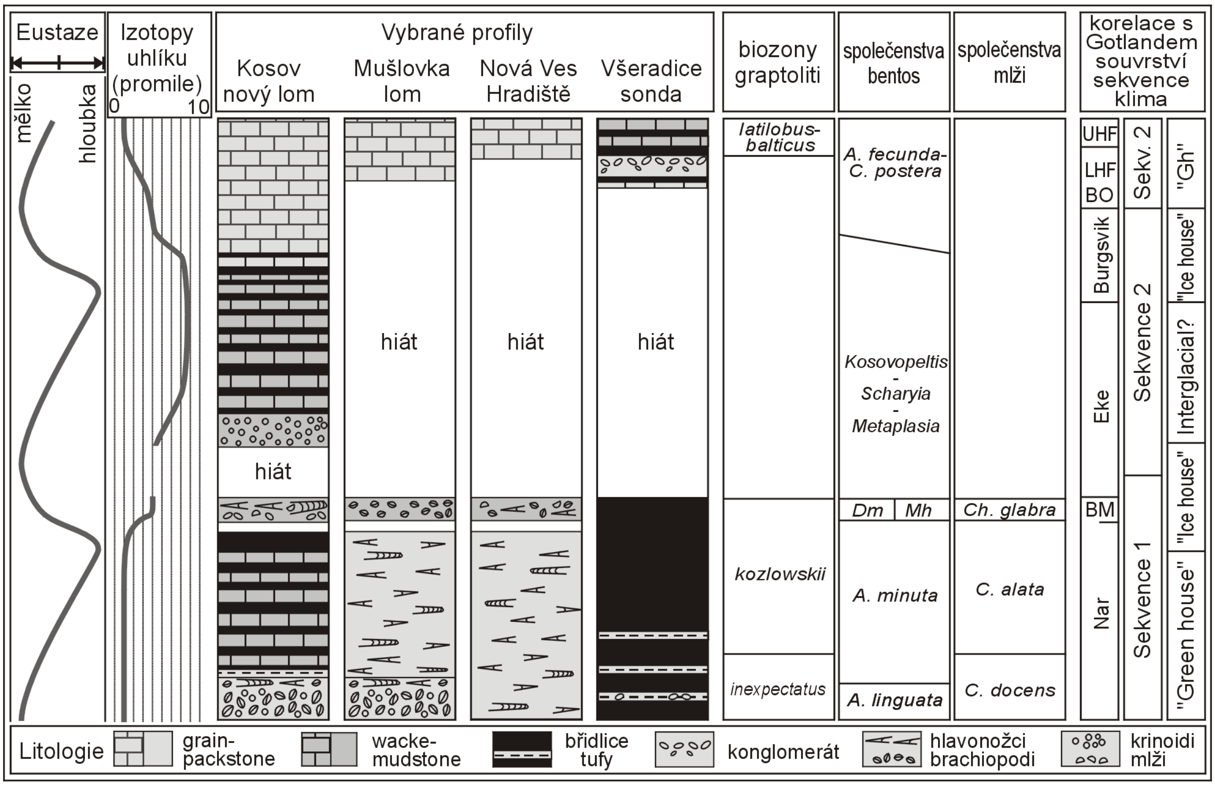
Jednou z nejvíce diskutovaných krizí je změna ve faunách ve svrchním ludfordianu, ludlowu. Poprvé byla popsána u graptolitů jako Kozlowskii event – podle druhového jména graptolita *Neocuculograptus kozlowskii* (Urbanek 1993, Koren 1993). Později byla popsána krize u konodontů a podle typové lokality na ostrově Gotland nazvána Lau event (Jeppsson a Aldridge 2000). Od začátku bylo zřejmé, že obě vymírání se odehrávala přibližně ve stejném časovém úseku. Obě vymírání koincidují se zvýšeným ukládáním organického uhlíku v sedimentech a největší izotopovou výchylkou $\delta^{13}C$ v celém fanerozoiku (Samptleben et al. 2000). Izotopy kyslíku dále prokázaly, že došlo k výraznému poklesu teploty vody v oceánech, které patrně odpovídá nástupu zalednění (Lehnert et al. 2007a, Ericsson a Calner 2008). Kozlowskii event byl popsán ze sledů s převahou břidlic z Polska, Podolí na Ukrajině a centrální Asie (souhrn Melchin et al. 1998). Lau event byl na základě konodontů identifikován v karbonátových sledech na Gotlandu, Skåne a Austrálie (souhrn Calner 2008). Izotopová exkurze izotopů uhlíku byla popsána z Skåne, Gotlandu, Estonska, Podolí na Ukrajině, Svatokřížských hor, Austrálie, severovýchodní části USA, Nevady i Čech (souhrn Calner 2008). Začátek izotopové výchylky ve všech oblastech odpovídá zhruba poslednímu výskytu konodonta *Polygnathoides siluricus*. Klíčovou oblastí je přitom karbonátová platforma Baltiky, konkrétně profily na ostrově Gotland. Na základě studia těchto profilů byl formulován model celé události, ten zjednodušeně dává vymírání do souvislosti s nástupem glaciální periody, vymírání pak koinciduje s obdobím před izotopovou exkurzí izotopu uhlíku. Glaciální perioda sama je oddělená interglaciálem. Z hlediska eustáze maximální zalednění odpovídají nízkým stavům hladiny a hiátům v sedimentárním záznamu (obr. 1, Ericsson a Calner 2008).

Pražská synforma je druhou klíčovou oblastí pro studium vymírání ve svrchním ludfordianu, umožňuje jej totiž studovat mimo tropické pásmo, dále je zde možná korelace s graptolitovými zónami, na které je fixovaná chronostratigrafie siluru. Faunu zóny *N. kozlowskii* popsal z lomu Kosov Štorch (1995b), ale vlastní vymírání, tedy svrchní hranici zóny, nezjistil. Později Lehnert et al. (2007b) popsali izotopovou výchylku ve v karbonátových sledech v různých částech pánve, její začátek spadá krátce nad poslední výskyt konodonta *P. siluricus*.



Obr. 1. Model Lau eventu podle dat na profilech ostrova Gotland (podle Ericssona a Calnera 2008 a Lehnerta et al. 2007a).

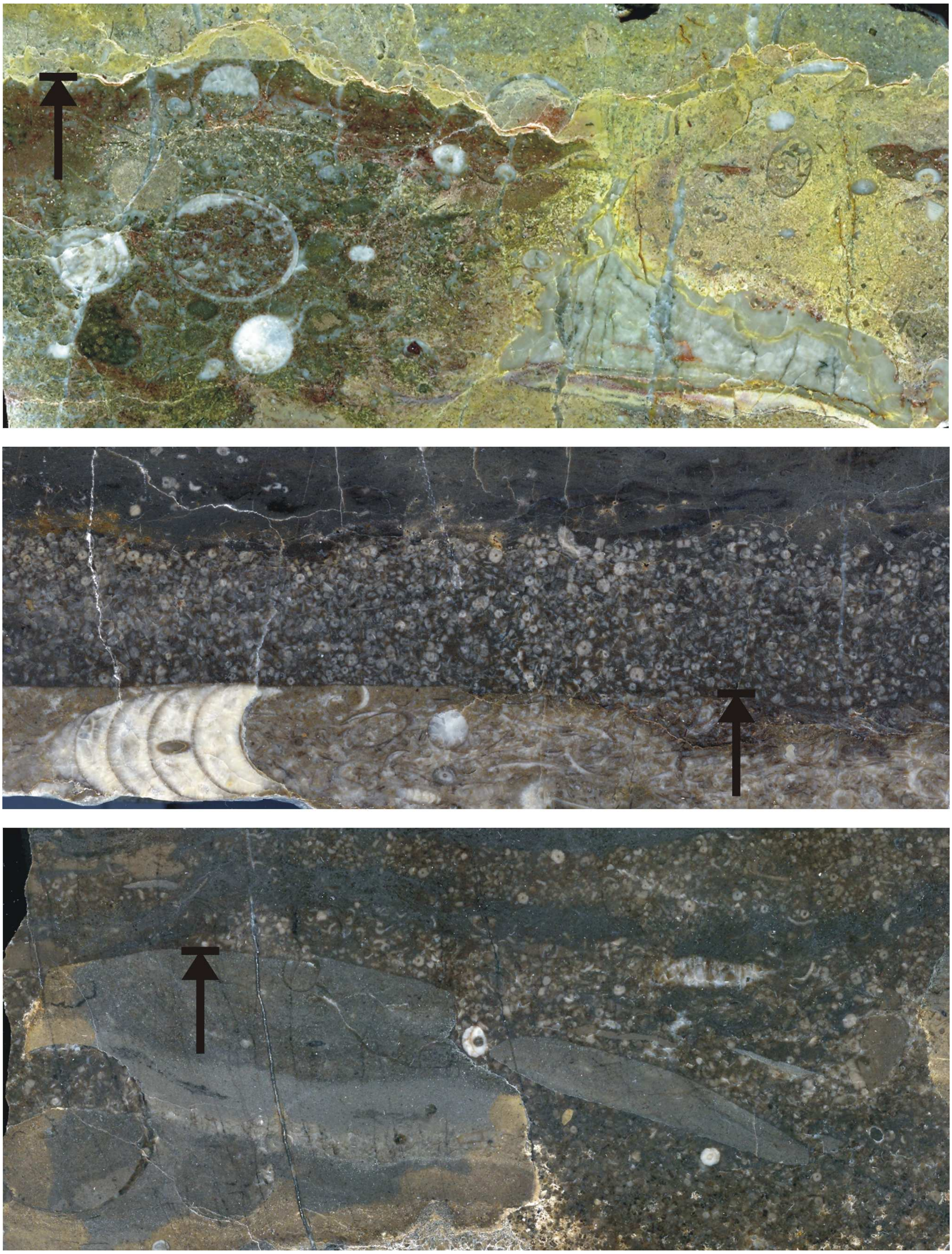
Manda a Kříž (2006) publikovali sekvenční analýzu intervalu v karbonátových sledech jednotlivých elevací a popsali výrazné sekvenční hranice napříč pánví, které odpovídají přerušením sedimentace v rozsáhlých oblastech pánve (obr. 2–4). Vlastní extinkční hranice je přitom zároveň sekvenční hranicí doprovázenou větším či menším přerušením sedimentace. Vlastní hranice má povahu erozní plochy nebo hardgroundu. Světlé vápence ukládané v dobře okysličeném prostředí jsou překryty tmavými vápenci s vysokým obsahem organické hmoty ukládanými v anoxickém prostředí. Kozlowskii (Lau) event spadá do krátkého období intenzivního vymírání, které současně postihlo i další faunu jako mlže, hlavonožce a trilobity, významná je i změna ve společenstvech. Během krize se objevila společenstva s nízkou diverzitou a jedním nebo dvěma převažujícími oportunistickými druhy.



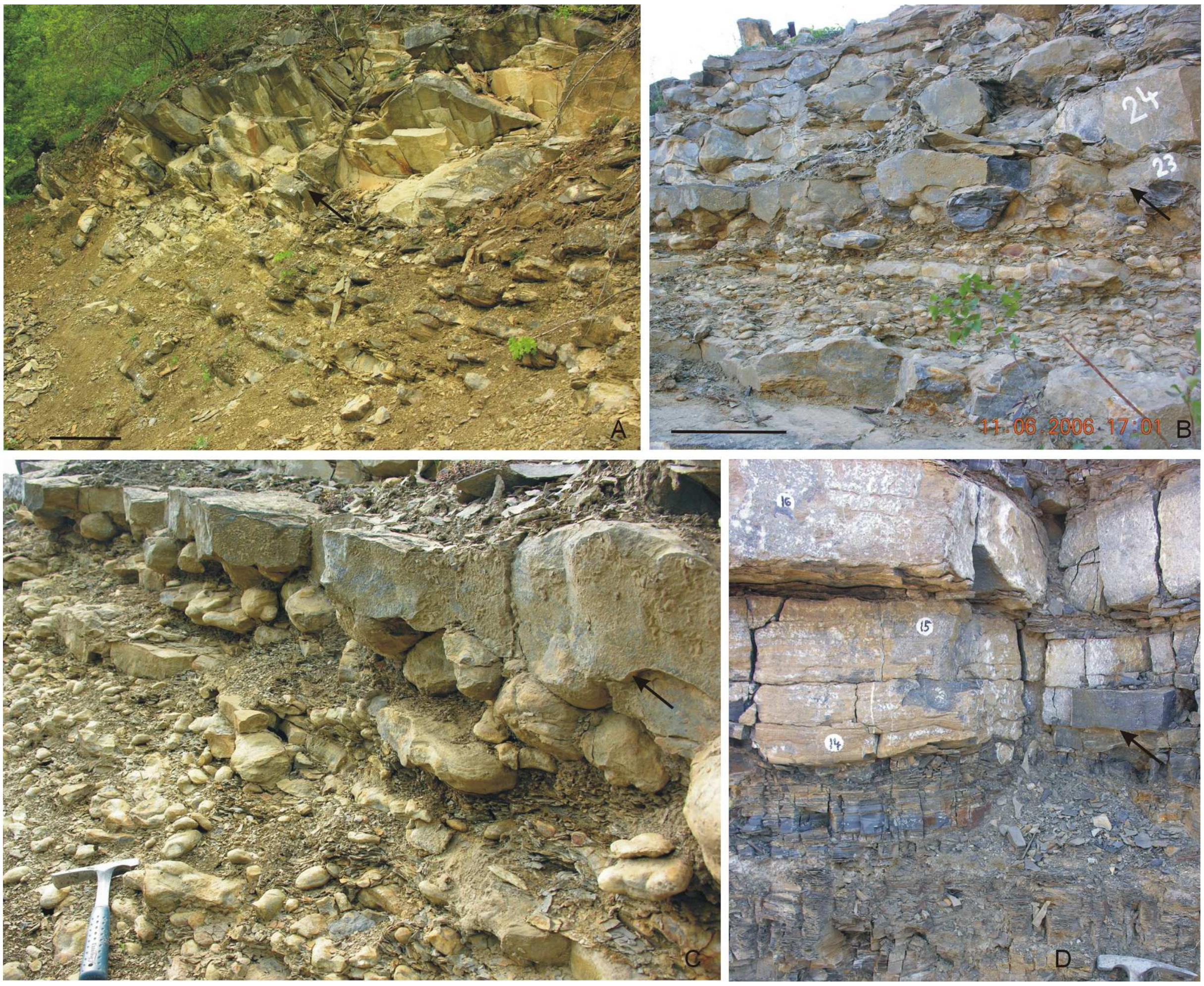
Obr. 2. Kozlowskii event v pražské pánvi, svrchní ludfordian. Eustatické cykly, vývoj izotopů uhlíku, vybrané profily (zjednodušeno, detailněji Manda a Kříž 2006) a společenstva v pražské pánvi a korelace se souvrstvími, sekvencemi a klimatickými stavy na Gotlandu, jak byly publikovány Ericssonem a Calnerem (2008). Zkratky: Dm = Dayia minor, *Mh =* Metaplasia hemicona*. Graptolitové zóny podle Mandy et al. (v tisku), mlžová společenstva podle Havlíčka a Štorcha (1990) a nepublikovaných dat, společenstva mlžů podle Kříže (1998, 1999a).*

* * *

Obr. 3. Sekvenční hranice (označené šipkou) spojené s přerušením sedimentace během Kozlowskii eventu. Odshora: Zadní Kopanina – Nad náhonem, kontakt hlavonožcových vápenců s trilobitovým packestone a s bakteriálními narůsty (hiát zahrnuje spodní část zóny latilobus-balticus*). Kozolupy, erozní hranice v hlavonožcovém packstone překrytá krinoidovým packstone s vysokým obsahem organické hmoty, krátkodobý hiát. Kosov, nový lom, hardground v hlavonožcovém wackestone překrytý krinoidovým wacke-packstone s intraklasty odvozenými z hardgroundu, na levé straně částečně rozpuštěná schránka hlavonožce vyplněná detritem, krátkodobý hiát. Přirozená velikost.*



Obr. 3. Vysvětlivky na předchozí straně.



Obr. 4. Náhlá litologická změna spojená s Kozlowskii eventem, ukázky profilů (označen šipkou). A: Liščí lom, B, C: Kosov 782, D: Kosov 924. Měřítko 50 cm.

Manda et al. (v tisku) popsali průběh Kozlowskii eventu z hlubších částech pánve. Vůbec poprvé bylo zdokumentováno vymírání u graptolitů a následná obnova graptolitových faun mimo tropickou zónu, to umožnilo doplnit graptolitové zóny nejvyššího ludlowu, popsaná fauna také spojuje fauny ludlowu a přídolí, takže evoluční linie graptolitů se staly zřejmějšími. Padla tak námitka Tellera (1987 a dále) proti stratotypu báze přídolí v pražské pánvi kvůli údajnému hiátu na této hranici, který měla dokládat nepřítomnost graptolitů v nejvyšším ludlowu v této oblasti. Polohy gravitačních uloženin pak umožnily korelaci graptolitových zón s faunami v karbonátových sledech (detailně v práci Manda et al. v tisku).

4. DÍLČÍ TÉMA „HLAVONOŽCI JAKO MODELOVÁ SKUPINA PRO STUDIUM MAKROEVOLUČNÍCH TRENDŮ, MORFOLOGICKÝCH ZMĚN A CHARAKTERU VYMÍRÁNÍ"

4.1. CHARAKTERISTIKA PROBLEMATIKY

Hodnotit extinkce a interakce mezi biotickou složkou a prostředím je v mnohém ohledu složitá záležitost. Jistě nejlepší je komplexní studium celých společenstev/faun. Takový přístup je nutný u studia globální biodiverzity, nicméně dostupná data jsou často různé kvality. Když specialista na nějakou skupinu nahlédne do patrně nejznámějšího kompendia Sepkoského z roku 2002, zdá se vše v pořádku až do chvíle, kdy nalistuje data o skupině, kterou zná, a tady není těžké objevit řadu nepřesností. Studia vývoje společenstev jako celku jsou také problematická, například proto, že se ve fosilním záznamu část organismů nezachovává nebo jen zřídka. Proto většinou studujeme modelové skupiny. Ve starším paleozoiku jsou oblíbenou skupinou graptoliti a konodonti. Ale obě tyto skupiny mají i řadu nevýhod, především to, že v kritických obdobích může být jejich diverzita relativně nízká. Jedná se o ekologicky víceméně homogenní skupiny, navíc způsob života a ekologické nároky těchto skupin jsou poměrně nejasné, protože nemají žádné současné potomky. Detailní studia u ostatních skupin jsou zatím spíše v začátku.

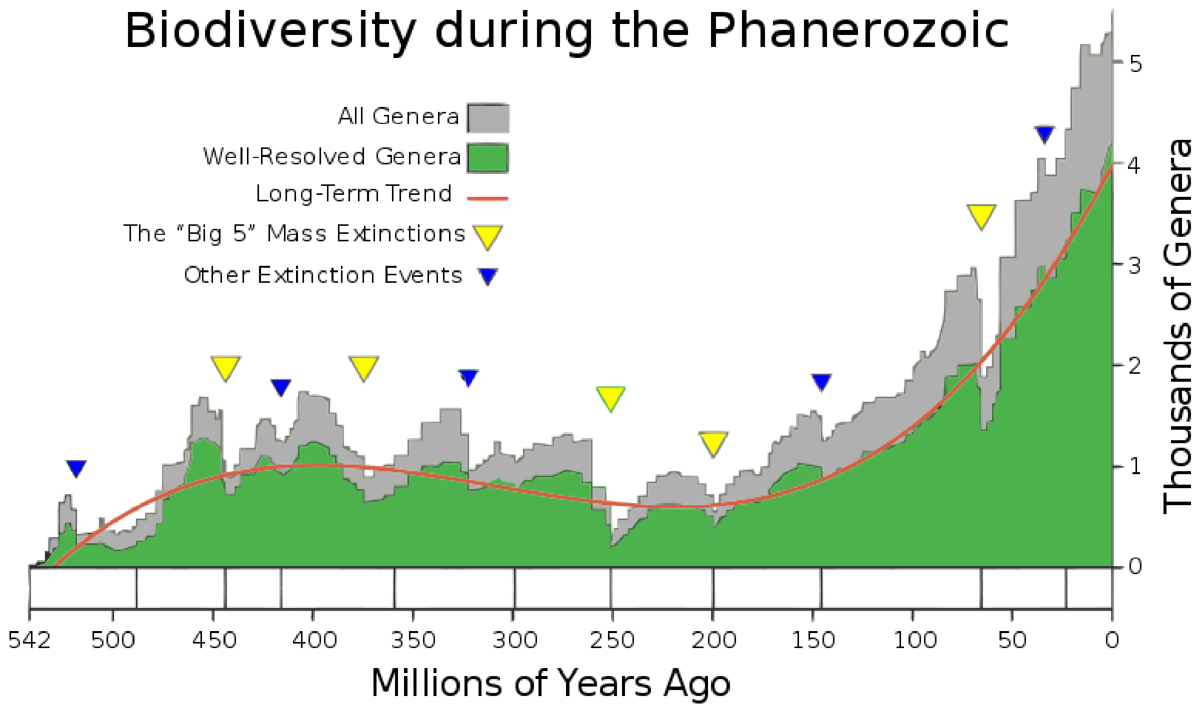
Hlavonožci, podobně jako ostatní měkkýši, představují jednu z nejslibnějších skupin. Jedná se o bohatě diverzifikovanou skupinu, jejich schránka poskytuje dostatek znaků pro definici taxonů a snadno se zachovává ve fosilním záznamu. Hlavonožci mají také žijící příbuzné zástupce, kteří umožňují srovnání a sledování makroevolučních trendů (nautiloidi jsou srovnáváni s rodem *Nautilus*, ale ortokonní hlavonožci s rovnou schránkou mají blíže ke coleoidům, jejichž jsou předky, viz Jacobs a Landman 1993). Většina hlavonožců jsou aktivní predátoři, v spodním paleozoiku byli na vrcholu potravní pyramidy. Jako aktivně se pohybující predátoři byli zvláště citliví na změny v prostředí a odrážejí stav společenstva jako celku (Barskov 1989, Frey et al. 2004). Ekologická konvergence mezi hlavonožci a rybami je obecně přijímána a jedná se o jeden z nejlepších příkladů interakce mezi dvěma skupinami ve fosilním záznamu (Packard 1972). Schránka hlavonožců, která plní kromě ochranné funkce (jako u všech měkkýšů) i funkci hydrostatickou, umožňuje poměrně spolehlivou funkčně morfologickou analýzu (Flower 1957, Chamberlain 1976, 1980, 1991, Westermann 1998). Co však činí hlavonožce zvláště vhodnou skupinou, je jejich hojnost ve fosilním záznamu, široké rozšíření v různých prostředích (Flower 1957) a především přítomnost různých evolučních strategií jak u juvenilních, tak u dospělých jedinců (Engeser 1990).

4.2. VYMÍRÁNÍ KOLEM HRANICE SILUR-DEVON: VÝZNAM RANÉ ONTOGENEZE A ZPŮSOBU ŽIVOTA HLAVONOŽCŮ

Vývoj biodiverzity rodů a čeledí v globálním měřítku je relativně dobře znám, i když je neustále zpřesňován: nejprve nárůst diverzity metazoí v kambriu, poté prudká diverzifikace ve spodním ordoviku, následovaná relativně dlouhým obdobím, kdy se diverzita relativně výrazně neměnila, patrná je globální krize na konci permu a finálně, v aproximaci, následuje nárůst diverzity trvající dodnes (obr. 5). Komentáře a statistické analýzy tohoto trendu naplňují stovky článků (přehled Stanley 2007). Silur a spodní devon je obecně obdobím diverzifikace následující svrchnoordovické vymírání, pokles diverzity v nejvyšším siluru je spíše sporný (Stanley 2007) a právě toto časové období patrně vyžaduje doplnění dat a detailnější studia, protože nejvyšší silur a nejnižší devon jsou celosvětově méně známá období.

Globální databáze taxonů mají své problémy a i studia diverzity na úrovni rodů a čeledí mají svá úskalí. Rody ani čeledě nejsou reálně existující přírodní entity jako druhy. Na druhou stranu databáze umožňující popsat druhovou diverzitu zatím nedosahují dostatečné kvality.

Individuální přístup badatelů, vlivy různých škol současných i minulých (mnohé skupiny byly revidovány naposledy před více než padesáti lety, tedy v období bez moderních klasifikačních metod a podobně), poněkud různé přístupy u jednotlivých skupin a útvarů, rozdílná regionální znalost, to vše je komplikujícím faktorem a stěží tomu bude někdy jinak. Slibným polem pro výzkum se tak stává studium jedné skupiny v různě dlouhém časovém úseku, a to v globálním nebo regionálním ohledu, kdy data ošetří jeden člověk nebo malý tým. Dále je třeba brát v úvahu, že globální databáze jsou poznamenané i nestejnou úrovní znalostí jednotlivých oblastí. Regionální studia umožňují v tomto ohledu podstatně vyšší rozlišení.



Obr. 5. Biodiverzita na úrovni rodů ve fanerozoiku (podle dat Sepkoského 2002). Zdroj Http://en.wikipedia.org/wiki/File:Phanerozoic_Biodiversity.png.

Takováto speciální studia diverzity druhů mají význam z několika důvodů. Mohou jednak testovat data získaná z analýz globální biodiverzity, dále umožňují lépe pochopit faktory ovlivňující danou skupinu během globálních krizí a dát je do souvislosti s ekologickou charakteristikou dané skupiny a jejím distribučním vzorcem. Celkově tak zpřesňují pochopení vývoje biodiverzity. Doposud takovéto studie byly provedeny jen u nemnoha skupin či v několika málo oblastech – ve starším paleozoiku například u graptolitů a trilobitů nebo řady skupin v oblasti Pobaltí či Skandinávie (například Kaljo et al. 1995, Calner 2008). Výsledky těchto studií jsou zatím rozptýlené a jejich význam nebyl shrnut do obecnějších modelů. Selektivní podstata některých vymírání tak zůstává otevřeným problémem. Pokud budeme například hledat v literatuře odpověď na otázku, proč došlo v nejsvrchnějším siluru k prudkému poklesu diverzity graptolitů, který víceméně trval až do období jejich konečného vymření v emsu (spodní devon), budeme patrně zklamaní. V nejvyšším přídolí dosáhla diverzita kritického minima, celosvětově jsou známé tři druhy (pokles z hodnoty kolem 20 druhů). Podobné krize jsou přitom známé i ze starších období, kdy ale došlo k prudké diverzifikaci a obnově (Jaeger 1991, Kaljo et al. 1995, Štorch 1995b, Melchin et al. 1998).

Tato událost v nejvyšším přídolí byla nazvána Transgrediens eventem (Urbanek 1993, viz též Kaljo et al. 1995, Melchin et al. 1998), následně byla pojmenována jako Klonk event (Jeppsson 1998) u konodontů a někteří autoři hovoří o silursko-devonském hraničním eventu (e.g. Walliser 1995). Celkově je nejlépe definovaný Transgrediens event těsně pod bází devonu, s kterou pak koinciduje post-extinkční obnova. Extinkce odpovídá také pozitivní výchylce $\delta^{13}C$ a zvýšenému ukládání uhlíku v sedimentech. Analýza biodiverzity hlavonožců (zahrnující embryonální strategie a strategie u dospělců) přídolí a nejnižšího devonu ukázala, že tato krize u graptolitů odpovídá vymírání u hlavonožců, přičemž vymírání postihlo převážně leucitrofní (s dlouhým embryonálním vývojem ve vajíčku bohatým žloutkem) demersální formy.

Extinkční interval odpovídá počátku změlčování, vzestupem primární produkce a rozsáhlými anoxiemi spojenými s poklesem aktivity mořských proudů. Následná obnova ale byla u hlavonožců spojená jen s mírnou diverzifikací v porovnání s předchozími krizemi (podobně jako u graptolitů). Důvod je patrně v celkovém stavu, na kterém se extinkce udála (viz níže u migrací). Z tohoto pohledu se zdá být vymírání zlomovým bodem ve faunách hlavonožců a počátkem vzestupu nektonních forem popsaným Klugem et al. (2010). Kröger (2008) rozčlenil u spodnopaleozoických hlavonožců dvě hlavní strategie a použil tyto skupiny pro vystižení makroevolučních trendů, ale nově vymezené strategie umožňují mnohem preciznější rozlišení: dva typy embryonálního vývoje (leuci-planktotrofní, tři typy u raně vylíhlých jedinců a celkem sedm strategií u dospělých jedinců. Toto rozdělení je přitom aplikovatelné na všechny spodnopaleozoické fauny hlavonožců a je slibným nástrojem pro makroevoluční studia hlavonožcových faun (Manda a Frýda 2010).

4.3. MIGRACE HLAVONOŽCŮ A JEJÍ DYNAMIKA: UTVÁŘENÍ SPOLEČENSTEV BIOFACIE SILURSKÝCH HLAVONOŽCOVÝCH VÁPENCŮ NA PERI-GONDWANĚ

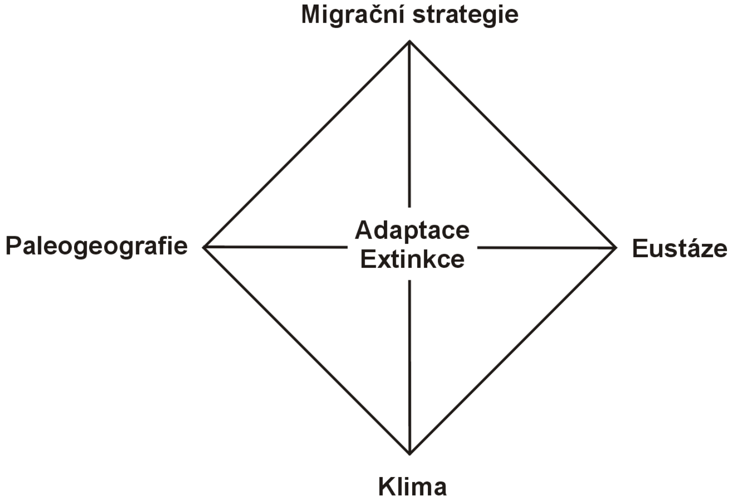
Migrace organismů neustále mění s větší či menší mírou charakter a povahu společenstev. Známé jsou sezonní migrace například mořských savců. Obecně ale do migrací patří i rozšiřování areálů jednotlivých druhů, někdy pomalé, jindy rychlé a nápadné (invazní druhy). Migranti mohou v nových oblastech vytlačit etablované druhy nebo zvýšit selekční tlak. Rozšiřovat se přitom nemusí jen jednotlivé druhy, ale i celé jejich skupiny (společenstva). V geologické minulosti je celá řada příkladů takovýchto migrací, i když ne vždy jsou dobře známé. Zdá se, že v některých obdobích docházelo ke zvýšeným migracím, které mohly zásadním způsobem změnit fauny na celých kontinentech nebo v mořských pánvích. Patrně nejznámějším příkladem je tzv. Velká výměna, ke které došlo během spojení Severní a Jižní Ameriky ve spodním terciéru. Změny areálů způsobují i klimatické změny (lesy s palmami na severní Sibiři by dnes hledal málokdo). Studovat dynamiku disperze a migrací umožňuje sledovat i adaptační trendy u jednotlivých kladů nebo obecné adaptační tlaky. Dalším výstupem může být relativní srovnávání klimatu v minulosti. Dynamiku rozptylu a migrace řídí interakce řady faktorů (obr. 6):

1) Migrační strategie, tedy způsob rozptylu, zda se děje pomocí larev (které mají různou délku života), nebo jestli jsou schopni migrovat i dospělí jedinci a v jaké míře.

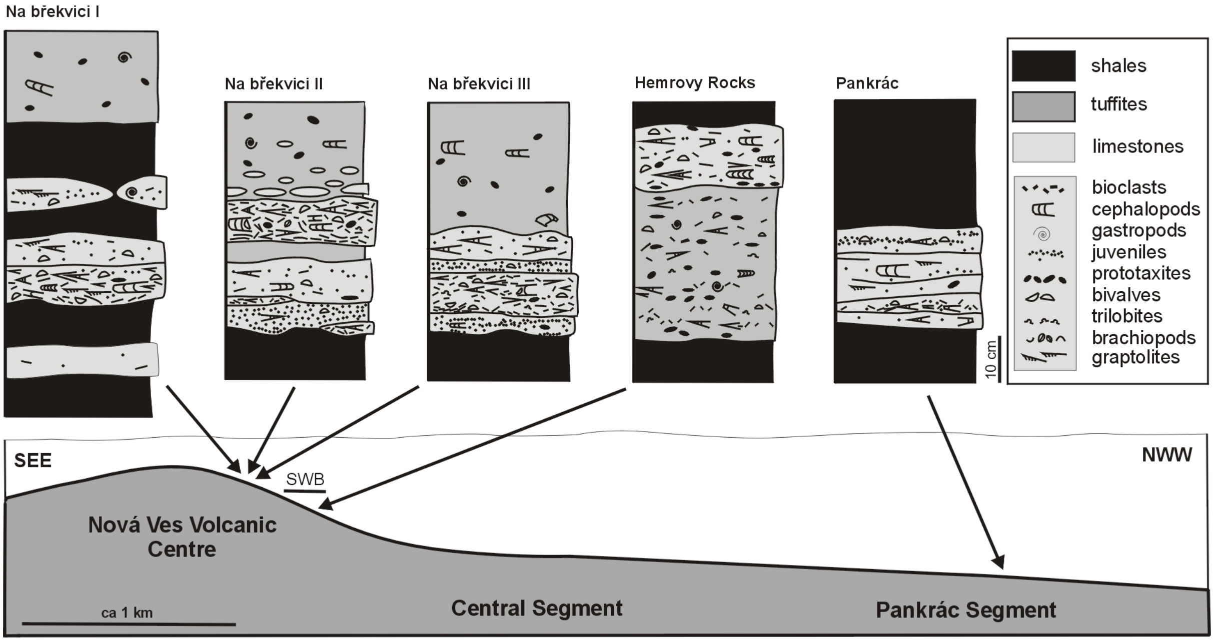
2) Paleogeografie, rozložení kontinentů a jejich vzdálenost; rozložení kontinentů se neustále pomalu mění a ve fosilním záznamu se období izolace nebo naopak rozsáhlejší výměny faun významně projevují.

3) Eustáze, eustatické pohyby jsou dalším pomalým faktorem, pohyby v řádu až desítek metrů podstatně mění migrační cesty a zároveň zvětšují a zmenšují vzdálenosti mezi mělkovodními oblastmi.

4) Klima je dalším faktorem; klima každé doby odráží řadu faktorů, o nichž se neustále vedou spory (např. extraterestrické vlivy tzv. Milankovičových cyklů, změny sluneční aktivity), klimatické podmínky souvisí i s paleogeografickým rozložením kontinentů díky systému oceánských proudů.



Obr. 6. Hlavní faktory ovlivňující úspěšnost a charakter migrací hlavonožců (orig.).



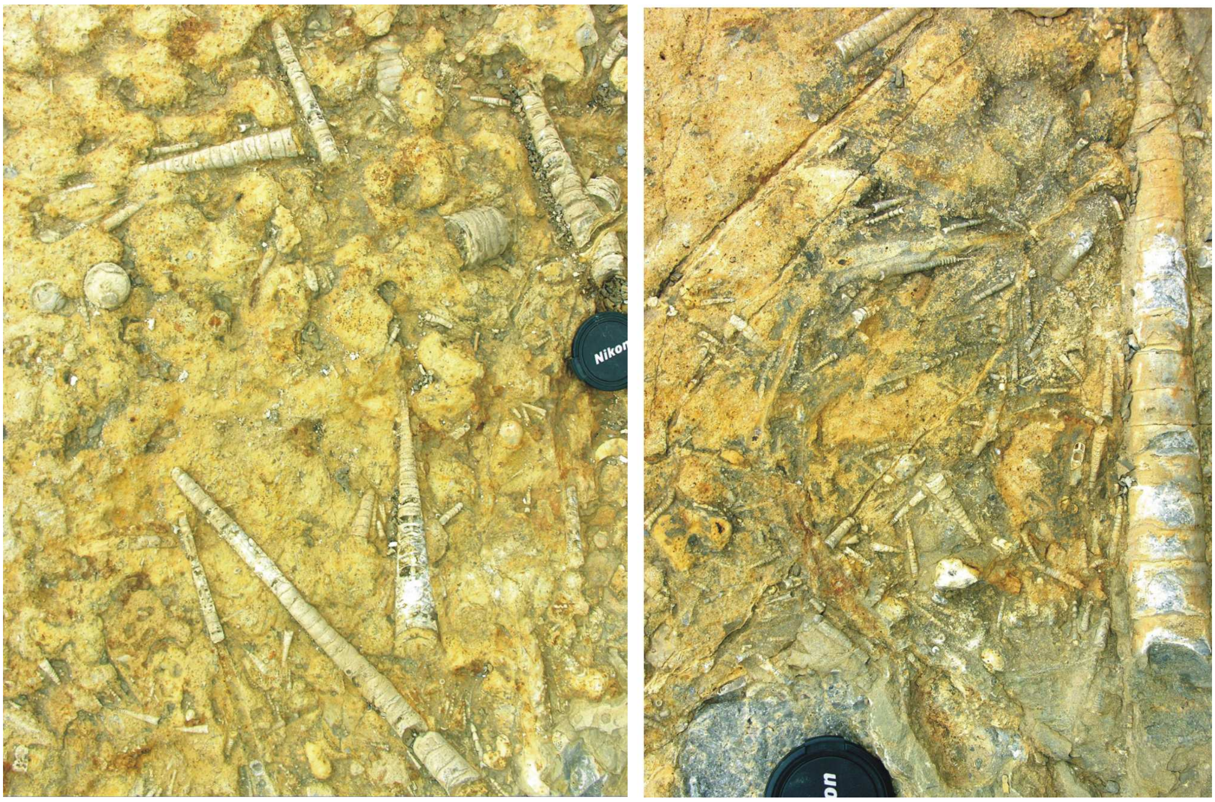
Obr. 7. Příklad vývoje hlavonožcových vápenců v nejnižším ludlowu, tenké polohy uvnitř sledu břidlic, rekonstrukce východní části pražské synformy.

Všechny tyto faktory je třeba brát v úvahu, chceme-li pochopit, jak se měnila biogeografie v minulosti; mají totiž zásadní vliv na makroevoluční procesy. Ve větší míře se přitom projevují v období globálních krizí a obnově ekosystémů, spodní silur je toho dobrým příkladem.

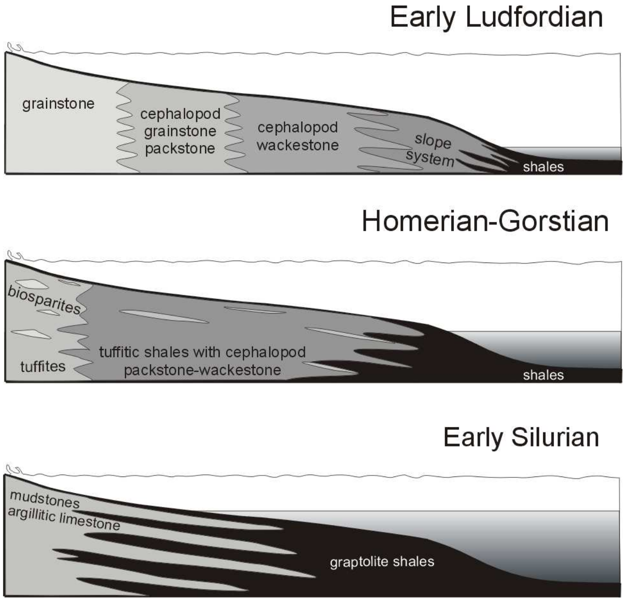
Po roztátí ledovců ve svrchním ordoviku došlo k rozšíření anoxických podmínek v rozsáhlých oblastech moří, které přetrvávaly během celého spodního siluru. Graptolitové černé břidlice jsou rozšířené od relativně mělkých částí pánví, zejména v chladnovodních oblastech (například Holland 1991, Kaljo et al. 1995). Anoxické prostředí u dna i ve vodním sloupci limitovalo život většiny organismů kromě graptolitů. Většina mořských společenstev se stáhla do úzkého tropického pásma kratonů Severní Ameriky, Baltiky, Kazachstánie, Sibiře a skupiny čínských bloků. Teprve v nejvyšším llandovery docházelo k postupnému narůstání aktivity mořských proudů a odeznívání anoxických podmínek (přibližně během wenlocku). V mělkých částech pánve se obnovila karbonátová sedimentace. Rozsáhlé prostory pánví představovaly volný ekologický prostor (Kaljo et al. 1995, Kříž et al. 2003, Verniers et al. 2008).

Nejmělčí části karbonátových plošin (větrané vlněním) obývala společenstva s převažujícími brachiopody a trilobity. Pod bází vlnění se ukládaly bioklastické vápence, patrně nejvýznamnější biofacií jsou hlavonožcové vápence.

Toto prostředí větrané nestabilními proudy a s častými anoxiemi u dna byly schopny obsadit jen některé organismy, převážně mlži a hlavonožci (Ferretti 1988, Gnoli et al. 1988, Ferretti a Kříž 1995, Kříž 1998). Hlavonožcové vápence jsou učebnicovým příkladem časově specifických facií a vyznívají ve spodním lochkovu, přičemž platí, že mnoho skupin, které je dlouhodobě obývaly, vymírá (například cardiolidní mlži) nebo jsou výrazně redukovány v diverzitě (Kříž 1998, 1999a, Manda 2001). V průběhu wenlocku se utvořilo několik rekurentních společenstev mlžů a hlavonožců, které jsou s biofacií hlavonožcových vápenců svázané (Kříž 1998, 1999a). Obecně platí, že během wenlocku a spodního ludlowu (gorstianu) hlavonožcové vápence tvoří tenké vrstvy (obr. 7), ale od svrchního ludlowu (ludfordianu) do spodního lochkovu tvoří již časově stabilní facie (obr. 8) a jejich rozšíření směrem do pánve i do mělčích facií agitovaných vlněním je dokladem stabilizace systému oceánských proudů (viz obr. 9, Manda a Kříž 2007).



Obr. 8. Ukázka hlavonožcových vápenců svrchního ludfordianu, ludlowu, zóna N. inexpectatus*, Kosov 782; proud směřoval od levého horního rohu do pravého dolního, vlevo několik proudem dobře usměrněných schránek, vpravo nahloučení neorientovaných malých schránek před velkou schránkou fungující jako překážka na dně. Malé schránky náleží pelagickým orthoceridům, větší schránky nektobentickým pseudorthoceridům.*

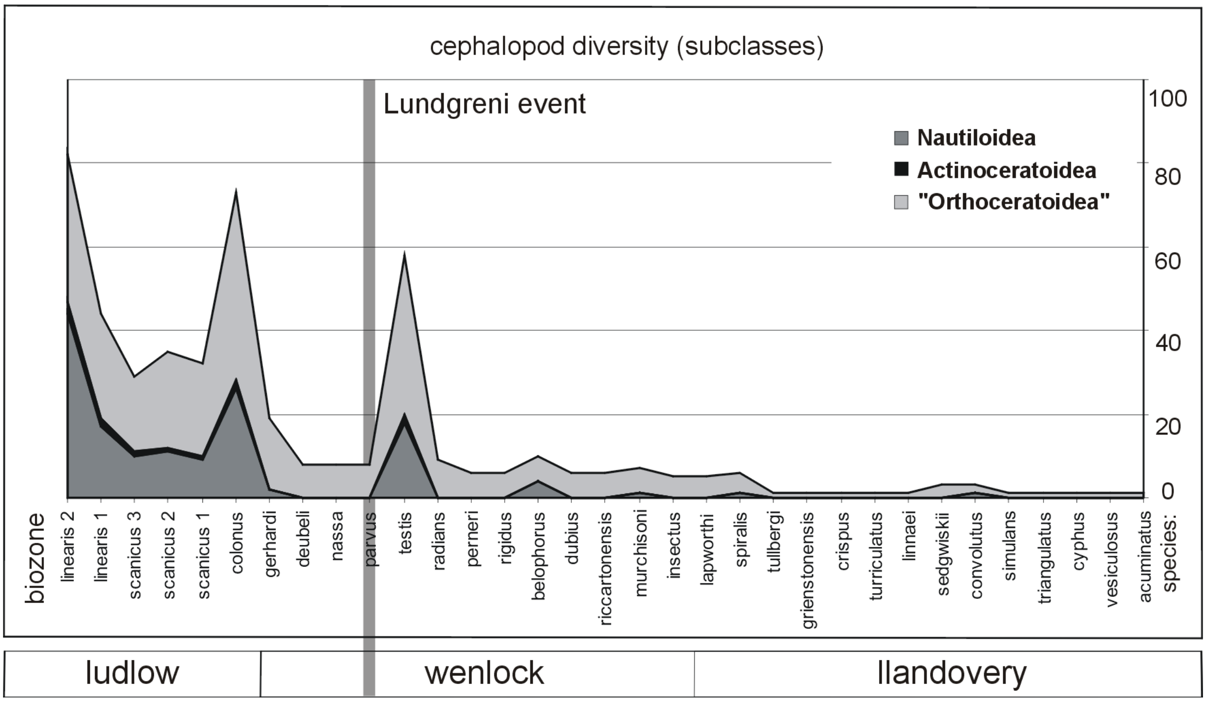


Obr. 9. Schematický vývoj sedimentace na svazích elevací v pražské pánvi v landovery až ludlowu, postupná stabilizace a expanze karbonátových facií.

Rozsah biofacie hlavonožcových vápenců se v průběhu času měnil, největšího rozšíření dosahují v obdobích nízkých stavů hladiny, kdy došlo ke změlčení na rozsáhlých podmořských elevacích peri-gondwanských teránů (Kříž 1998). Horizonty hlavonožcových vápenců, často oddělené výraznými hranicemi, umožňují sekvenční korelaci napříč pánvemi (Manda a Kříž 2007, Brett et al. 2009), celkem je z peri-Gondwany popsáno sedm významnějších úrovní, další jsou známé jen z izolovaných pánví (Ferretti a Kříž 1995, Kříž 1998, 1999a, Kříž et al. 2003, Kröger 2008, Lubeseder 2008). Příklad hlavonožcové biofacie vázané na lokální vulkanickou elevaci byl popsán Mandou a Křížem (2007). O tom, že „pulsování" biofacie hlavonožcových vápenců do jisté míry řídilo makroevoluci hlavonožců a mlžů, svědčí fakt, že každý horizont má specifické společenstvo (Kříž 1998, 1999a, Manda a Kříž 2007) a některé druhy (např. ancestor ve starším a descendent v mladším horizontu). Refugium hlavonožcových vápenců popsaných Mandou a Křížem pak může dokládat, že zvýšená vymírání, anagenetické změny a speciace jsou vázány právě na období refugií, kdy byly populace značně zmenšené.

Pozoruhodným aspektem společenstev biofacie hlavonožcových vápenců je jejich vznik. U mlžů se touto otázkou zabýval Kříž (1999a, b, 2007), který dokládá, že larvy mlžů přinášené proudy z tropů se usazovaly v biofacii hlavonožcových vápenců a postupně se zde vyvinuly specifické adaptace řízené r-selekční progenezí (nadřád Nepiomorphia).

Hlavonožci mají poněkud jiný migračně-evoluční vzorec. Hlavonožci nemají druhé larvální stadium jako většina ostatních měkkýšů, schránka se tvoří již ve vajíčku a líhnou se jedinci podobní dospělcům (Engeser 1996, Kröger 2006, Manda a Frýda 2010). Hlavonožci jsou též ve větší či menší míře aktivně plavající živočichové. Hlavonožci na jižní polokouli také postupně migrovali z tropického pásma (Stridsberg 1998, Manda 2008a).



Obr. 10. Vývoj diverzity (počty druhů) na zónu či její část v llandovery až spodním ludfordianu pražské synformy, patrný nárůst diverzity po odeznění anoxických podmínek s vrcholy během regresí, patrná je také diverzifikace demersálních nautiloidů.

Pelagičtí (planktotrofní) hlavonožci se objevují již ve svrchním llandovery a jejich migrační vzorec je jednoduchý, představují nenáročné oportunistické taxony žijící ve vodním sloupci, zejména podél svahů elevací. Pelagičtí hlavonožci tvoří horninotvornou část hlavonožcových vápenců, diverzita je nízká (do 5 druhů). Někdy ve svrchním wenlocku u nich vznikly adaptace umožňující přechod k životu u dna v pozdních ontogenetických stadiích. Takové formy tvoří významnou část společenstva, diverzita je přitom vyšší (ca 10 druhů).

Podstatně složitější migrační vzorec ukazují nautiloidi. Nautiloidi tvoří menší populace, v porovnání s pelagickými hlavonožci jsou specializovaní a mají delší život, jejich juvenilní stadia se podobají dospělcům, vývoj ve vajíčku je relativně dlouhý. To znamená, že vajíčka jsou delší dobu vystavena prostředí i predátorům. Areál, kde kladli vajíčka, je menší než u dospělců, kteří jsou schopni migrovat na relativně větší vzdálenosti. Celkově je možné rozpoznat tři stadia migrací z platforem směrem k pólům. Podobný vzorec vykazují všichni nautiloidi, i když jednotlivá stadia se u jednotlivých kladů nekryjí, to odráží patrně míru tolerance ke změnám prostředí a inkubační dobu, ale také migrační schopnosti dospělců (nektonní svinuté formy *versus* demersální). Migrace z tropů do chladnějších moří je charakteristická pro většinu měkkýšů (Valentine a Jablonski 2010). Pro většinu měkkýšů také platí, že v teplých mořích převládají planktotrofní formy a v chladných leucitrofní (Valentine a Jablonski 2010), zajímavé je, že u paleozoických hlavonožců je to naopak, diverzita leucitrofních forem (nautiloidi) je vyšší v teplých mořích.

Stadia migrace byla detailně studována u nautiloidů rodu *Phragmoceras*, řád Discosorida (Manda 2007, 2008a). Jedná se o relativně velké hlavonožce se zahnutou nebo svinutou schránkou, dospělí jedinci mají zúžená ústí. Nejstarší phragmoceři se objevují v nejspodnějším siluru na tropických platformách a postupně se rozšířili po většině kontinentů v tropech kromě jihočínské desky. Po odeznění anoxie v spodních šířkách začala jejich migrace z tropického pásma (obr. 10).

1) Zbloudilí migranti. V prvních fázích migrovali ojediněle dospělí jedinci (Stridsberg 1988) nebo i celé populace. Takovéto nálezy jsou vzácné a vázané na některé vrstvy. Příkladem takové masové migrace je jedna lamina s hojným druhem *Phragmoceras munthei* (druh známý z Gotlandu) ve spodním wenlocku pražské pánve (Manda 2007, 2008a). Podobný zajímavý případ patrně představuje neobvyklý výskyt svinutého tarphicerida *Trocholites* v dobrotivu (střední ordovik) peri-Gondwany. Poprvé byl popsán ze Španělska, později i z Portugalska, Francie a Bolívie (Babin a Marco 1992, Babin et al. 1996), naposledy byl popsán z pražské pánve (Manda 2008b). Zbloudilí migranti byli schopni přežít v novém prostředí jen krátce a pravděpodobně se zde nedokázali

rozmnožovat. Jejich migrace zřejmě odráží krátké periody s lepšími podmínkami v celkově nepříznivém prostředí (Manda 2008a).

2) Ve druhé fázi phragmoceři vytvářejí stabilní populace v jistém časovém období, jejich druhy se shodují s druhy na tropických platformách, odkud migrovali (mateřské populace), podmínky tedy již umožňují rozmnožování (to dokládají nálezy schránek časně vylíhlých jedinců). V této fázi se migranti také musí adaptovat na nové prostředí, biofacie, než původně obývali. V peri-gondwanských pánvích je to spojené s adaptací na biofacii hlavonožcových vápenců, původně přitom většinou obývali prostředí kolem tropických rifů. Populace migrantů ale nejsou dlouhodobě stabilní, jejich výskyt je spojen s nízkými stavy hladiny a během následného vzestupu hladiny vymírají (Manda 2008a).

3) Ve třetí fázi dochází ke vzniku stabilních místních populací migrantů a vzniku nových druhů, často doprovázených adaptivní radiací. Obecně u měkkýšů je expanze kladů z tropů do chladnějších moří často vedena cestou speciace (Valentine a Jablonski 2010).

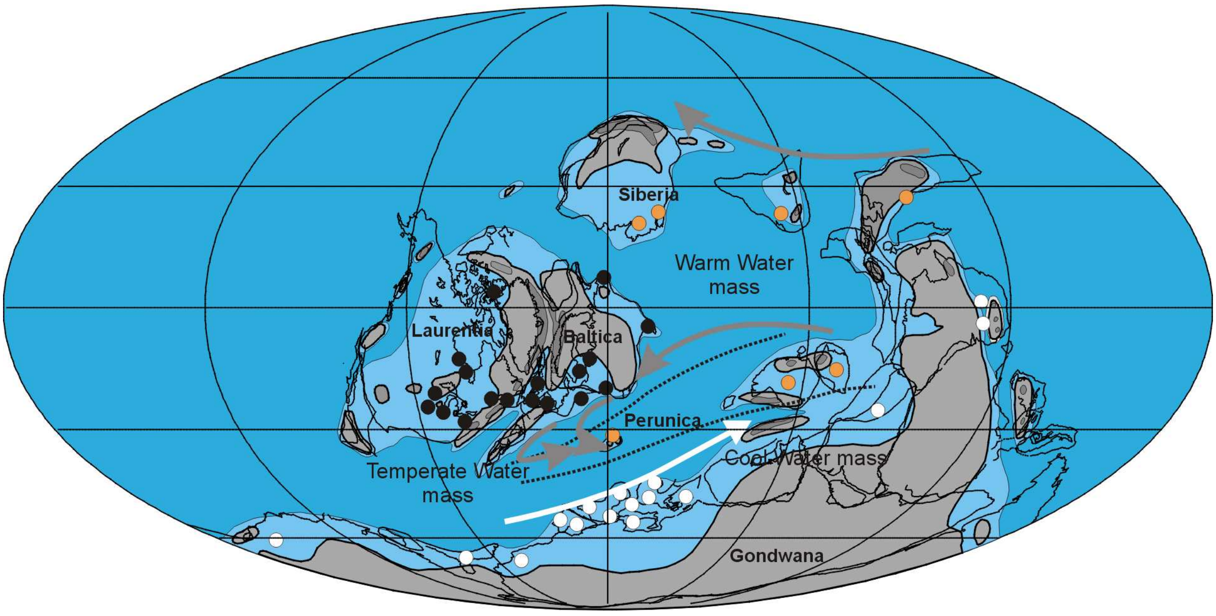
Migrační stadia mají na jižní polokouli zřetelný vztah k zemské šířce, v pražské pánvi, která se nacházela na severním okraji peri-Gondwany, se zbloudilí migranti objevují v nejvyšším llandovery, krátkodobé populace ve středním–svrchním wenlocku a stabilní populace ve svrchním wenlocku až spodním ludfordianu (u jednotlivých skupin různě). Jižněji na peri-Gondwaně (Sardinie, Karnské Alpy) se zbloudilí migranti objevují ve svrchním wenlocku až ludlowu, stabilní populace teprve ve svrchním ludlowu až spodním lochkovu, a to pouze u tolerantnějších skupin nautiloidů (onkoceridi). Zatímco v pražské pánvi se etablovaly zprvu baltské, popřípadě laurentské druhy, migranti do jižněji položených oblastí jsou z drtivé většiny s afinitou k pražské pánvi (Gnoli 2003, Manda 2008a). Časování migračních fází patrně odráží mimo změn prostředí i posouvání peri-Gondwany směrem k severu a postupné uzavírání Rheického oceánu (Manda 2008a).

Migrace z tropického pásma směrem k jižnímu pólu a jejich jednotný ráz jsou důvodem, že fauny jižní polokoule jsou značně uniformní na celé jižní polokouli, charakteristický je přitom gradient zeměpisné šířky: směrem k pólům klesá diverzita a ubývá demersálních nautiloidů. Celkově jsou migrace nautiloidů do chladnějších moří překvapivé, vycházíme-li ze srovnání s žijícími rody *Nautilus* a *Allonautilus*. Zdá se, že migračně-adaptační potenciál paleozoických nautiloidů byl mnohem větší než u potriasových nautilidů, podobně jako jejich tolerance ke změnám prostředí (teploty, okysličení apod). Geografická distribuce nautiloidů se zvýšila i oproti ordoviku. Důvodem jsou patrně kompetiční tlaky mezi predátory, protože od devonu a později výrazněji od mezozoika progresivně expandují pokročilejší predátoři, jako ryby, mořští plazi či coleoidní hlavonožci (Signor a Brett 1984, Vermeij 1993). Nicméně i v kenozoiku během teplotního eocenního maxima nautiloidi migrovali výrazně směrem k pólům do Anglie, Antarktidy a severní Sibiře (Dzik a Gadzicky 2001), ovšem rozsah této migrace a diverzifikace nesnese srovnání s masivními migracemi v siluru.

4.4. PALEOGEOGRAFIE: VÝZNAM HLAVONOŽCOVÝCH FAUN PRO REKONSTRUKCE ROZLOŽENÍ KONTINENTŮ A SYSTÉMU PROUDŮ

Paleogeografické rozložení kontinentů je důležitým dlouhodobým faktorem pro evoluci bioty. Na tomto pozadí se odvíjejí všechny další změny. Rozložení kontinentů určuje charakter mořského proudění, souvisí s ním plocha šelfů a mělkých moří, kontinenty a jejich vzdálenost působí jako disperzní bariéry a podobně. Přestože základem pro paleogeografické rekonstrukce je geofyzika, strukturní geologie a charakter sedimentů, rozložení biogeografických provincií je jedním z klíčových dostupných dat pro testování stávajících modelů. Paleobiologie se zde ale trochu pohybuje v kruhu, na jednu stranu sice paleogeografické modely testuje, na druhou stranu z nich i částečně vychází. Vývoj peri-Gondwany je jedním z klíčových problémů paleogeografie paleozoika. Peri-Gondwana tvoří skupinu mnoha teránů mezi Gondwanou na jihu a Rheickým oceánem oddělenou Baltikou+Avalonií na severu. Peri-gondwanské terány se oddělily od severní Gondwany během riftogeneze ve spodním ordoviku a zanikly při kolizi Gondwany a Laurusie během variského vrásnění ve svrchním paleozoiku (pro souhrn Stampfli a Borel 2002, Raumer a Stampfli 2008, Linnemann et al. 2008). Je tedy jistou analogií Tethydního oceánu následujícího Wilsonova cyklu (někdy se proto hovoří o Paleotethys, např. Stampfli a Raumer 2002).

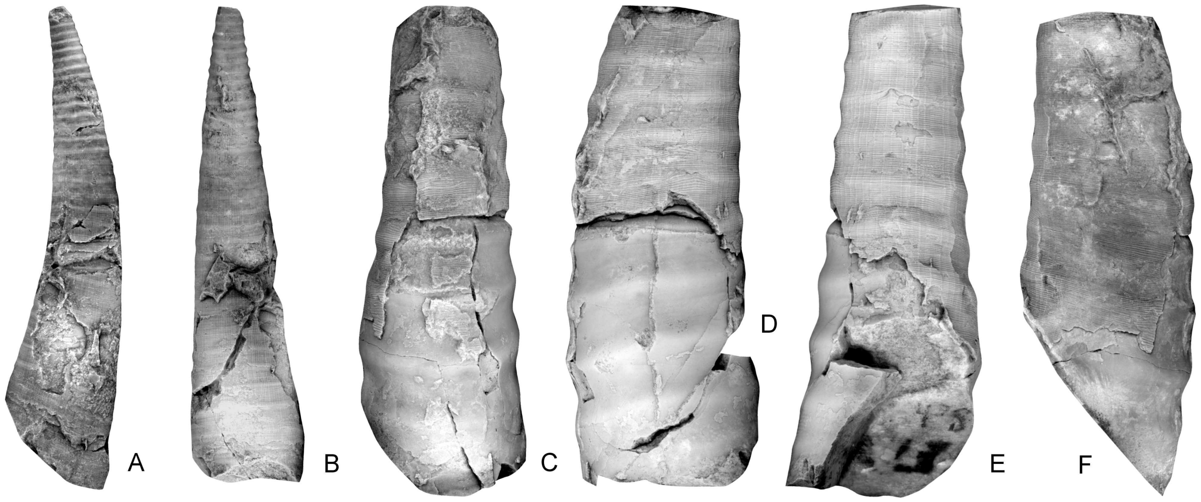
Není zde možné detailně rozebírat problémy paleogeografie paleozoika a navíc by to i vybočovalo ze záměru práce. Cílem je jen poukázat na některé aspekty, které je třeba brát v paleogeografických modelech ve vztahu k pražské pánvi a peri-Gondwaně v úvahu. V poslední době diskuse o paleogeografii určuje rozdělení na geofyzikální a komentující paleontologickou část. To je důsledek specializace, paleontologové příliš nerozumí geofyzice a strukturnímu pojetí a na druhou stranu pro všechny geofyziky platí to samé. Základní otázkou rekonstrukce peri-Gondwany je, z kolika samostatných teránů či desek a mikrodesek se vlastně skládá a jaká byla jejich vzájemná pozice. Na jedné straně je představa mnoha malinkatých desek a na druhé střízlivější odhady, které je sdružují do větších celků. Otázka pozice tepelsko-barrandienského teránu s pražskou pánví je přitom jednou z nejviditelnějších kontroverzí (přehled viz Fatka a Mergl 2010). Je toto malé území součástí saxothuringika či moldanubické zóny, nebo tvoří malý mikrokontinent (nazvaný Perunikou) ležící poněkud stranou od ostatních uprostřed Rheického oceánu? Většina střízlivě uvažujících geologů i paleontologů je ve své odpovědi spíše rozpačitá.



Obr. 11. Paleogeografická situace ve svrchním ludlowu (ludfordianu) podle Scotese a McKerrowa (Worldmap projekt). Pozice Peruniky podle Cockse a Torsvika (2006).

Proč se zdá pozice pražské pánve v rámci peri-Gondwany tak specifická? Základní vymezení Peruniky se opírá o ordovické fauny, jsou zde opakovaná období izolace a komunikace s ostatními částmi peri-Gondwany a Avalonie, respektive Baltiky. Definice teránu je tedy spíše biologická než geologická, jak by bylo žádoucí. Žádná jiná pánev peri-Gondwany podobný vzorec neukazuje

(Havlíček et al. 1994, Fatka a Mergl 2009, Cocks a Torsvik 2002, 2006). V siluru byla podrobně analyzována pouze fauna mlžů, ta ukazuje silné vztahy pražské pánve s ostatními oblastmi peri-Gondwany, mnoho sdílených druhů i celých společenstev, i když celková diverzita je výrazně větší (Kříž 1999b). Mělkovodní fauny mlžů ale mají překvapivou afinitu k Baltice a Laurentii (Kříž 2008). Afinitu s Laurentií ukazuje i nově doložený výskyt fylokarida *Cetratiocaris papilio* (Budil et al. 2010) nebo mechovky *Stictoporella* (Ernst et al. 2011). Problémem paleobiologického přístupu k paleogeografii je fakt, že ne všechny skupiny mají stejný distribuční vzorec, proto je třeba zhodnotit více významných skupin s různou strategií disperze. Dosud byl kladen důraz na bentické fauny – převážně brachiopody, trilobity a mlže, kteří se rozšiřují pomocí larev (například Robardet 2003).

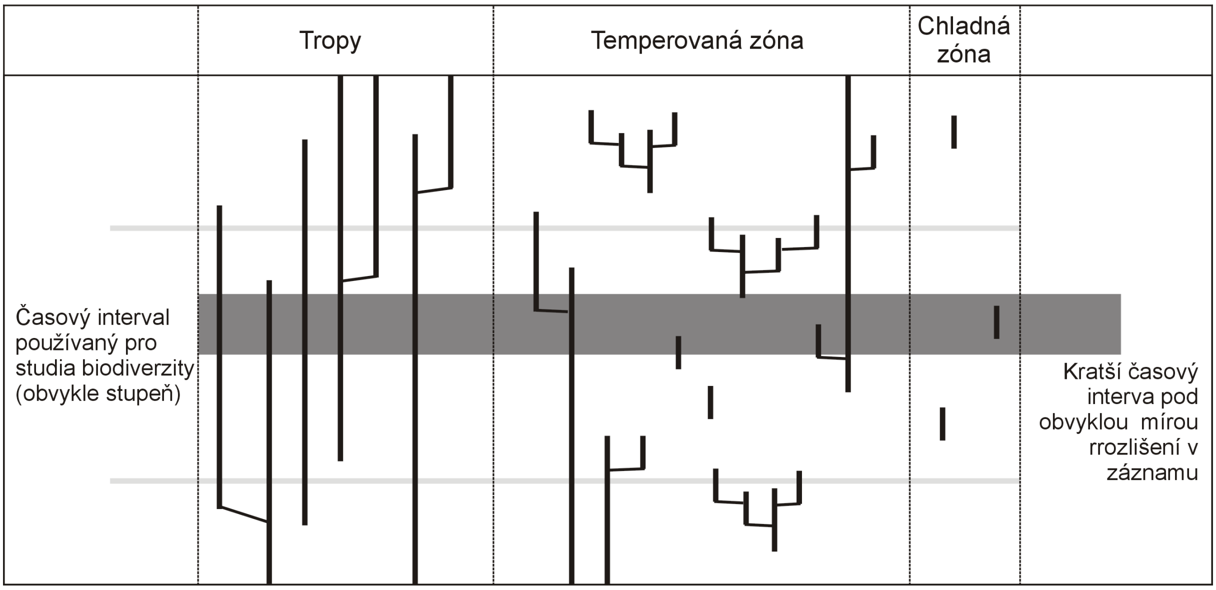


Obr. 12. Příklad endemických hlavonožců ze svrchního lochkovu pražské synformy. A, B: Spyroceras pugio *(Barrande, 1877), laterální a dorsální pohled, patrně nejstarší známý zástupce vysoce diverzifikované devonské čeledi Spyroceratidae. C–F:* Nephriticerina perornatum *(Barrande, 1877), ventrální, laterální (pravý), dorsální a laterální (levý) pohled, jediný známý barrandeocerid z lochkovu, z morfologicky podobných forem se odštěpil v givetu první nautilid. Lokalita Lochkov. Přirozená velikost.*

Hlavonožcové fauny peri-Gondwany jsou obecně velmi podobné (Gnoli a Serpagli 1991, Kříž 1998, Gnoli 2003, Kröger 2008). Drtivá většina druhů (více než 90 %) je sdílená mezi peri-Gondwanou a pražskou pánví. Jedná se vesměs o tolerantní taxony s přímou schránkou. Společenstva jsou podobná jen z části, obecně společenstva z hlubších částí pražské pánve odpovídají těm z ostatních částí peri-Gondwany. Mělkovodní společenstva mají spíše podobnost s faunami tropických oblastí Baltiky, nejzřetelnější je to ve wenlocku, později mají společenstva známá z pražské pánve specifičtější charakter. Tato mělkovodní společenstva jsou vysoce diverzifikovaná, je zde mnoho nektobentických forem, zejména nautiloidů (Manda 2008a).

Základní schéma oceánských proudů v Rheickém oceánu je zřejmé: od východu na západ směřoval podél Baltiky a Avalonie jižní subtropický proud, který se stáčel do oblasti Rheického oceánu, kde vyzníval. Od západu na východ směřoval podél severního okraje Gondwany jižní studený proud (Wilde et al. 1991). V současnosti existují dva hlavní paleogeografické modely: jeden prezentuje Peruniku (pražskou pánev) jako osamocenou mikrodesku položenou poněkud severněji od ostatních peri-gondwanských pánví (Havlíček et al. 1994, Cocks a Torsvik 2002, 2006, obr. 11). Druhý model prezentuje oblast pražské pánve jako součást těsného uskupení peri-Gondwany podél severního okraje Gondwany, poblíž saxothuringika a grazské oblasti, ale i zde je území umístěno vcelku severněji a na okraji peri-Gondwany (Stampfli a Borel 2002, Raumer a Stampfli 2008).

Fauny teplotně citlivých hlavonožců z pražské pánve říkají jen tolik, že tato oblast musela být v dosahu teplého proudu a ostatní části peri-Gondwany nikoliv (Manda 2008a). Něco takového je v podstatě možné u obou modelů, i když model Cockse a Torsvika se zdá poněkud pravděpodobnější. Podle analogie s recentními nautilidy by pro paleozoické hlavonožce vzdálenosti s Baltikou-Avalonií nepředstavovaly disperzní bariéru ani v jednom z případů (viz Manda 2008a). Jiným specifickým rysem pražské pánve je vysoká míra endemicity, tedy počet druhů a rodů (Barrande 1877, Gnoli 2003), které jsou známé jen z tohoto území, celkově se jedná o mnoho desítek taxonů; a něco takového je ve fosilním záznamu obecně velmi neobvyklé. Kříž in Kaljo et al. (1995) přirovnává izolované mělkovodní elevace (vulkanická centra a tektonické prahy kolem bývalých vulkanických center tvořící archipelág) pražské pánve ke Galapágám. Představa „silurských Galapág“ je vcelku užitečná, zdá se, že nautiloidi vázaní na malé mělkovodní domény obklopené hlubšími částmi pánve mohli snadno podléhat adaptivní radiaci. Obzvláště když množství těchto druhů tvoří jen malé populace a vyskytuje se ve fosilním záznamu jen krátce v řádu desítek tisíc let (Manda a Turek 2009a). Představa „silurských Galapág“ také spíše odpovídá jisté separaci pražské pánve od ostatní peri-Gondwany. Četnost některých nautiloidů je velmi vysoká, to dokládá vysokou úroveň živin a primární-sekundární produkce charakteristické spíše pro studenější vody (hlavonožci jsou sekundární a vyšší predátoři). Vzato dohromady, zdá se, že pražská pánev leží na pomezí teplovodní a chladnovodní oblasti.



Obr. 13. Jedno z možných vysvětlení vyšší diverzity nautiloidů v temperované zóně oproti tropům jako artefakt časového dělení.

Hlavonožcové fauny pražské pánve mají i další specifický charakter, ve svrchním siluru kolidovala Baltika+Avalonie s Laurentií, v důsledku toho došlo k ústupu mělkovodních facií v oblasti, v okrajových mořích se ukládala klastika a vznikly rozsáhlé brakické pánve, taková prostředí jsou pro hlavonožce zcela nevhodná (preferují čistou vodu s nízkým obsahem suspenze, tolerance ke změnám salinity je velmi malá), v důsledku toho hlavonožcové fauny z celé oblasti mizí či jsou fauny výrazně redukovány. Zbylé oblasti získávají endemický charakter s omezenou diverzitou (části anglo-waleské pánve a Podolí na Ukrajině, Holland 2000, Zhuravleva 1974).

V tomto období je celá řada čeledí a řádů známa z jediné oblasti – pražské pánve (obr. 12). Z tohoto pohledu je pražská pánev něco jako refugium pro mnoho kladů, tedy „hot spot“. Zdá se přitom, že je zde možno doložit předky některých rozšířených devonských čeledí (Manda 2001, Manda a Turek 2009b, Manda a Frýda 2010).

Biodiverzita měkkýšů obecně vykazuje jeden charakter důležitý pro paleogeografické rekonstrukce. Obvykle je diverzita nejvyšší v tropickém pásmu a směrem k pólům klesá. Exsistují ale i výjimky, například u některých skupin mlžů, kdy je diverzita nejvyšší v temperované zóně, v tropech mírně klesá, zatímco směrem k pólům je pokles výrazný (Valentine a Jablonski 2010). Zmínění autoři to vysvětlují vyšší rychlostí extinkce v temperované zóně. Siluršti nautiloidi patrně představují stejný případ, i když v podstatě jedinou dobře dokumentovanou oblastí v temperované zóně je pražská pánev (a částečně Kazachstánie, Kiselev et al. 1993). Nicméně diverzita je zde mnohem vyšší nežli na tropických platformách Baltiky. Vyší rychlost extinkce a adaptivní radiace migrantů v pražské pánvi nicméně mohou být vysvětlením stejně jako přítomnost různých prostředí na podmořském archipelágu. Časové rozšíření druhů na platformách Baltiky je výrazně delší než u druhů v pražské pánvi (např. Manda 2008a), a to i v případě, že se jedná o sdílené druhy, které migrovaly do temperované zóny. Tito migranti, bez výjimky, mají v pražské pánvi podstatně kratší časové rozšíření a často zde tvoří nové druhy cestou adaptivní radiace (Stridsberg 1985, Manda 2007, 2008a, Manda a Turek 2009a, Turek a Manda 2011). Podobný gradient diverzity nebyl doposud u hlavonožců zaznamenán, nicméně další studia jsou potřebná před konečným zhodnocením (například možnost artefaktu časového rozlišení a podobně, obr. 13).

4.4. EVOLUČNÍ ZMĚNY JAKO DŮSLEDEK ZMĚN PROSTŘEDÍ A SPOLEČENSTEV

Morfologie těl živočichů odráží celou řadu faktorů a je výsledkem dlouhodobé evoluce. Dlouho se věřilo, že výsledná morfologie je striktně odrazem adaptace organismu na prostředí. Dnes je ale zřejmé, že vývoj morfologie těla odráží celou řadu faktorů, kromě klasické adaptace na abiotické prostředí je i výsledkem řady dalších interakcí v ekosystémech (např. predátor–kořist), neutrální molekulární evoluce, náhodných faktorů evoluční historie, zejména při extinkčních událostech, a fyzikálních a biologických omezení, která limitují, co je ještě možné a co už nikoli. Určit faktor, který je určující při vzniku morfologické struktury, je proto složité, ve většině případů je morfologie daná interakcí řady faktorů.

Studia makroevolučních trendů nicméně ukazují, že ve fosilním záznamu můžeme rozlišit obecné trendy v morfologii. Pevné schránky měkkýšů schopné fosilizace umožňují trendy v morfologii studovat lépe než u mnoha jiných bezobratlých. Schránka hlavonožců má dvě základní funkce: ochrannou (jako u ostatních měkkýšů) a hydrostatickou (schránka obsahuje přepážky s plynnou směsí, která schránku nadnáší a usnadňuje tak plavání, v české literatuře tzv. plynové komory; gas chambers v angličtině; na základě poznámek jednoho z německých recenzentů, který upozornil na šovinistický charakter tohoto označení, byť věcně správného, dále používám termín fragmokonové komory). Obě tyto funkce jsou nicméně v rozporu, schránka je tím bezpečnější, čím je silnější, ale naopak tím se stává i těžší a znesnadňuje vznos. U coleoidů nakonec došlo k redukci schránky na vnitřní a posléze k její úplné redukci. U staropaleozoických hlavonožců ale byla schránka vnější a plnila obě tyto funkce větší či menší měrou.

Tvar schránky, morfotyp, do značné míry určuje způsob života. Každý tvar schránky má své hydrodynamické vlastnosti, které určují jednak možnosti pohybu (aktivní plavci versus demersální formy) a také pozici schránky, a tedy orientaci ústí (těžiště schránky); přehled viz Flower (1957), Chamberlain (1991) a Westermann (1998). Obecně svinuté schránky jsou efektivní při plavání a jejich ústí směřuje na stranu, naopak schránky s vyšším úhlem rozšiřování, rovné či mírně zahnuté, neumožňují tak aktivní pohyb, ale jejich ústí směřuje víceméně ke dnu (demersální predátoři). Tyto základní typy mají i kombinace, například svinutá schránka se může v dospělosti rozvinout a tím dochází k orientaci apertury více ke dnu. Zcela samostatnou skupinou jsou pak rovné a pomalu expandující schránky, u kterých je otázka jejich biologické pozice dána umístěním balančních zátěží v komorách fragmokonu (pelagické formy s vertikální orientací *versus* nektonní formy s horizontální orientací).

Během ordovické radiace se objevila celá řada morfotypů. Byl obsazen prakticky celý morfologicky možný prostor. Vysoká morfologická disparita přetrvávala až do nejvyššího siluru, následuje mírný pokles ve variabilitě schránek a ve svrchním paleozoiku převládají v rovině vinuté schránky s posílením tohoto trendu v triasu, kdy vrcholí (Ward a Bandel 1987, Barskov 1989). Protože tvar schránky do značné míry determinuje způsob života, vyskytují se řady konvergencí mezi jednotlivými klady. Neexistují žádné klady s jedním typem schránek, i když existují jisté preference dané patrně ranou embryogenezí. Nejvyšší variabilita schránek je u nautiloidů, orthoceratoidi mají naopak většinou rovné schránky (vyloučíme-li ovšem amonity se svinutými schránkami, kteří se od nich odštěpili v devonu). Vzhledem k charakteru raných stadií (bilaterálně symetrická a mírně zahnutá schránka u nautiloidů) jsou některé typy schránek vysloveně unikátní. U nautiloidů je takovým ontogenetickým omezením například prostorově vinutá schránka. Takové schránky byly doposud známé především u tzv. aberantních amonitů, ale nově byly popsány i u devonských rutoceridů z pragu (Manda a Turek 2009b). Je přitom zajímavé, že takováto změna morfotypu, tedy z 2 do 3D vinuté schránky je velmi rychlá v řádů menším než milion let. Obecně evoluční plasticita schránky je u nautiloidů velmi vysoká. Něco takového ale neplatí pro amonity nebo nautilidy. V čem může být důvod vysoké morfologické disparity u spodnopaleozoických hlavonožců a její náhlý pokles od svrchního devonu? Zdá se, že hlavním důvodem je celkový vývoj ekosystémů, tedy kompetiční tlak ze strany jiných skupin. To by vysvětlovalo úbytek demersálních forem počínaje devonem a posilování podílu svinutých nektonních forem (Kröger 2005, Manda a Turek 2009b, Klug et al. 2010).

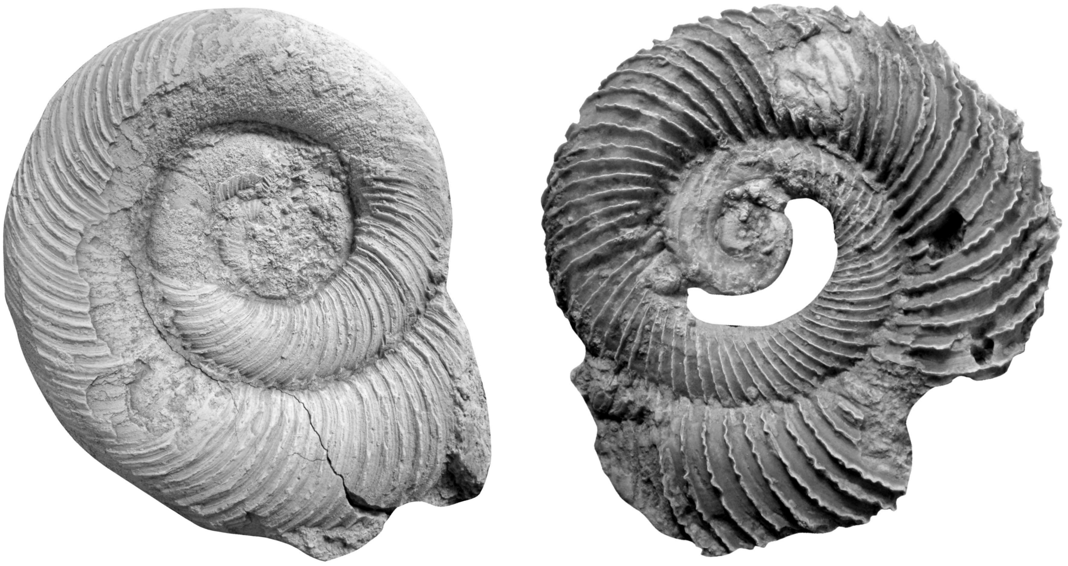
Podceňovaným faktorem je i velikost schránky, která podstatně ovlivňuje mechanické vlastnosti schránky. S narůstající velikostí schránky narůstá její křehkost, a je zajímavé, že mnoho vývojových linií v siluru drží například podobné maximální velikosti dospělců (Manda a Turek 2009c, v tisku), ale naopak u spodnodevonských nautiloidů dochází k postupnému vzrůstu velikosti schránky (Manda a Turek v tisku). Naopak u některých forem, kde je bezpečně možné určit dospělost (uzavřené ústí), je variabilita velikosti dospělců vysoká;

patrně to odráží prostředí a jeho kvalitu, vývoj velikosti schránek se zdá být zajímavým, ale doposud málo studovaným tématem. V následující části jsou ve větší podrobnosti diskutovány tři vybrané morfologické parametry hlavonožců a jejich možný význam.

4.4.1. Posílené skulptury: antipredační znak?

Schránka měkkýšů přirůstá akrečně, v oblasti apertury je vylučována okrajem pláště nová schránka. Tento růst zanechává na schránce viditelné linie, přírůstkové zóny. V obdobích s větším zdrojem potravy schránka může přirůstat rychleji a naopak ve stresových obdobích se sekrece schránky může zpomalit nebo zastavit. Schránky měkkýšů ale vykazují celou řadu modifikací této základní přírůstkové struktury. Kromě přírůstkových vrásek různé velikosti se vyskytují radiální žebra nebo vznikají dokonce různé výrůstky jako trny a podobně. Často dochází i k periodickému zvětšování a zmenšování ústí a schránka je pak v řezu zvlněná – anulovaná. Jindy jsou přírůstkové vrásky redukovány, takže schránka působí, jako by byla hladká. Všechny tyto variace ve skulptuře musí mít nějaký důvod. Zmíněná sezonalita (změna rychlosti tvorby schránky) je nemůže plně vysvětlit. Navíc zmíněné posílené skulptury se vyskytují u mnoha navzájem nepříbuzných skupin, mohou tedy představovat adaptivní konvergence a vypovídat o makroevolučních tlacích.

Vermeij (souhrn 1987, 1993) v řadě prací ukázal, že u mořských gastropodů dochází v průběhu mezozoika k zesílení schránek a posílení jejich skulptur. Tento trend dává do souvislosti s radiaci durofágních predátorů schopných destruovat schránky měkkýšů (například ryb, krabů, coleoidů nebo hvězdic). Vermeij (1987) hovoří o mezozoické marinní revoluci a tento názor byl obecně akceptován. Signor a Brett (1984) nicméně zpozorovali podobný trend již v devonu a hovoří o události předcházející vlastní mezozoické revoluci, autoři dokládají vznik a rozvoj antipredačních znaků u řady skupin, mezi měkkýši u plžů a hlavonožců. Podle těchto autorů dochází u hlavonožců v devonu k rozvoji posílených skulptur (zesílené přírůstkové valy, radiální a příčná žebra a podobně) a různých výrůstků na schránce (různé trny, výstupky známé jako nody, zvlněné nebo rovné límce, křídlovité struktury, popřípadě jejich kombinace), a to údajně u více vývojových linií.



Obr. 14. Tarphyceridi Graftonoceras *sp. A (vlevo) a* Graftonoceras *sp. B (vlevo), wenlock, Gotland. Příklad rychlé fixace posílené skulptury u mělkovodních forem. Lehce naznačené přírůstkové valy u ancestora a zvlněné vystupující límce u descendenta. Přirozená velikost. Podobné posílené skulptury se vyskytují i u třech dalších druhů, které se vyskytují v rifových vápencích s* Graftonoceras *sp. B. To dokládá, že vznik zesílených skulptur odpovídá adaptaci na mělkovodní prostředí.*

Analýza rozvoje skupin s posílenými skulpturami nicméně dokládá (Manda a Turek 2009b, v tisku), že takové skulptury se vyskytují již u ordovických a silurských hlavonožců (obr. 14), v devonu jsou sice takovíto hlavonožci hojnější, ale bez výhrady se jedná o příslušníky jednoho kladu, který prodělal rychlou adaptivní radiaci ve spodním devonu. Zesílené schránky navíc nepřinášejí u hlavonožců podobný efekt jako u ostatních měkkýšů, protože hlavonožci jsou aktivně plavající živočichové a predátoři, jakékoliv zesílení schránky tedy klade nároky na jejich metabolismus a omezuje pohyb. V souhrnu se zdá posílení skulptur v devonu spíše jako důsledek adaptace na mělčí, a tedy dynamičtější prostředí, posílené skulptury dále mohly zvyšovat stabilitu schránky při aktivním pohybu (Manda a Turek 2009b). Dále mělkovodní populace v souladu s tímto vysvětlením vykazují posílenější skulptury než časově současné populace téhož druhu z hlubších částí pánve. To ukazuje ekotypický charakter částečného posílení skulptur u mělkovodních populací. Není to překvapení, protože v mělčím a teplejším prostředí představuje vylučování posílených skulptur menší metabolickou zátěž. Koexistence mělkovodních a relativně hlubokovodnějších populací s rozdílně vyvinutými skulpturami pak dokládá teritorialitu některých nautiloidů a omezenou migraci mezi populacemi, a to spíše z mělčího prostředí do hloubky než naopak (Manda a Turek v tisku).

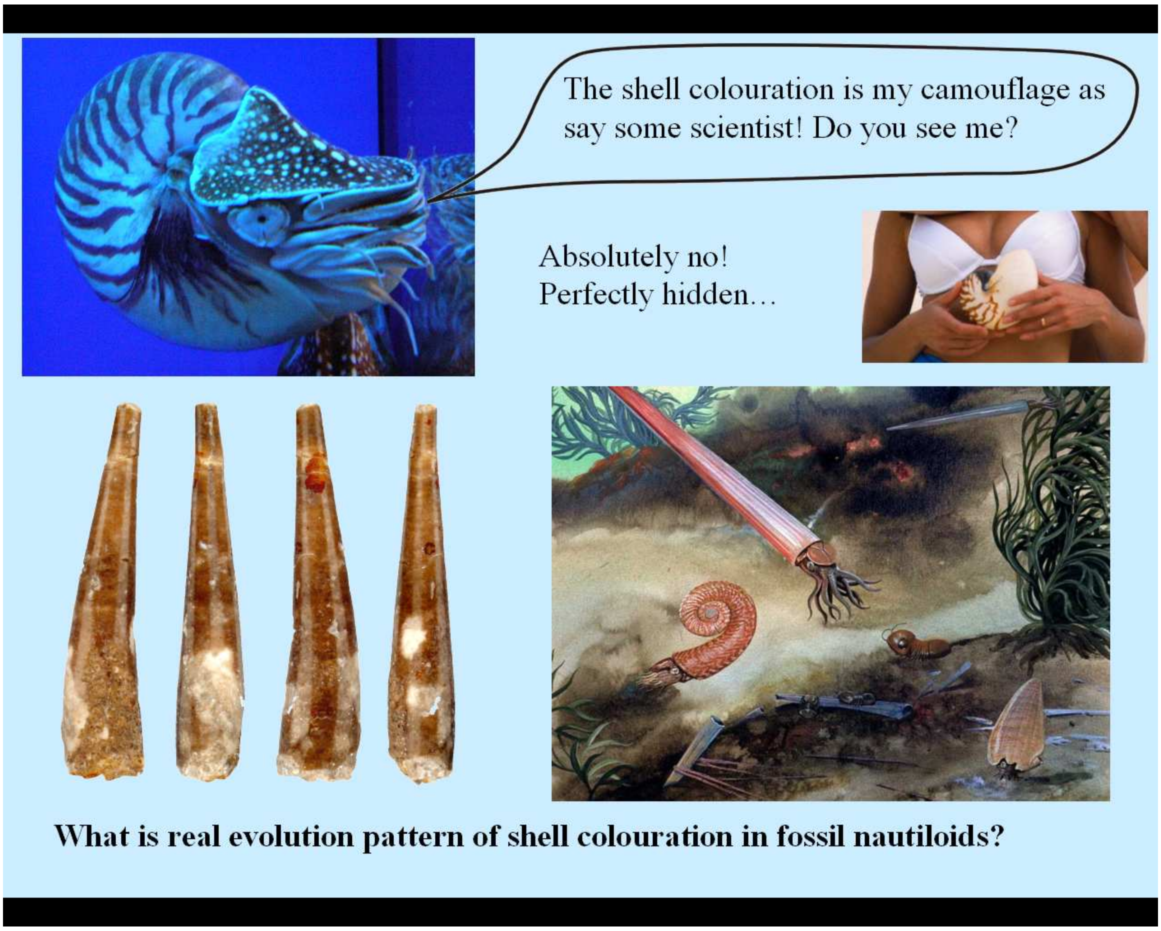
4.4.2. Zbarvení schránek

Zbarvení schránek měkkýšů vzniká pravděpodobně jako důsledek ukládání metabolického odpadu (Kobluk a Mapes 1989). U mnohých měkkýšů nemá zbarvení schránky žádnou funkci, protože během života nijak neovlivňuje úspěšnost organismu, platí to například pro hrabavé mlže a některé gastropody. Naopak u měkkýšů, kteří se aktivně pohybují, může zbarvení druhotně získat ochranou funkci (exaptace). U recentního nautila zbarvení slouží jako kamufláž a podobně tomu bylo i u vymřelých nautiloidů, a o tomto faktu panuje obecná shoda, i když přesvědčivé důkazy chyběly (obr. 15, Cowen et al. 1973, Kobluk a Mapes 1989, Westermann 1998). Zbarvení nautiloidů je velmi variabilní, známé jsou radiální a příčné pruhy, dále lomené vzory, zvlněné pruhy, a samozřejmě jejich kombinace (Foerste 1930). Zbarvení se může výrazně lišit i u příbuzných druhů nebo někdy dokonce v rámci druhu. Nemůže být tedy důsledkem větších anatomických změn. Z tohoto důvodu byl navržen neurosekreční model produkující zbarvení v závislosti na prostředí (Boettinger et al. 2009). Naprostá většina druhů nautiloidů má druhově specifický barevný vzor, to samo o sobě podporuje jeho adaptační význam. Nicméně evoluční vzorec barevných vzorů u jednotlivých kladů je dosud špatně znám.

Radiální barevné pruhy jsou u nautiloidů extrémně vzácné, naopak časté jsou u orthoceratoidů s rovnou schránkou (má podobnou funkci jako analogické barevné pruhy u ryb). Turek a Manda (2009c) popsali zajímavý případ konvergence mezi nautiloidy a orthoceratoidy. Malá, jen slabě zahnutá schránka onkocerida *Pomerantsoceras*, která silně připomíná orthoceratoidy, vykazuje pravidelné radiální pruhy. Konvergence morfotypu a zbarvení je zřejmým dokladem adaptivního charakteru zbarvení. Ten samý vzor byl navíc u tohoto dlouho žijícího druhu stabilní kolem sedmi milionů let. Na druhou stranu u zahnutého onkocerida *Eurizocerina* došlo během rychlé speciace k velmi rychlé změně barevného vzoru z pravidelných transverzálních na nepravidelné pulzující pruhy, současně došlo i k rychlé změně zahnutí schránky, a tedy změně biologické orientace během života (Manda a Turek 2009a).

Polymorfismus v barevném vzoru měkkýšů byl popsán zejména u některých gastropodů, kde slouží jako adaptace na různá prostředí, např. barvu substrátu a podobně. První případ polymorfismu u nautiloidů byl popsán u rodu *Phragmoceras* ze siluru. Další možné případy byly diskutovány u dalších nautiloidů. Zdá se, že polymorfismus a celková světlost (poměr mezi pigmentovanou a nepigmentovanou částí schránky) schránky jsou řízeny prostředím. Nautiloidi obývající hlubší prostředí mají spíše tmavší schránky než jejich příbuzní z mělkovodních nik. Zajímavé je zastupování dvou vzorů u nezávislých kladů: širších a řidších pruhů paralelních s přírůstkovými strukturami v mělkovodním prostředí *versus* kombinace úzkých a hustších transverzálních-longitudinálních pruhů v hlubším prostředí (Turek a Manda 2010, 2011).

Celkově se ukazuje, že evoluce barevného vzoru byla podstatně komplexnější, než se předpokládalo, a její poznání může vést k poznání interakcí ve fosilním záznamu (vztah dravec–kořist, adaptace na hloubkové poměry, kvalita vidění predátorů a podobně).



The shell colouration is my camouflage as say some scientist! Do you see me?

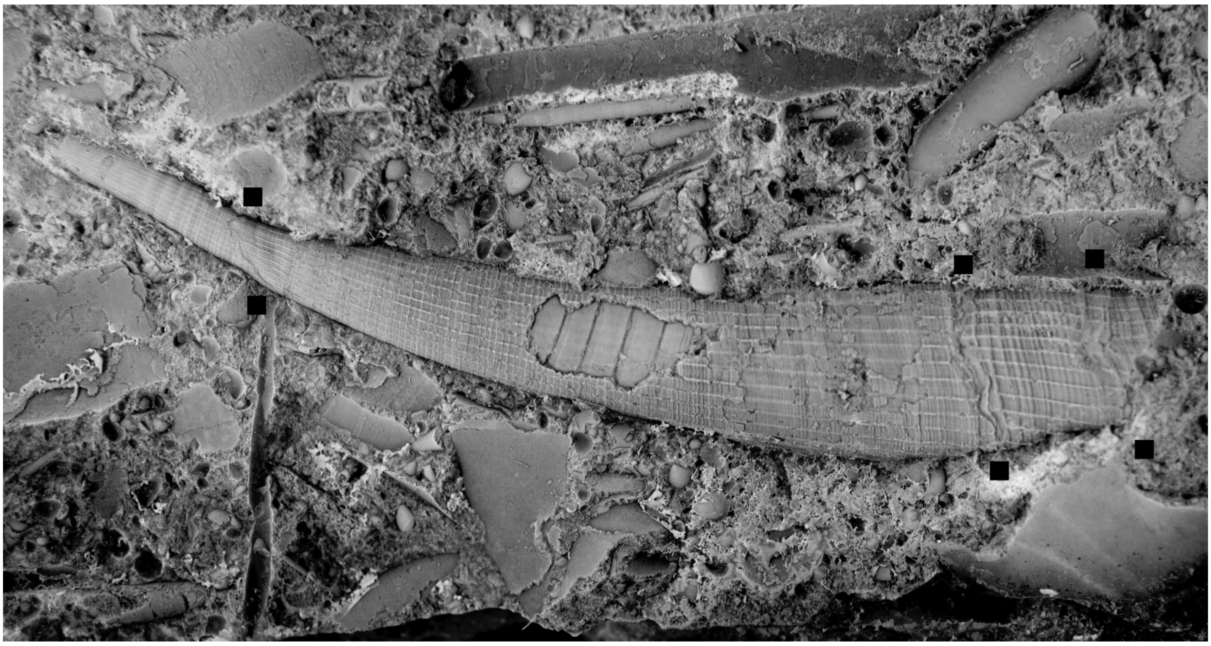
Absolutely no!
Perfectly hidden…

What is real evolution pattern of shell colouration in fossil nautiloids?

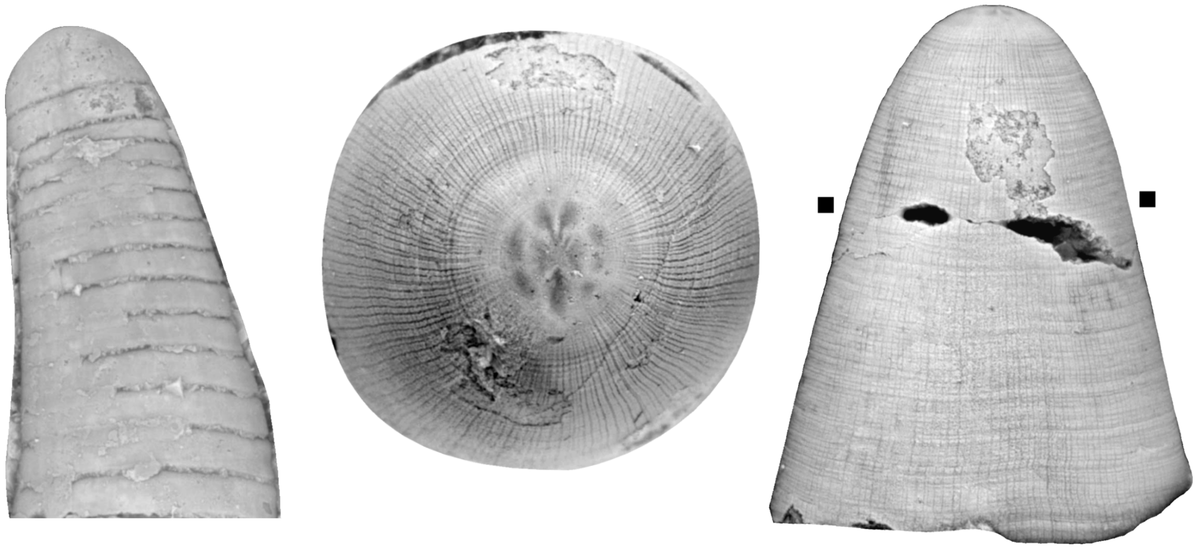
Obr. 15. Úvodní stránka prezentace na Mezinárodním paleontologickém kongresu v Londýně 2010, ukázky zbarvených hlavonožců.

4.4.3. Embryogeneze nautiloidů

Embryonální vývoj nautila je relativně dobře znám, *Nautilus* klade relativně veliká, žloutkem bohatá vejce v kryptických místech (skalních trhlinách a podobně). Vývoj ve vajíčku je relativně dlouhý, v řádu mnoha měsíců. Z vajíčka se líhne malý jedinec podobný dospělému a schránkou s jedním závitem. Vylíhnutí způsobuje náhlou změnu, která se projevuje krátkodobým zúžením schránky nazvaným nepionická konstrikce (souhrn Ward 1987, Landmann et al. 1996). Podobným způsobem se utvářela raná embryogeneze u všech nautilidů (řád Nautilida) přinejmenším od jury (Chirat a Rioult 1998). Jaká ale byla embryogeneze spodnopaleozoických nautiloidů? I když byla popsána řada apikálních částí schránek v období popisného období paleontologie, tyto nálezy nebyly doposud interpretovány na rozdíl od embryonálního vývoje orthoceratoidů s rovnými schránkami (Erben 1960, 1964, 1965, Ristedt 1968, 1971, Kolebaba 1973, 1975, 1977, Kröger 2006). Převážná část embryonálních schránek přitom byla popsána právě ze siluru a devonu Čech (Barrande 1865–1877).



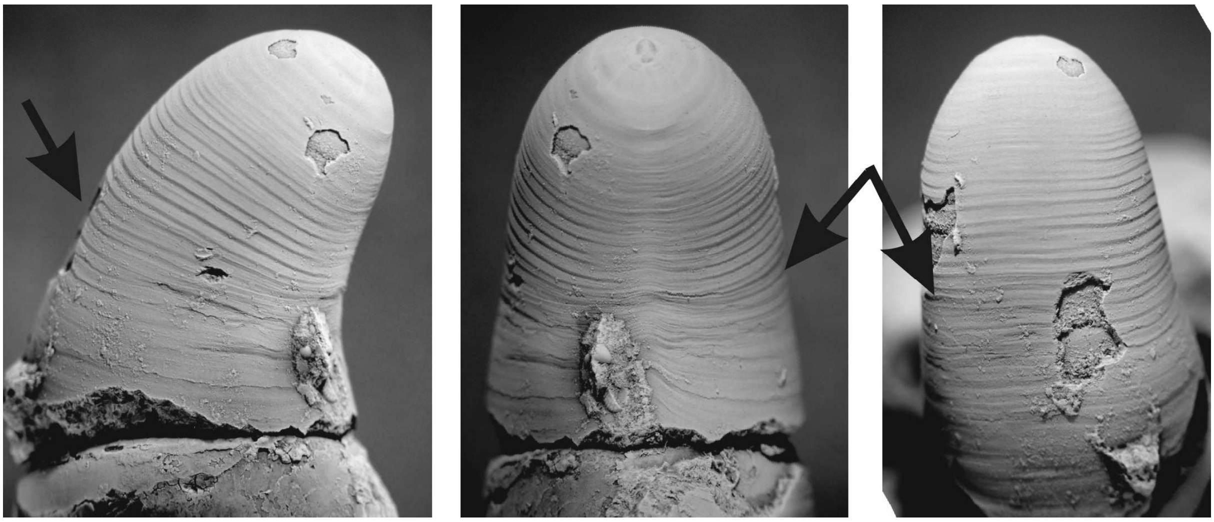
Obr. 16. Raná schránka orthocerida „Orthoceras" mimus *Barrande. Výrazné vyhojené zranění v apikální části (označeno čtverečkem) dokládá, že k vylíhnutí muselo dojít již dříve, příklad orthocerida s planktotrofním raným stadiem a pozdější adaptací na nektobentický způsob života (konvergence s rodem* Kionoceras*). Báze ludlow, Butovice. Maximální průměr schránky je 4 mm.*



Obr. 17. Příklad embryonální schránky u silurských onkoceridů. Vlevo raná část schánky Oonoceras *sp., laterální pohled, výrazné snížení velikosti fragmokonových komor indikuje líhnutí; maximální průměr schránky 5 mm, lokalita Lochkov. Uprostřed a vlevo* Rizosceras mundum *Barrande, apikální a ventrální pohled, zranění a densita sept indikuje líhnutí při průměru schránky 4 mm (označeno čtverečkem), lokalita Karlštejn.*

Všichni svrchnopaleozoičtí nautilidi a také devonský *Centroceras* (nejstarší nautilid) vykazují zcela odlišný embryonální vývoj než recentní *Nautilus*. Raná schránka je zahnutá a nikoliv stočená, pokrytá je přírůstkovými vráskami a její konec je zašpičatělý, první komora je velmi nízká. Líhnutí probíhalo dříve než u potriasových nautilidů, podle druhu a rodu zhruba, když závit dosáhl poloviny až tří čtvrtin (Ruzhentsev a Shimansky 1954, Flower 1952, Mapes et al. 2007). U triasových nautilidů líhnutí probíhalo později, když schránka dosáhla jednoho závitu (Sobolev 1989).

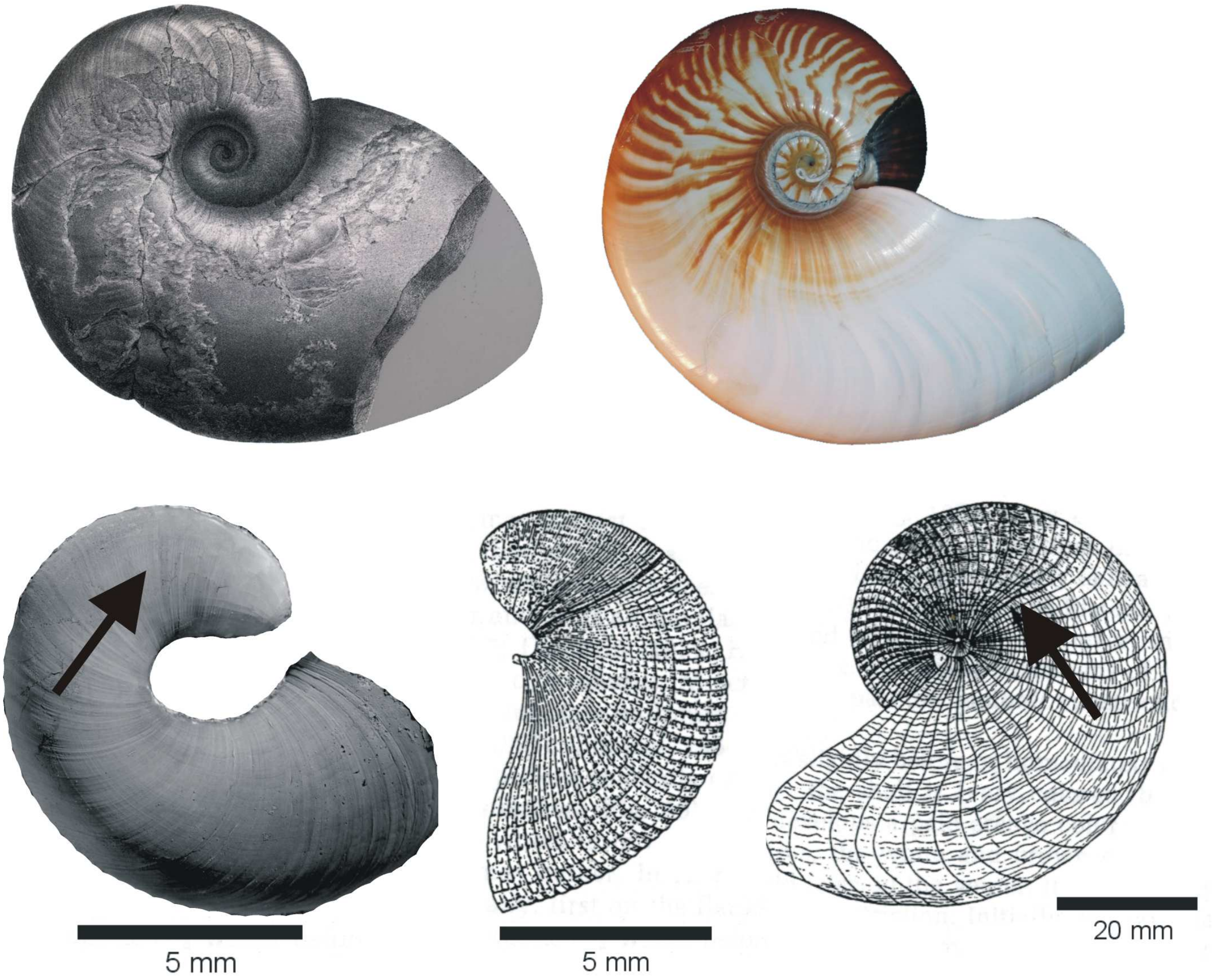
Situace u spodnopaleozoických nautiloidů (řády Oncocerida, Discosorida a Tarphycerida) je podstatně složitější. Onkoceridi a diskosoridi mají velmi podobná raná stadia, která se tvarem příliš neliší od nautila, nicméně velikost u jednotlivých druhů/rodů se značně liší, průměr schránky u prvního septa je mezi 2 až 10 mm; první komora je relativně vysoká. Tupý apex je rovný nebo zahnutý. Cicatrix není eliptický jako u nautila*,* ale kruhový, nebo je tvořen eliptickým polem s radiálními strukturami, které se ale zachovávají jen velmi vzácně. Původ těchto radiálních struktur je nejasný, ale patrně dokládají ranou segmentaci hlavového komplexu (obr. 17). Tyto struktury vcelku odpovídají rané segmentaci u *Nautila,* která je interpretována jako pozůstatek archetypálního plánu měkkýšů. Je to pozoruhodný důkaz evoluční stability této segmentace v rané embryogenezi. U *Nautila* ale dochází ke komplexní metamorfóze tohoto archetypálního plánu (Shigeno et al. 2008).



Obr. 18. Raná schránka u druhu Phragmoceras imbricatum *Barrande, spodní ludlow, lokalita Butovice, laterální, ventrální a dorsální pohled, doba líhnutí odpovídá šířce schránky 4 mm a je označena šipkou.*

Onkoceridi a diskosoridi nicméně vykazují i jiný znak seriality, a sice segmentaci svalových polí na anulární elevaci, zatímco nautilidi mají jeden pár laterálních retraktorů (Kröger a Mutvei 2005). Rozložení svalových vtisků a utváření ústí (zúžení) nicméně dokládají, že hlavový komplex u těchto nautiloidů nevyplňoval celou oblast ústí (Kröger 2007, Manda 2008a). Onkoceridi a diskosoridi tak náleží bazálnímu kladu nautiloidů s úzkým vztahem ke kambrijským ellesmeroceridům (Chen a Teichert 1983). Diference řádu Oncocerida a Discosorida (Flower a Kummel 1950) na základě sifonálních struktur (tedy aditivních znaků), která doposud nebyla zpochybněna, se tak zdá být spíše sporná.

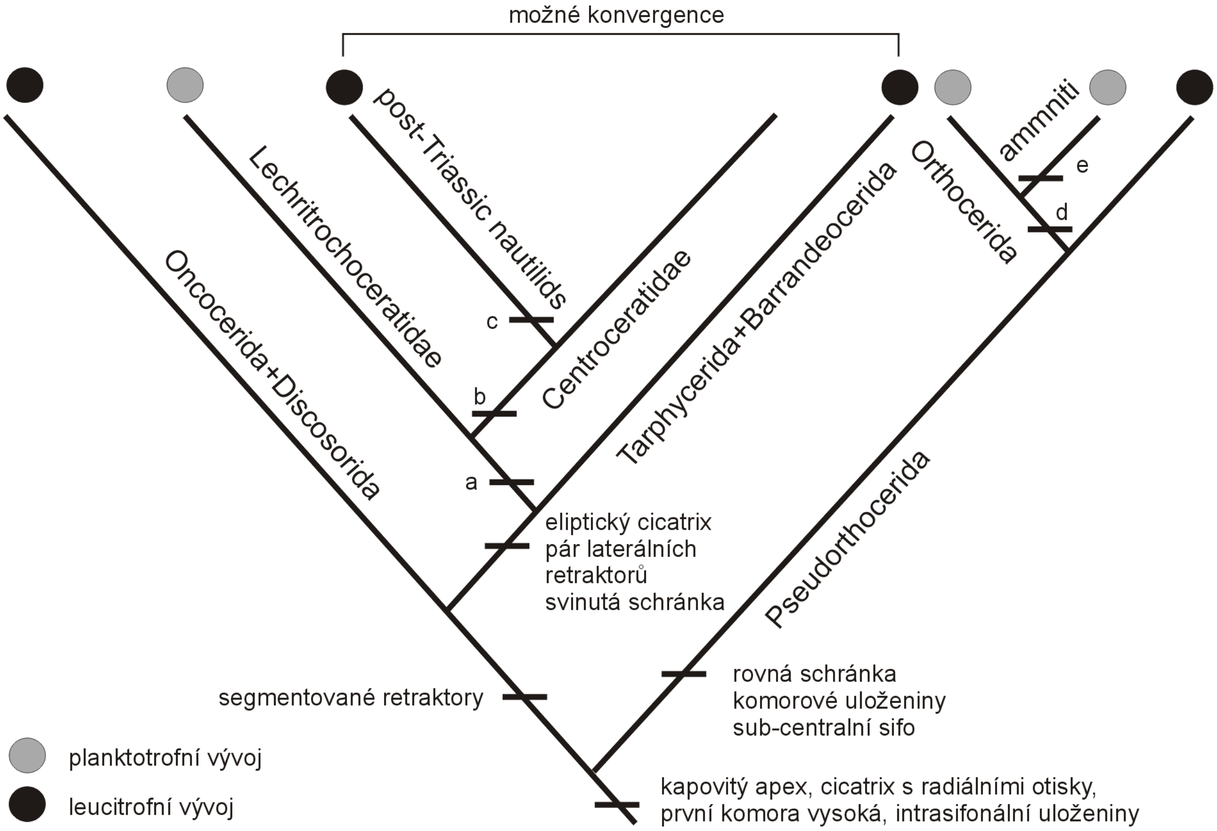
Podstatnou informaci může poskytnout i doba líhnutí, a tedy délka inkubační doby a velikost kladených vajíček. Určit dobu líhnutí u spodnopaleozoických nautiloidů je složité, nepionická konstrikce (jinak známá u všech nautilidů) chybí, ale je zde řada dalších znaků zahrnující změny



Obr. 19. Konvergence mezi silurským barrandeoceridem Boionautilus *(vlevo) a recentním nautilem (vpravo, kresba podle Hyatta 1894). Patrný je rozdíl ve velikosti schránky během líhnutí (označena šipkou) navzdory tvarové podobnosti (podle prezentace Turka a Mandy 2009).*

skulptury, hustoty sept či výskyt vyhojených zranění (obr. 16). Posouzení těchto znaků ukázalo, že diskosoridi rodu *Phragmoceras* se líhli, když schránka byla velmi malá (obr. 18). Raná stadia tak připomínala monoplakofory a její šířka se pohybovala kolem 4 mm, výška kolem centimetru. To znamená, že inkubační doba byla podstatně kratší než u před- i potriasových nautilidů.

Jaký je vývoj u barrandeoceridů (Tarphycerida), skupiny, ze které se odštěpili nautilidi? Vyskytují se zde dva základní typy embryonálních stadií. První typ je nejlépe znám u silurského rodu *Boionautilus*, který tvarem schránky výrazně připomíná recentního nautila. Rovněž tvar embryonální komory obou rodů je podobný; zásadní rozdíl je ale v době, kdy docházelo k líhnutí. Vylíhlý



Obr. 20. Model fylogeneze nautiloidů podle rané ontogeneze. a: redukovaná velikost apexu, první komora nízká, retikulátní skulptury na apexu; b: zašpičatělý apex, apikální schránka s příčnými žebry, nepionická konstrikce doprovázená změnou vinutí, zvlněné sutury; c: prodloužení inkubace, apex větší, embryonální komora s radiálními žebry, nepionická konstrikce nedoprovázená změnou schránky; d: chybí cicatrix, pelagická stadia po vylíhnutí, protokoncha sférická, redukce uloženin; e: protokoncha sférická se zaškrcením, sifo marginální, sutury zvlněné.

Boionautilus měl kápovitou schránku s průměrem kolem 4 mm, tedy opět podstatně méně než nautilidi (obr. 19). Navzdory podobnosti *Boionautila* a nautila nejsou členy stejné linie, svrchnodevonští nautilidi se oddělili od lechritrochoceratidů (Dzik a Korn 1994), kteří mají v dospělosti svinutou schránku, ale jejich rané stadium je jen mírně zahnuté s radiálními a příčnými žebry. K jejich líhnutí docházelo, když schránka měla průměr méně než 2,5 mm (Turek 2010) a na rozdíl od sesterské linie s *Boionautilem* byla druhotně planktotrofní (Manda a Frýda 2010).

Celkově fylogeneze nautiloidů byla podstatně složitější, než se předpokládalo (obr. 20), a k jejímu poznání je nutné revidovat další materiál.

Z hlediska makroevolučních trendů je u nautiloidů patrný trend k prodlužování vývoje ve vajíčku. Tento trend byl již dříve rozpoznán u gastropodů (Frýda et al. 2008). Čerstvě vylíhlí spodnopaleozoičtí nautiloidi měli malou a monoplakoforům podobnou kápovitou schránku, přestože podle posledních studií tyto skupiny nejsou fylogeneticky příbuzné. U svinutých forem, které postupně převládly (viz výše), to znamenalo značný problém, protože přechod od demersálního mladého jedince s nesvinutou schránkou do dospělce se svinutou schránkou, a tedy aktivního plavce byl patrně problematický a jedinci mohli být vystaveni většímu predačnímu tlaku. U nautila se líhne jedinec s už svinutou schránkou a tento problém odpadá (na úkor prodloužení inkubační doby, během níž je vajíčko vystaveno změnám prostředí a predátorům). Celkově kratší vývoj ve vajíčku u paleozoických nautiloidů je patrně důvodem jejich podstatně většího rozšíření než potriasových nautilidů. Krátká inkubační doba totiž činí vajíčko méně náchylné proti změnám prostředí a sezonalitě, vejce s menším počtem živin také umožnují zvětšit jejich počet. Kratší embryonální vývoj také patrně umožňoval větší morfologickou pestrost nautiloidů, embryonální stadia nautiloidů jsou totiž velmi podobná a k změnám morfotypu dochází většinou v raných stadiích (pokud má vylíhlý jedinec svinutou schránku, je její transformace do jiného morfotypu nepravděpodobná). Tento trend patrně odráží vývoj narůstajících kompetičních a predačních vztahů v siluru a devonu.

5. ZÁVĚR

Tato disertační práce se zabývá studiem globálních změn v období siluru a spodního devonu. Tento časový úsek v historii Země je pozoruhodný v mnoha ohledech, neboť zahrnuje obnovu ekosystémů po globální krizi ve svrchním ordoviku a následné rozsáhlé změny v biotě, jakými byl rychlý rozvoj predátorů/nektonních forem v devonu a výstup/expanzi živočichů a rostlin na souši. Klasickým územím, kde byly mořské uloženiny tohoto období studovány, jsou střední Čechy, proslavené již od počátku 19. století.

Detailní studium doposud nedostatečně známé svrchnoludfordianské krize (Kozlowskii/Lau event) dokládá, že vymírání proběhlo relativně rychle a odpovídá změlčení spojenému s glaciací a nárůstu $\delta^{13}C$ v sedimentech. Vymírání postihlo nejen graptolity/konodonty, ale i ostatní faunu a je doprovázeno výraznou změnou společenstev. Obnova ekosystémů doprovázená masivní imigrací proběhla až během následného nízkého stavu hladiny. Extinkční intervaly jsou zvýrazněné sekvenčními hranicemi spojenými s přerušením sedimentace.

Dosud značně opomíjení hlavonožci byli vybráni jako modelová skupina pro studium evolučních změn a ekosystémů v siluru a devonu. Nově vymezené skupiny hlavonožců lišící se embryonální strategií a způsobem života dospělců umožnily sledovat makroevoluční trendy v paleozoiku. Raně ontogenetické strategie a velikost vajíček (doba inkubace) hlavonožců ovlivňují přežití a vývoj diverzity během krizí, což bylo doloženo pro vymírání v nejvyšším siluru, kdy začala růst diverzita nektonních forem, a tento trend pokračoval i v devonu.

Ustupující anoxie ve spodním siluru zahájila rozsáhlé migrace hlavonožců z tropické zóny směrem k pólům. Byly rozeznány jak ojedinělé migrace dospělců, tak i výskyt lokálních populací a nakonec i masivní migrace doprovázené speciací. Migrace ovlivňovalo paleogeografické rozložení kontinentů a eustatické pohyby (jsou zvýšené během nízkých stavů). Diverzita hlavonožců na archipelazích temperované zóny byla vyšší než v tropech, patrně díky vyšší rychlosti extinkce. Složení fauny silurských hlavonožců pražské pánve dokládá ovlivnění teplým subtropickým proudem, na rozdíl od ostatních částí peri-Gondwany. Ústup moří z kolidující Laurentie/Avalonie a Baltiky v nejvyšším siluru vedl ke zúžení geografického areálu mnoha skupin hlavonožců. Desítky rodů jsou známé jen z pražské pánve (zvýšené vymírání hlavonožců na hranici silur-devon může odrážet i tento fakt, protože post-extinkční obnova bývá spojena s migracemi z tropů).

Vybrané morfologické charakteristiky schránek byly využity pro studium makroevolučních trendů hlavonožců. Posílené skulptury u některých hlavonožců jsou spíše adaptací na mělkovodní prostředí než antipredační adaptací, jak se předpokládalo. Porovnání skulptur u současných populací dokládá omezené migrace mezi populacemi v mělkém a hlubším prostředí (to ovlivňuje i rychlou speciaci hlavonožců). Studium silurských hlavonožců doložilo, že zbarvení schránek hlavonožců je řízeno jako sekundární adaptační znak (exeptace). Poprvé byl doložen polymorfismus barevných vzorů u hlavonožců, konvergence barevných vzorů u nepříbuzných skupin, vztah zbarvení k hloubce a biologické orientaci.

Bylo doloženo postupné prodlužování embryonálního vývoje nautiloidů vrcholící u současného *Nautila*. Spodnopaleozoičtí nautiloidi měli po vylíhnutí malé kápovité (tvarem podobné monoplakoforům) schránky a během růstu se měnila jejich biologická orientace i tvar schránky. U potriasových nautilidů se líhl jedinec s již svinutou schránkou, žijící podobně jako dospělci. Prodlužování embryonálního vývoje patrně odráží narůstající kompetiční tlaky u demersálních organismů a postupnou radiaci predátorů. Tento makroevoluční trend podstatně ovlivňuje i disperzi nautiloidů: vajíčka jsou déle vystavena prostředí/predátorům a jejich počet je menší. Proto je geografické rozšíření spodnopaleozoických nautiloidů výrazně větší než u mladších nautilidů. Kápovitý tvar schránky ovlivňuje i schopnost změny tvaru schránky během následného růstu. Otisky radiálních struktur na apexu silurských nautiloidů řádů Onkocerida a Discosorida dokládající ranou segmentaci těla známou i u *Nautila*. Tyto řády náleží bazálním kladům nautiloidů: serialita svalů a hlavový komplex vyplňovaly jen část ústí. U řádu Tarphycerida (od kterého se odštěpili nautilidi) je embryonální komora bez radiálních struktur, svaly jsou redukované na pár retraktorů jako u *Nautila*, ale vajíčka byla menší a embryonální vývoj kratší. Vylíhlí jedinci byli u pokročilých tarphyceridů (předků nautilidů) planktonní.

Evoluce hlavonožců v paleozoiku byla tedy komplexnější, než se předpokládalo. Prodlužování embryonálního vývoje, omezování obývaného areálu a pokles morfologické plasticity byl patrně způsoben narůstajícími kompetičními tlaky u demersálních organismů a radiací moderních predátorů.

6. PODĚKOVÁNÍ

Závěrem bych rád poděkoval své rodině, která mě navzdory svému přesvědčení, že studovat tak dlouho něco tak ekonomicky neperspektivního a zbytečného, jako je paleobiologie, hraničí s blbostí, soustavně podporovala. Za velkou část toho, co vím, vděčím Jiřímu Křížovi, kterému tímto coby nehodný žák srdečně děkuji. Za svědomité vedení své disertace děkuji Jiřímu Frýdovi, k němuž jsem nastoupil jako první student-průkopník, nedbaje rizika, a který mě zasvětil i do tajemství „managementu" výzkumu a trpělivě snášel můj odpor završit tuto tezi. Dále bych rád poděkoval spoluautorům publikací, které jsou součástí této teze, na prvním místě Vojtěchu Turkovi, který odolával mým drastickým pracovním metodám s trpělivostí hodnou pravého křesťana a nezištně poskytoval rady i studijní materiál, dále Petru Štorchovi, Ladislavu Slavíkovi a Petru Budilovi. Dík patří i recenzentům těchto publikací, zejména D. H. Evansovi, který trpělivě opravoval mé zločiny na anglickém jazyku, dále Ch. Klugovi, B. Krögerovi, M. Calnerovi, H. P. Schönlaubovi, J. Dzikovi, A. Balinskému, K. Histonové, D. Loydellovi, M. Melchinovi a M. Gnolimu. Za lekci vědecké práce a mezinárodní kooperace děkuji německým kolegům O. Lehnertovi, A. Munneckemu a A. Nützelovi. Dík patří i kolegům R. Lojkovi a Z. Tasáryové, kteří s porozuměním naslouchali mému spílání na některé z výše uvedených.

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Příloha 1

Publikovaná práce

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Environmental and biotic changes in subtropical isolated carbonate platforms during the Late Silurian Kozlowskii Event, Prague Basin

ŠTĚPÁN MANDA[1] and JIŘÍ KŘÍŽ[1]

Manda, Š. & Kříž, J., 2006: Environmental and biotic changes in subtropical isolated carbonate platforms during the Late Silurian Kozlowskii Event, Prague Basin. *GFF*, Vol. 128 (Pt. 2, June), pp. 161–168. Stockholm. ISSN 1103-5897.

Abstract: The Kozlowskii Event extinction in the Prague Basin is not prominent in number of extinct taxa among Ludfordian extinctions, but by its short duration and changes in community structure in both nektonic, pelagic and benthic faunas of different depth zones. The number of taxa going extinct is relatively low because some sensitive benthic and nectobenthic organisms (e.g., trilobites, cephalopods, gastropods, brachiopods) disappeared already at the base of the *Neocucullograptus kozlowskii* Zone contemporaneous with the beginning of a sea level highstand. The Kozlowskii Event includes two phases of extinction coinciding with two erosional sequence boundaries. The event also coincides with climatic changes and alterations of the ocean current regime. Sedimentary facies indicate that the first phase of extinction in the upper *N. kozlowskii* Zone took place during a sea level highstand situation. A lowstand with associated reduction in current activity occurred during the second phase of extinction in the lowermost *Pseudomonoclimacis latilobus* Zone. Recovery was completed in the upper *P. latilobus* Zone. The Kozlowskii Event is in the Prague Basin is accompanied by an abrupt change of benthic and pelagic communities and by immigrations from Baltica, Avalonia and Laurentia. The initial δ^{13}C excursion correlates in the Prague Basin with the uppermost *N. kozlowskii* Zone after the last appearance datum of the conodont *Polygnathoides siluricus*.

Keywords: Prague Basin, Kozlowskii Event, environment, biotic changes, communities, biostratigraphy, oceanic circulation, faunal immigrations.

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Introduction

The early Palaeozoic Prague Basin (Fig. 1) represents a rift type basin located at the northern margin of peri-Gondwana on the Perunica Microplate, which during the Silurian drifted across the south subtropical zone (Kříž et al. 2003). The first shallow-water limestone facies in the basin formed on Wenlock volcanic elevations and reflect warming and increased ventilation of the ocean after the widespread anoxia in Llandovery (Kříž 1991). Thereafter, from the early Ludfordian (Ludlow) to the early Přídolí, substantial carbonate sedimentation took place on structural highs of the sea bottom. These highs were produced by previous volcanic activity in the volcanic centres (Fig. 1) or by the rising of smaller individual basin subsegments along the deep synsedimentary faults in the Central Segment of the Prague Basin and in the adjoining Western Segment (Figs. 1–3). The resulting isolated carbonate platforms represent a unique carbonate system with various and abundant shell beds. The main slope facies are brachiopod or crinoidal grainstones, platy grainstones and packstones rich in benthos, cephalopod limestones enriched with benthos, cephalopod mudstones and wackestones, shales including mudstones with some discrete skeletal accumulations (allodapic limestones), and hemipelagic shales. The prominent Ludfordian change in facies and fauna occurs in the Prague Basin just before the last appearance datum (LAD) of the graptolite *Neocucullograptus kozlowskii* and in the *Pseudomonoclimacis latilobus* graptolite Zone and coincides with the Kozlowskii Event (Kříž 1991). In the Prague Basin, this change has been known for a long time as the boundary between the trilobite horizon with *Cromus beaumonti* and *Ananaspis fecunda*, recognised first by Jahn (1902) and studied in detail by Horný (1955).

The extinctions during the Kozlowskii Event, following the Ludfordian *N. kozlowskii* Zone, eliminated both conservative graptolite taxa (*Bohemograptus*) and highly specialized taxa (*Neocucullograptus, Neolobograptus* and *Polonograptus*) and have been recognised by Urbanek (1993) and by Koren (1993) who named it the Podoliensis extinction event. The term Kozlowskii Event has been widely accepted and determined in several shale sequences globally (see Štorch 1995a, 1995b; Melchin et al. 1998). Contemporaneous faunal changes in the shallow-water shelf settings have been described from a number of European locations. For example, Schönlaub (1986) distinguished the Cardiola Event in the Carnic Alps. Talent et al. (1993) proposed the name Pentamerid Event for the same event.

Jeppsson (1990) in his model of Silurian ocean regimes expressed oceanic cycles as changes between more humid low latitude and cooler high latitude climates (primo episodes), and

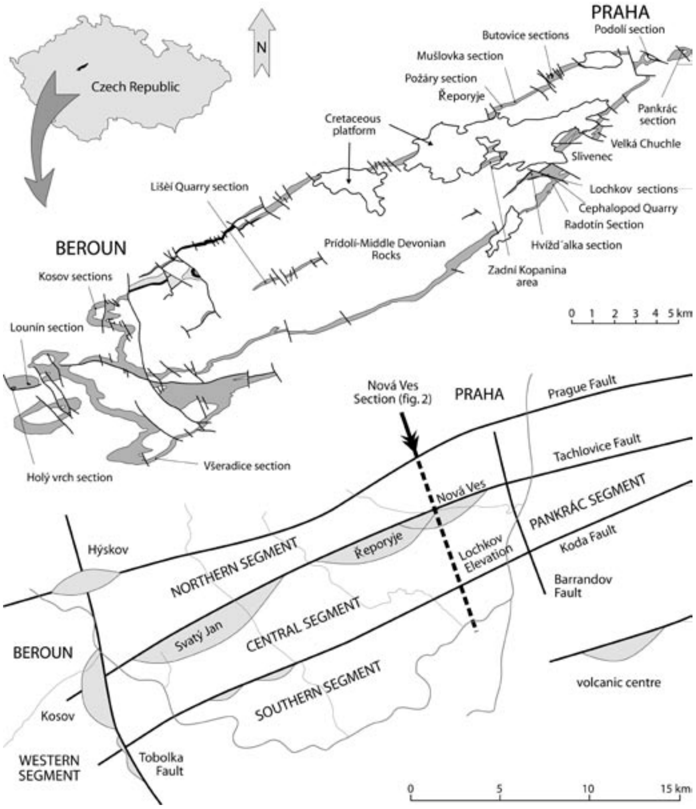

Fig. 1. Distribution of Silurian rocks in the Prague Basin including the position of studied sections and Silurian synsedimentary tectonics, volcanic and tectonic elevations, and segments (sub-basins) in the preserved parts of the Prague Basin (after Kříž 1991). Arrow indicates the Nová Ves section.

drier low latitude and warmer high latitude climates (secundo episodes) that caused also changes in water temperature, content of dissolved gases, character of sedimentation and nutrient supply. P–S transitions are associated with extinctions. At the end of the Ludfordian *Polygnathoides siluricus* Zone, Jeppsson (1993) defined the Lau Primo-Secundo Event on Gotland, Sweden. Jeppsson & Aldridge (2000) draw the beginning of the event slightly before the LAD of the conodont *P. siluricus*. On Gotland, the event is synchronous with an increase in δ^{13}C values (Samtleben et al. 2000). This interval marks the top of the *P. siluricus* Zone and comprises five steps of extinction in conodonts, graptolites, chitinozoans, and fishes. The earliest occurs within the *Dayia* flags in the uppermost Hemse Group and coincides with the initial increase of δ^{13}C. The second phase of extinction, located within the uppermost part of the *Dayia* flags, is associated with the LAD of *P. siluricus* (Samtleben et al. 2000). According to Calner (2005) the strata deposited during and shortly after the Lau Event in the Baltic Basin represent an anachronistic period characterized by a substantial increase of microbially mediated facies in the Eke and Burgsvik formations comparable to those in the aftermath of the end-Ordovician and end-Permian mass extinctions. He suggested that this anomalous period may be identified elsewhere by the positive carbon isotope excursion and the LAD of *P. siluricus*.

In the Prague Basin the LAD of *P. siluricus* occurs below the LAD of *N. kozlowskii* and the taxon has been recorded in the Marble Quarry and Mušlovka sections by Schönlaub *in* Kříž et al. (1986), below the top of cephalopod limestone yielding the *Cardiola alata* Community, and correlated with shale of the *N. kozlowskii* Zone by Kříž (1998). Lehnert et al. (2003) detected the initial δ^{13}C peak in limestone of the uppermost *N. kozlowskii* Zone exposed in the Mušlovka Section at level no. 16, together with *Dayia minor* and *Metaplasia hemicona*, above the LAD of *P. siluricus* (Kříž & Schönlaub 1980).

We conclude that the Lau Event on Gotland started earlier than the Kozlowskii Event in Bohemia. Jeppsson & Aldridge (2000) draw the beginning of the Lau Event slightly before the LAD of *P. siluricus*. According to Urbanek (1993) Kozlowskii Event started after the LAD of *N. kozlowskii,* later than the LAD of *P. siluricus* in Bohemia.

The Ludfordian of the Prague Basin

The Ludfordian carbonate facies of the Prague Basin reflect changes in tectonics, eustasy and climate. There are principal differences between former volcanic centres (Fig. 1) with thick and rapidly changing sedimentary successions and tectonic elevations between synsedimentary faults (Fig. 1) with successions dominated by cephalopod limestone (Fig. 3). Relative water depths have been inferred from facies and biotic changes (Fig. 2).

Synsedimentary tectonic movements affected sedimentation in the Prague Basin and this sensitive system reflects depth changes of each order. Changes in facies across sub-segments of the basin are considered not to represent local controls. The presented sea level curve (Fig. 2) differs from that published by Johnson et al. (1998) in showing an additional lowstand in the *N. inexpectatus* Zone, separating two highstands in the *B. bohemicus tenuis* and *N. kozlowskii* zones, respectively. The Ludfordian of the Prague Basin is below subdivided into nine sequences termed L1–L9 (Figs. 2, 3). Prominent erosional surfaces are developed on the bases of the L6, L7, and L8 sequences.

The lower Saetograptus linearis *Zone sequence (L1)*

This sequence represents a shallowing-up succession of tuffitic shale and limestone formed on volcanic centres and contains rich communities of brachiopods and trilobites. On the tectonic elevations shales and wackestones with *Bleshidium* were deposited (Kříž 1992; Manda 2003). Some new taxa appear in the early Ludfordian (brachiopods, index graptolite). Minor extinctions of e.g., brachiopods, cephalopods, and gastropods are recorded in the uppermost part of the sequence (Fig. 2).

The upper S. linearis *Zone sequence (L2)*

The L2 sequence is characterised by an expansion of carbonate sedimentation, activation of sea currents, and a faunal radiation suggesting a lowstand (Figs. 2, 3). Packstone and grainstone with cephalopods, trilobites and brachiopods occur in the central part of the elevations ("*Metacalymene* bank"). Cephalopod limestone occurs on slopes, namely packstone with common brachiopods in shallow and cephalopod wackestone in slightly deeper environments, respectively. The diverse fauna includes locally evolved organisms as well as many immigrants restricted mainly to the shallow-water environment (e.g., the trilobite *Metacalymene* and the cephalopods *Phragmoceras, Protophragmoceras,* and *Ascoceras*).

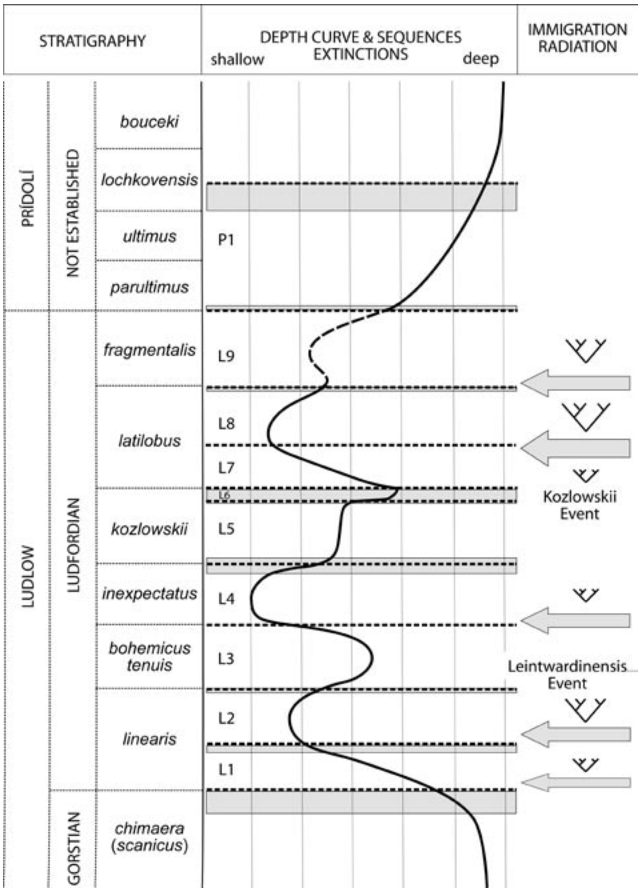

Fig. 2. Ludfordian sequences, extinctions, immigrations, and eustatic curve in the Prague Basin. Facies and communities indicate relative bathymetry of the sea-level curve. Arrows indicate immigrations and diverging lines indicate faunal radiation.

The Bohemograptus bohemicus tenuis *Zone sequence (L3)*

The L3 sequence reflects a deepening during which shales, containing mudstone and cephalopod wackestone, were deposited over the shallow-water limestone formed on the volcanic elevations. On tectonic elevations the cephalopod wackestone with bivalves overlay the cephalopod packstone (Fig. 3). The faunal turnover detected in this sequence is known as the Leintwardinensis Event (Urbanek 1993; Štorch 1995a). Except for graptolites, the extinction particularly affected immigrants appearing in the underlying *S. linearis* Zone (e.g., *Metacalymene, Systrophoceras, Phragmoceras*, *Protophragmoceras*).

The Neocucullograptus inexpectatus *Zone sequence (L4)*

The L4 sequence marks the extension of the brachiopod limestone with *Atrypoidea linguata* over the elevations during shallowing. Brachiopod limestones graded basinward to cephalopod packstone and wackestone and further into cephalopod wackestone and mudstone close to the platform margin (Figs. 2, 3).

The N. kozlowskii *Zone sequence (L5)*

The lower part of the sequence (base of the *N. kozlowskii* Zone) coincides with extinction affecting organisms in shallow-water brachiopod limestones (with the *A. linguata* Community) and the adjacent domain of the cephalopod limestones (that includes e.g., cephalopods, and the trilobite *Cromus beaumonti*). During a sea level highstand in the *N. kozlowskii* Zone, cephalopod limestone and shale rich in benthos extended over the elevations (Kříž 1998).

The uppermost N. kozlowskii *Zone sequence (L6)*

This up to 0.5 m thick sequence consists mainly of mud-rich shell beds with a restricted fauna above an erosional surface. It reflects an additional short-term highstand situation (Figs. 2, 3). The sequence is characterized by the occurrence of the *Cheiopteria glabra* Community (Kříž 1999a).

The lower P. latilobus *Zone sequence (L7)*

The L7 sequence is developed only on the Kosov (Fig. 4) and Svatý Jan elevations (i.e. the former horizon with *Scutellum haidingeri* of Horný 1955) and is represented by platy limestone and shale. A contemporary gap occurs in the eastern part of the Central Segment (Fig. 3; Manda 2003). The *P. latilobus* Zone is used as the zone of partial range between the *Bohemograptus* extinction and the *M. fragmentalis* Zone; the FAD of the index taxon occurs 0.5 m above the extinction of *Bohemograptus*.

The upper P. latilobus *Zone sequence (L8)*

The L8 sequence is a thick unit of shallow-water skeletal limestone and stromatactis mudstone that grade basinward into cephalopod packstone and grainstone that are rich in benthos and were deposited during a lowstand. In most areas, the sequence covers an erosional surface, above which accumulations of trilobites or cephalopods and bivalves occur. Platy limestone reflecting renewed sea level rise overlie massive limestone (Figs. 2, 3). The sequence is correlated with the former horizon with *Ananaspis fecunda* (Horný 1955). Before the end of the sequence much of the characteristic fauna of the *P. latilobus* Zone, especially many trilobites (e.g., *A. fecunda*, *Decoroscutellum heidingeri, Scharyia micropyga, Ryckholtia ryckholti*), brachiopods and cephalopods go extinct (Havlíček & Štorch 1990).

The Monograptus fragmentalis *Zone sequence (L9)*

This sequence corresponds with the expansion of cephalopod limestone over the elevations and basinward (Fig. 3). Brachiopod-cephalopod grainstone were deposited in the most shallow parts of the volcanic elevations. The sequence probably corresponds with a short-term shallowing and subsequent slowly deepening accompanied by current activation (Fig. 2). The base of the sequence approximately correlates with the base of the *M. fragmentalis* Zone (Kříž et al. 1986).

Offshore depositional environments

In the deepest setting in the Western and Southern segments (e.g., Lounín section, Fig. 1) the *N. kozlowskii* and *P. latilobus* zones are characterized by hemipelagic, laminated calcareous shales. Common graptolites, pelagic cephalopods and pelagic ostracod *Entomis migrans* occur prior to the Kozlowskii Event while a restricted graptolite fauna and locally common mazuelloids occurs after. The small-scale carbonate platforms appear within the hemipelagic facies realm during shallowing in the upper *P. latilobus* Zone (Fig. 4). An erosional surface at the base of the L8 sequence is covered with a deepening-up succession of crinoidal grainstones and grades to brachiopod mudstones that terminate just below the base of the Přídolí (L8, max. 8 m thick, Lounín section, Fig. 1). The steep slope deposits of elevations are characterised by slumps of carbonate rock derived from the platform margin (Holý vrch section, Fig. 1) or canalised debris flows with pebbles from the eroded slope (Všeradice section, Fig. 1).

Transitional depositional environment

As the transitional facies we consider strata in areas in which carbonate sedimentation extended basinward close to the Kozlowskii Event.

The Pankrác Segment (Pankrác and Podolí sections)

This part of the basin is characterized by continuous sedimentation of shale from the late Wenlock until the *N. kozlowskii* Zone when mudstone with *Cheopteria glabra* appears (L6, max. 1 m thick). Higher up, the deepening-up succession of cephalopod limestone covers the erosional surface. The following, 0.3 m thick cephalopod limestone (L8 sequence) consists of packstone and grainstone with large shells, bivalves, brachiopods and trilobites, indicative of the *P. latilobus* Zone. The most diverse fauna occurs close the erosive surface in infills of erosional depressions and includes the large bivalve *Dualina excisa*. Mostly pelagic cephalopods and the *C. conformis* Community (Kříž 1999a) of the *M. fragmentalis* Zone characterize the overlaying sequence (L9) of 1 m thick cephalopod wackstone and packstone. The cephalopod limestone terminates with the early Přídolí transgression, only locally thin beds (up to 0.1 m thick) of the cephalopod limestone with *Cardiolinka bohemica* Community (Kříž 1999a) occur at base of the Přídolí.

The Southern Segment (Mořinka and Cephalopod Quarry sections)

Continuous shale exists from the Llandovery up to the Kozlowskii Event in this part of the basin. Some ball slumps including well-sorted remains of shallow-water fauna and a laminated, ca 3 m thick mudstone (L8 sequence) appear within shales in the *P. latilobus* Zone on the lower slope of an elevation (Mořinka section, Fig. 1). In the upper *N. kozlowskii* Zone, close to the Central Segment (Cephalopod Quarry section, Fig. 1, Kříž 1992), a 1 m thick mudstone containing the bivalve *Ch. glabra* Community appear (Kříž 1999a) (L6 sequence). Higher above the erosional surface, a thin deepening-up succession of trilobite grainstone and trilobite-cephalopod wackestone (0.25 m thick) begins. This thin unit yields a fauna of the *P. latilobus* Zone (L8 sequence) and is overlain by a 1.6 m thick cephalopod limestone of the *M. fragmentalis* Zone (L9 sequence) (Fig. 3).

Carbonate platform depositional environments

The Lochkov Elevation (Lochkov sections)

Sedimentation of (maximally 4 m thick) cephalopod wackestone and packstone continued from the *S. linearis* Zone up to the *N. kozlowskii* Zone (L2–5 sequence) when the long-ranging *Cardiola docens* Community (Kříž 1999a) was replaced by the *C. alata* Community (Kříž 1998) (L5 sequence) which have common *Ch. glabra* in its uppermost part (Lochkov sections, Fig. 1). Above the erosional surface, at the base of the L8 sequence, a thin cephalopod limestone terminated with laminated shale-mudstone in the latest Ludlow and earliest Přídolí. The 0.4 m thick rusty cephalopod packstone-grainstone of the *P. latilobus* Zone (L8 sequence) contains common nectobenthic cephalopods, common brachiopods, bivalves (just above erosional surface *Dualina excisa* is common), ostracods, and gastropods. The overlying, maximally 1.5 m thick, cephalopod wackestone of the *M. fragmentalis* Zone (L9 sequence) contains mainly pelagic orthocerids and common bivalves of the *C. conformis* Community (Kříž 1999a).

The Zadní Kopanina area

This area is located close to the basin axis and strata here reflect the transition between the Lochkov Tectonic Elevation and former Řeporyje Volcanic Elevation (Figs. 1, 3). Similarly to the situation in the Lochkov Elevation, a 4.2 m thick cephalopod limestone appears in early Ludfordian and continue up to the *N. kozlowskii* Zone (L2–5 sequences), when a 0.8 m thick mudstone with interbeds of packstone yielding the *Ch. glabra* Community and the restricted *C. alata* Community appear (L6 sequence). Above the erosional surface, at the base of L8 sequence, a 0.3 m thick wackestone unit with accumulations of the trilobite *A. fecunda* (filling depressions on the erosional surface) appear. Higher up in the L8 sequence this is followed by a 3 m thick unit consisting of platy grainstone and packstone with microbial mats (stromatolites) and brachiopods in the *P. latilobus* Zone. Separate beds contain diverse communities dominated by brachiopods; e.g., the: *A. fecunda-Cyrtia postera* Community (Havlíček & Štorch 1990) or local communities characterised by *Atrypoidea modesta, Septatrypa verna* or *Cadudium sphaerulites*. A 0.15 m thick cephalopod packstone and grainstone bed enriched in brachiopods, trilobites and gastropods forms the upper part of the succession. As in the Lochkov Elevation, this bed is overlain by a 1.5 thick cephalopod wackestone of the *M. fragmentalis* Zone (L9 sequence).

Řeporyje Volcanic Elevation (Mušlovka and Požáry sections)

A 2.85 m thick cephalopod packstone, and locally a poorly washed grainstone (enriched in brachiopods and trilobites), with common hardgrounds and erosional surfaces occurs in the *N. kozlowskii* Zone (L5 sequence). The cephalopod limestone is replaced by maximally 0.7 m thick succession of brachiopod limestone in the uppermost *N. kozlowskii* Zone (L6 sequence). Brachiopod

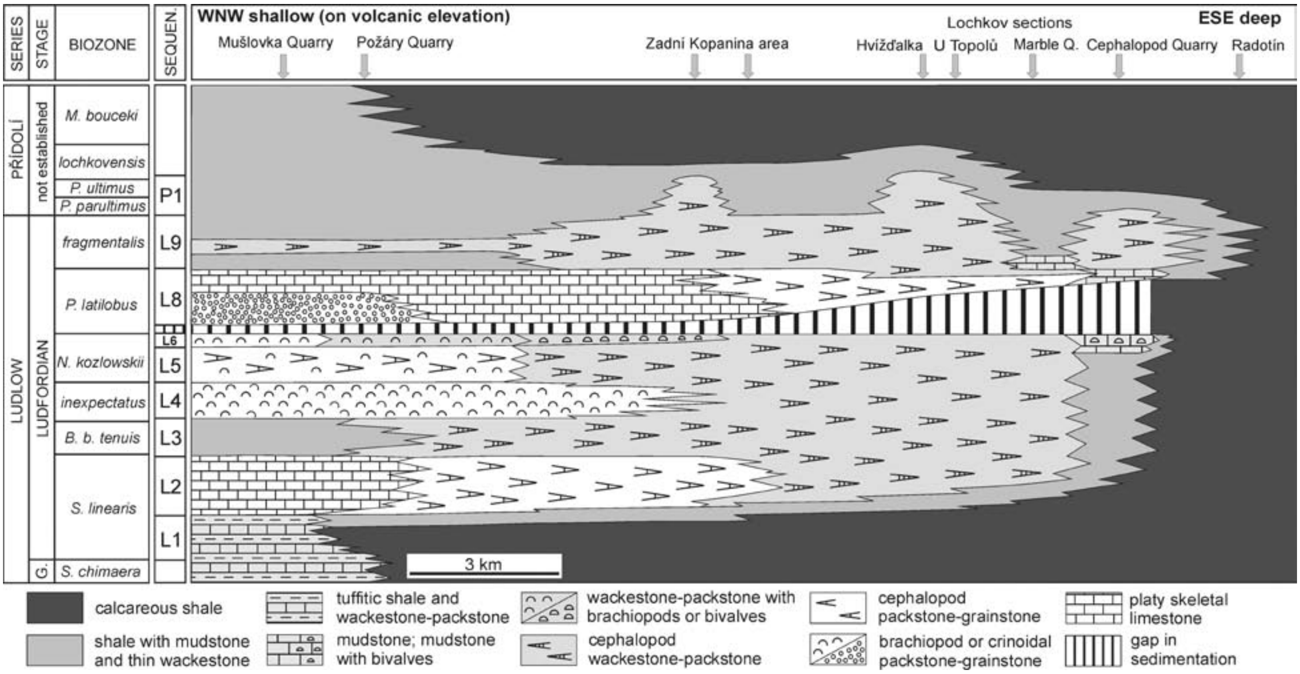

Fig. 3. The facies distribution of the Ludfordian isolated carbonate platform in the eastern part of the Prague Basin in Prague territory (in the Nová Ves section, location shown in Fig. 1).

grainstone with the *D. minor* Community occurs in the Mušlovka section (Figs. 1, 3) on the shallower part of the elevation, above the wave-base, while brachiopod-cephalopod packstone with the *M. hemicona* Community occurs in the Požáry section (Figs. 1, 3) reflecting deeper, and thus less ventilated bottom environments. A 6.6 m thick beds of crinoidal grainstone (L8 sequence) with a diverse fauna reflect very shallow-water sedimentation/accumulation in the *P. latilobus* Zone. Just above the erosional surface the large spiriferid *Cyrtia* (occurs in slightly shallower settings) or the minute strophomenid *Plectodonta moderatrix* (occurs in slightly deeper settings). A well-diversified community of brachiopods, trilobites and crinoids (*A. fecunda-C. postera* Community) occurs in the crinoidal grainstone. The overlaying platy wackestone-packstone facies (maximally 1.5 m thick) reflects deepening in the uppermost *P. latilobus* Zone (L8 sequence) and are terminated by a maximally 5.3 m thick shale-mudstone or cephalopod limestone unit in the latest Ludlow (L9 sequence).

Nová Ves Volcanic Elevation (Butovice sections)

The ca 1.2 m thick cephalopod limestone range from the upper *S. linearis* Zone to the *N. kozlowskii* Zone identified by the presence of the *C. alata* Community (L5 sequence). The cephalopod limestone is overlain by a thin wackestone-packestone unit (L6, max. 0.3 m) with a fauna including the *Ch. glabra*, *M. hemicona* and *C. alata*. The *P. latilobus* Zone started above the erosional surface and is covered by a 0.2 m thick packstone unit (L8 sequence) with accumulations of the trilobite *A. fecunda*. Higher up, a packstone and grainstone unit that never exceeds a thickness of 2 m, and which includes trilobites and brachiopods, reflects maximum shallowing of sea level (L8 sequence). This unit is followed by a 3.8 m thick stromatactis mudstone with slabs of *A. modesta* (L8 sequence) and by a 1.9 m thick platy mudstone (L8 sequence). Cephalopod limestone (0.3 m thick) appears in the uppermost *P. latilobus* Zone (L8 sequence) and continues across the *M. fragmentalis* Zone (L9 sequence) in which it is ca 1.3 m thick. Just below the Ludlow-Přídolí boundary, intercalations of laminated shale and mudstone start (Fig. 3).

Kosov Volcanic Elevation (Kosov sections)

Here the sequence of shale and limestone is 6 m thick and yields trilobites and brachiopods of the *Acanthalomina minuta* Community (L5 sequence). It terminates with the appearance of a maximally 0.25 m thick cephalopod-bivalve wackestone of the *Ch. glabra* Community (L6 sequence) and both correspond to the *N. kozlowskii* Zone (Fig. 4). The *P. latilobus* Zone starts above the erosional surface with a wavy laminated brachiopod limestone bed with a maximum thickness of 0.5 m that yields *Plagiorhyncha thisbe* (L7 sequence). The section continues with a shallowing-up succession of a maximally 6 m thick unit of dark grey mudstone and wackestone intercalated with shale (L7 sequence). The limestone contains a high density and low diversity assemblage with *K. svobodai, S. micropyga* and ostracods. The shale contain diverse communities reflecting a rapidly changing, but restricted environments, e.g. ostracod-dominated community, monospecific community with *M. hemicona* or relatively rich community with *Protoshaleria mucronata* and *Gladiostrophia gladiola*. A platy packstone-grainstone (maximally 8 m thick) with numerous hardgrounds and a rich *A. fecuda-C. postera* Community (including over 55 species) mark a sea level lowstand in the upper *P. latilobus* Zone (L8 sequence).

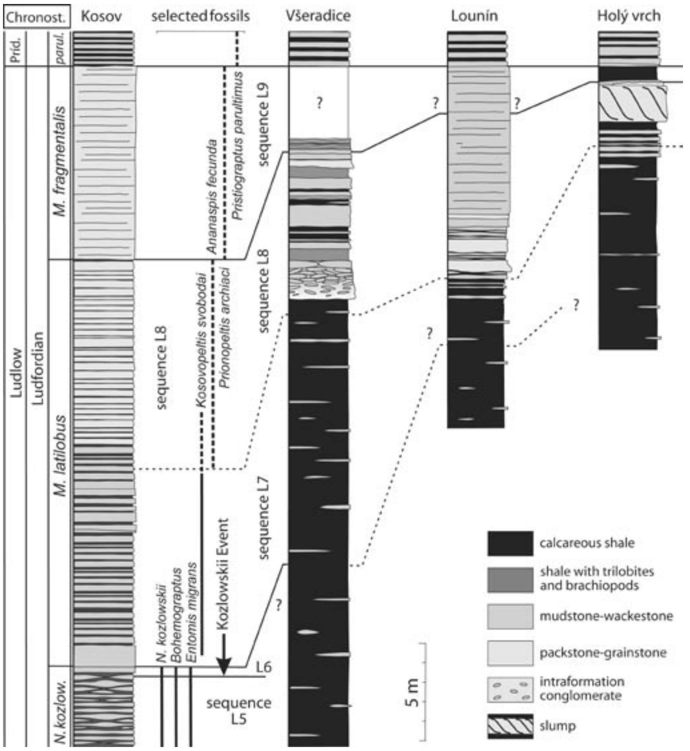

Fig. 4. Selected Ludfordian sections in the Western Segment of the Prague Basin. Kosov section (Kosov Elevation), and sections of the small-scale isolated carbonate platforms within the hemipelagic sedimentation setting (Všeradice, Lounín, and Holý vrch sections).

Slope of Svatý Jan Volcanic Elevation (Liščí Quarry section)

The central part of this elevation was covered by a basalt sheet and was emerged in the latest Wenlock (Kříž 1991). Five meters of thick rusty, fine-grained crinoid-brachiopod grainstone (dolomite) represent the shallow-water sediments of the Ludfordian deposited on the upper part of the slope close to the shoreline. The limestone consists of thin cross-bedded grainstone separated by numerous erosional surfaces and a few hardgrounds. The fauna is represented mainly by *Atrypa*-type brachiopods. Within the limestone succession a prominent hardground with cavities filled by laminated micrite and calcite occurs. Just above the hardground, in mud-rich interbeds, a high diversity and brachiopod dominated community, including mainly atrypids, rhynchonellids and large spiriferid *Cyrtia* occurs, reflecting an *P. latilobus* Zone age.

The sedimentary succession of the distal slope of the Svatý Jan Volcanic Elevation (Liščí Quarry section, Fig. 2) is similar to that of the Kosov Elevation. A ca 4 m thick unit of grainstone with *Atrypoidea* (L4 sequence, *N. inexpectatus* Zone) is covered by a maximally 3 m thick unit of laminated shale and limestone with trilobites and brachiopods of the *Acanthalomina* Community (L5 sequence, *N. kozlowskii* Zone). They are overlain by a 2 m thick succession of shale and mudstone with scolecodonts, which may be correlated with the horizon with *K. svobodai* in the Kosov Elevation (L7 sequence) (Horný 1955). Above the erosional surface (in contrary to continuous sedimentation in Kosov Elevation), 1.5 m thick crinoid-brachiopod grainstone (L8 sequence) continue up to the early Přídolí when shale and mudstone appear.

The Kozlowskii Event

Before we discuss our conclusions concerning the Kozlowskii Event we should point out that we identify and correlate this event within the Prague Basin using graptolites in the shale facies and contemporaneous bivalve communities and cephalopod assemblages in the cephalopod limestones and transitional facies. The correlation with conodonts was established by H. P. Schönlaub (Schönlaub *in* Kříž et al. 1986) in the Marble Quarry section where the top of the *P. siluricus* Zone approximately coincides with the top of the *C. alata* Community (uppermost *N. kozlowskii* Zone).

Conodonts in many regions cannot be used since "uncertainties remain because of the low frequencies of many taxa and gaps in their ranges, and it is therefore currently difficult to identify datum points" (Jeppsson & Aldridge 2000, p. 1144). We are not convinced by the correlation of the *N. kozlowskii* Zone with conodonts (Jeppsson & Aldridge 2000, p. 1144, fig. 1 and Jeppson (2005, p. 127, fig. 2) on Gotland.

The Kozlowskii Event in the Prague Basin is not prominent in terms of numbers of extinct taxa compared to other Ludfordian extinctions, but is noteworthy because of its short duration and changes in community structure in nektonic, pelagic and benthic faunas of each depth zone (Fig. 2). The number of extinct taxa is relatively low because some sensitive benthic and nectobenthic organisms (e.g., trilobites, cephalopods, gastropods, brachiopods) already disappear at the base of the *N. kozlowskii* Zone contemporaneous with the beginning of deepening (Fig. 2). The Kozlowskii Event includes two phases of extinction coinciding with two erosional sequence boundaries, respectively.

The first phase of extinction

The first phase of extinction during the Kozlowskii Event coincides with the base of the L6 sequence in the uppermost *N. kozlowskii* Zone. It affected especially organisms surviving a previous extinction at the base of the *N. kozlowskii* Zone (e.g., *A. linguata, Prionopeltis praecedens* and some cephalopods). During the first extinction phase, the stable communities with *C. alata* in the cephalopod limestone and *A. minuta* in shale are replaced by restricted low diversity communities, namely the *D. minor* Community (upper slope probably above the wave-base), *M. hemicona* Community (mid-slope below the wave-base), the restricted *C. alata* Community (mid-slope below wave-base, temporarily within the reach of surface currents), and the low diversity and high density *Ch. glabra* Community (lower slope, slightly ventilated).

The first phase of extinction is contemporaneous with short-term decrease of current activity, probably related to deepening. On the upper slope of the elevations, restricted communities were affected by a possible temperature increase, whereas in deeper slope environments the cephalopods and bivalves were less affected. This phase in the Prague Basin is contemporaneous with the beginning of the $\delta^{13}C$ increase (Lehnert et al. 2003, in press).

The second phase of extinction

The second and main phase of extinction during the Kozlowskii Event coincides with a sequence boundary in the lowermost *P. latilobus* Zone (base of the L7 sequence). Extinction affected graptolites of the *Bohemograptus* and *Neocucullograptus* stocks (see Štorch 1995a, 1995b) and the long-ranging pelagic ostracode *E. migrans*. Simultaneously, pelagic cephalopods and phylocarids became less abundant. Among benthos the extinction affected especially bivalves, e.g., *C. alata, C. tix, C. ornithopsis, Tenka bohemica* and *Ch. glabra* (Kříž 1999a, 1999b), and trilobites (e.g., *A. minuta, Otarion diffractum* and *Balisoma transiens*). The most severely affected were the nektonic communities of cephalopods, especially nectobenthic forms (e.g., *Phragmoceras beaumonti, Glossoceras gracile, Oonoceras baculoides, Pentameroceras mirum*).

According to Melchin et al. (1998) extinction of pelagic graptolites corresponds to the regressive episode following the *N. kozlowskii* Zone. The data from the Prague Basin confirm this explanation. However, there may be additional reasons for the changes of the ocean surface currents. While the majority of regressive episodes are associated with activation of sea currents and bivalve-cephalopod radiation, the shallowing-up after the Kozlowskii Event in the Prague Basin elevations is connected with a decrease of current activity and increase in temperature. This in turn is reflected by a decrease in the diversity of bivalve and cephalopod dominated communities.

The substantial sedimentary and faunal changes during the Kozlowskii Event are documented within Gondwanan Europe in the Carnic Alps Basin of Austria. In the Wolayer facies, dark shale with limestone interbeds containing current oriented pelagic cephalopods of the Cardiola Formation, including the *C. docens* Community, is replaced by limestone with a restricted *C. alata* Community–*Cardiola pectinata* Subcommunity, corresponding to the uppermost levels of the *N. kozlowskii* Zone (Kříž 1999b). They are overlain by the Alticola Limestones with low diversity pelagic cephalopods and reflecting stable conditions of a pelagic setting (Schönlaub in Kříž et. al. 2003). This environmental change corresponds to a prominent shallowing-up succession in the Carnic Alps Basin just after the Kozlowskii Event (Schönlaub in Kříž et. al. 2003, fig. 27). Just above the Kozlowskii Event tuff and coarse tuffite occur in the North Balkhash region of the Silurian in Kazakhstan (Kazakhstania) indicating a nearby volcanic activity (Nikitin & Bandaletov 1986).

On Gotland, the uppermost part of the Hemse Group, characterized by marls and the *Dayia* flags, is followed by shallow-water carbonates of the Eke Formation. The unconformity between the Hemse Group and Eke Formation (Cherns 1983) corresponds to the shallowing-up succession (Samtleben et al. 2000).

Recovery after the Kozlowskii Event

The process of recovery and change of communities may be seen in strata formed on the lower slope settings of the Kosov Volcanic Elevation (Figs. 1, 4) where the lower *P. latilobus* Zone is locally preserved due to intensive subsidence. The erosional surface on the base of the *P. latilobus* Zone is overlain by a 0.5 m thick bed of limestone with the monospecific community of *P. thisbe*, which reflects restricted and rapidly changing conditions. Brachiopod communities of the *N. kozlowskii* Zone re-appear shortly after the Kozlowskii Event (except smooth atrypids). Above the bed with *P. thisbe* other brachiopods, forming different monospecific communities, appear successively (*M. hemicona, P. mucronata, G. gladiola*). In the shale layers brachiopod dominated communities occur while in the limestone interbeds low diversity and high density trilobite assemblage with scutelid *Kosovopeltis* (burrowing) and the minute proetid *Scharya* (pelagic?) occurs. In contrast to the brachiopod fauna, the trilobite assemblages strongly differ from that before the Kozlowskii Event where the trilobite assemblage with the proetid *Otarion* (epibenthic) and odontopleurid *Acanthalomina* (pelagic?) was restricted to the shale.

Shallowing connected with better ventilation of the bottom probably by wave or weak currents caused the change in communities in the lower *P. latilobus* Zone. The interbeds of limestone, containing a specific assemblage of trilobites, show periodic and rapid sedimentation of unconsolidated carbonate mud derived from more shallow areas.

In other parts of the basin (except Kosov and Svatý Jan elevations) a gap in sedimentation occurs during the lower *P. latilobus* Zone (Fig. 3).

Upper P. latilobus Zone radiation

The rapid, but successive radiation can be seen in the Kosov Elevation (Figs. 1, 4) where shales and mudstones and wackestones yielding restricted communities are replaced by packstones and grainstones. These shallow-water limestones contain a rich *A. fecunda-C. postera* Community including 48 species of brachiopods (Havlíček & Štorch 1990), trilobites (over 15 species), gastropods, rugose corals, and 13 species of crinoids (Prokop 2001). These communities colonised frequent hardgrounds and firmgrounds.

Just above the erosional surface at the base of L8, in the eastern part of the Central and Pankrác segments, accumulations of relatively large organisms such as the trilobite *A. fecunda*, the bivalve *D. excisa* or the spiriferid brachiopod *Cyrtia* occur. Further above the sequence boundary a deepening-up succession starts containing diverse and already well-structured communities.

The shallow-water rich benthic communities of the upper *P. latilobus* Zone contain a few taxa surviving from the *N. kozlowskii* Zone (namely pelagic orthocerids, pristiograptid graptolites, the ostracod *Cryptophyllus*, the crinoid *Pisocrinus pilula,* and the brachiopods *P. mucronata* and *Joniomya flexa*) or the lower *P. latilobus* Zone (some trilobites, brachiopods and ostracods). A distinct part of the fauna in the upper *P. latilobus* Zone is represented by local taxa rapidly evolved during recovery. Most of these stocks locally disappear before the Kozlowskii Event. Their ancestors occur rarely below the LAD of *N. kozlowskii* (e.g., *A. linguata, O. diffractum*). In the cephalopod limestone facies a restricted *C. conformis* Community occurs. The bivalves in this community evolved from the ancestors occurring before the Kozlowskii Event and the community became more diversified in the *M. fragmentalis* Zone.

The fauna after the recovery was strongly enriched by immigrants. Brachiopods, trilobites and cephalopods document the radiation of these exotic immigrants from the Laurentian, Avalonian and Baltic areas. In the upper *P. latilobus* Zone, 24 species of trilobites occur. Most of them occur in the Prague Basin for the first time, including the most characteristic trilobite *A. fecunda*. The genus *Ananaspis* is known from the Wenlock and Ludlow of Avalonia and Laurentia. Similarly to trilobites, the cephalopod faunas were strongly enriched by immigrants (four species of nautiloids in the *N. kozlowskii* Zone versus over twenty species in the upper *P. latilobus* Zone). While cephalopod immigrants from Baltica and Avalonia were common from the Wenlock (Manda 2004) the immigrants from Laurentia started to appear in the late Ludfordian. In addition, two crinoid immigrants from Laurentia (*Lampterocrinus*) and Baltica (*Lecanocrinus facietatus*) are known (Prokop 2001). The immigrants to the Prague Basin from Avalonia, Baltica and Laurentia after the Kozlowskii Event document large-scale change in ocean circulation.

The radiation of fauna in the upper *P. latilobus* Zone reflects widespread favourable conditions for benthic organisms during sea level lowstand (Fig. 2). The well-diversified communities on the elevations were dominated by brachiopods, trilobites and crinoids and reflect stable ventilation of the bottom by surface currents or by wave action. During the *P. latilobus* Zone crinoidal grainstones replaced the brachiopod grainstones with *Atrypoidea*. The depositional areas of the cephalopod limestone facies was strongly reduced during the lowstand, and became unusually enriched by benthic taxa (trilobites, brachiopods, corals, gastropods) while bivalves were reduced in diversity. All these changes are interpreted to reflect short-term warming as well as a low current activity episode in the upper *P. latilobus* Zone.

Conclusions

The short duration of the Kozlowskii Event is prominent among Ludfordian extinction events (Fig. 2). The extinctions during the Kozlowskii Event took place in two phases, in the uppermost *N. kozlowskii* and lowermost *P. latilobus* zones, respectively. The event affected the pelagic as well as the benthic fauna (especially ostracods, graptolites, bivalves and cephalopods) at several different depths in the marine environment. The faunal turnover during the event is thus connected with rapid eustatic oscillations and climatic changes. Prior to the Kozlowskii Event the widely distributed *C. alata* Community and low diversity cephalopod fauna reflect stable, but cooler surface currents ventilating the elevations in the *N. kozlowskii* Zone. The succeeding distinctive facies of the subsequent *P. latilobus* Zone reflect a warmer episode, change in circulation pattern and immigration of new fauna. The lowstand and warming episode during the Kozlowskii Event (after the LAD of *N. kozlowskii*) in the Prague Basin has also been detected on Gotland, in the uppermost part of the Hemse Group (characterized by marls and *Dayia* flags) and the overlying Eke Formation (shallow-water carbonates) (Samtleben et al. 2000).

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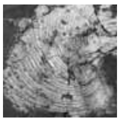
PŘÍLOHA 2

Publikovaná práce

Manda, Š. 2007. New Silurian nautiloids Phragmoceras Broderip, 1839 and Tubiferoceras Hedström, 1917 from the Prague Basin (Bohemia). Bulletin of Geosiences 82, 119–131.

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.

MANDA, Š. 2007. New Silurian nautiloids *Phragmoceras* Broderip, 1839, and *Tubiferoceras* Hedström, 1917, from the Prague Basin (Bohemia). *Bulletin of Geosciences 82(2)*, 119–131 (9 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received May 14, 2007; accepted in revised form June 15, 2007; issued June 30, 2007. • DOI 10.3140/bull.geosci.2007.02.119

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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

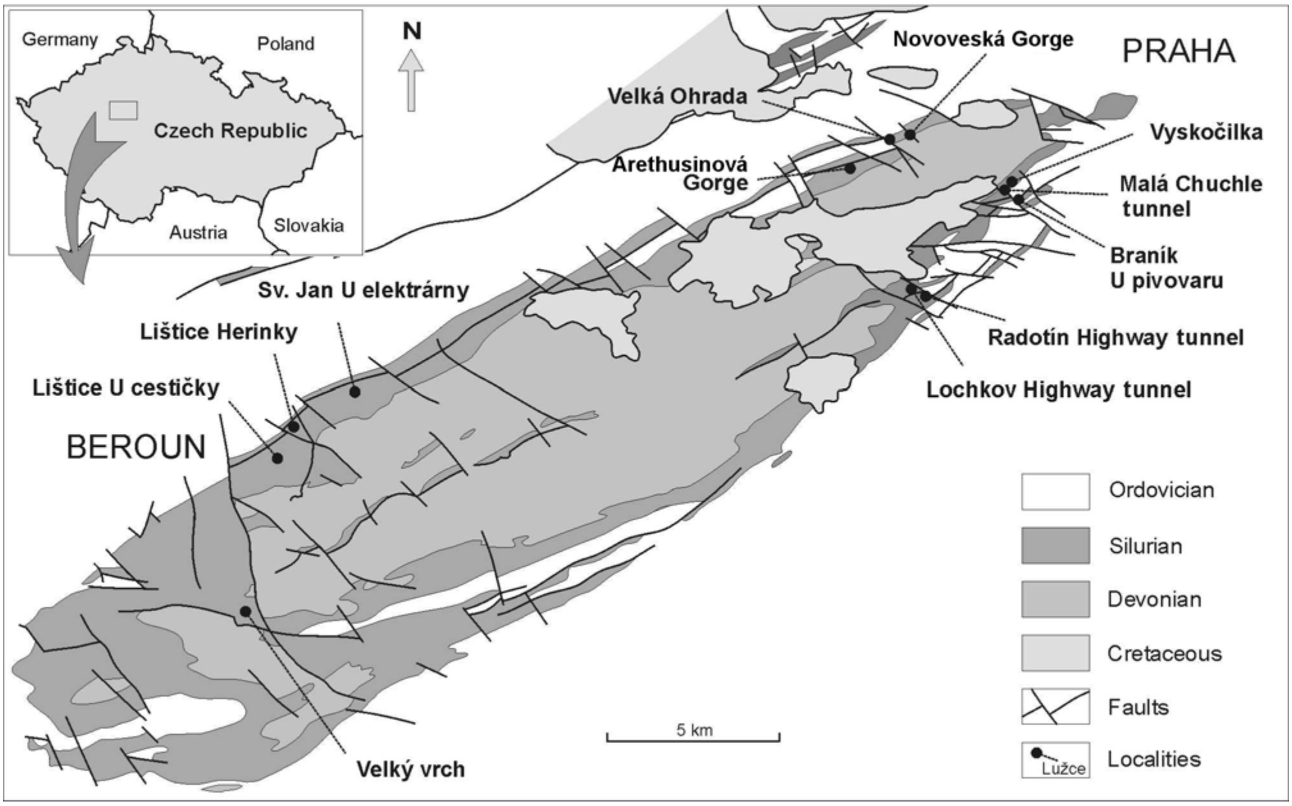

Figure 1. Distribution of Silurian rocks in the Prague Basin and position of the mentioned sections.

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.

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.

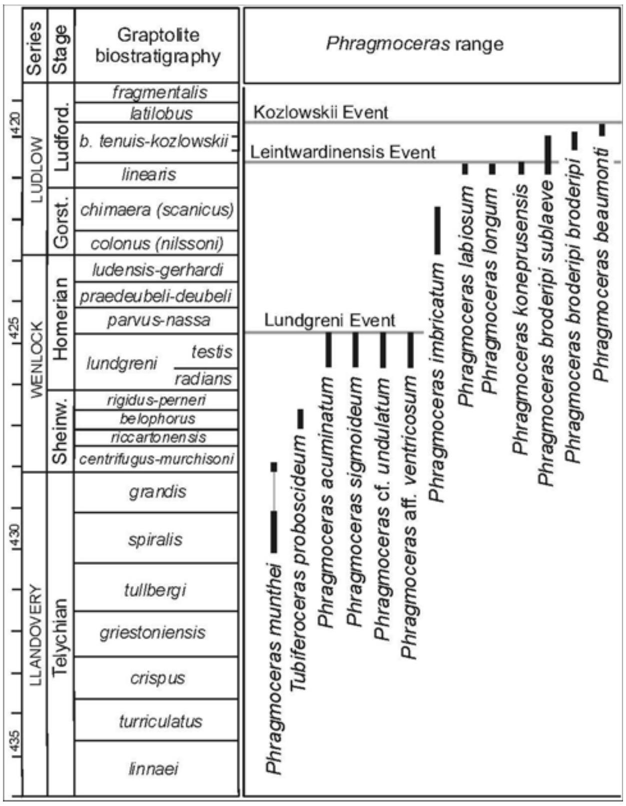

Figure 2. Range of phragmocerids in the Silurian of the Prague Basin. Graptolite biostratigraphy adopted from Kříž (1991), Manda & Kříž (2006), Štorch (2006).

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

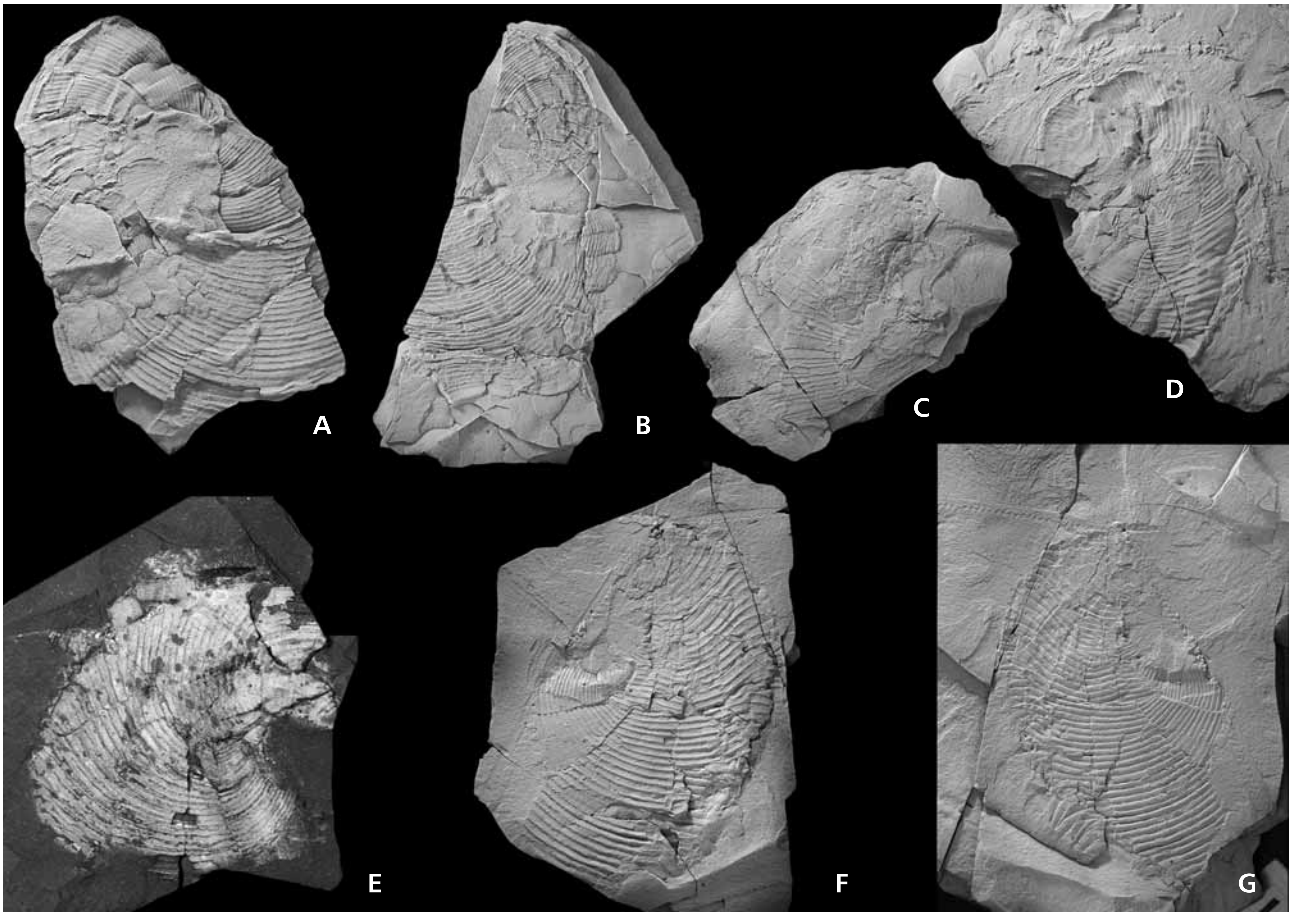

Figure 3. *Phragmoceras munthei* Hedström, 1917, from the latest Llandovery and earlier Wenlock of the Prague Basin, all specimens come from the Motol Formation. • A, B – lateral views, part and counterpart, specimen SM 82a, b; Nová Ves Section; Llandovery, Telychian, *O. spiralis* Zone. • C – lateral 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).

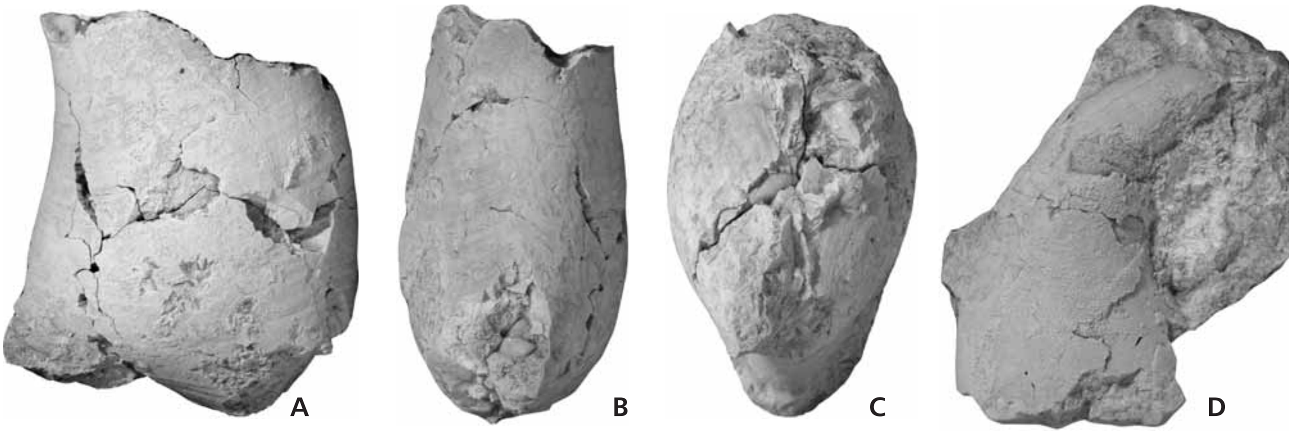

Figure 4. *Phragmoceras acuminatum* Hedström, 1917; Lištice, Herinky Hill, Barrande's pit; Wenlock, Homerian, *C. lundgreni* Zone, *T. testis* Subzone; Motol Formation; A–C (SM 58), D (SM 91). • A – lateral view. • B – ventral view. • C – apertural view. × 1. • D – lateral view; × 1.

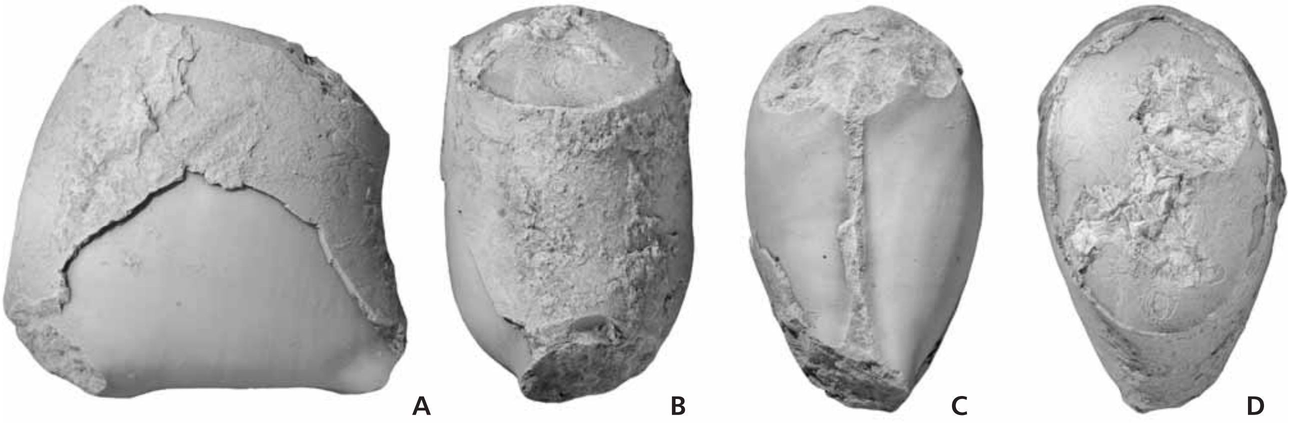

Figure 5. *Phragmoceras sigmoideum* Hedström, 1917; Malá Chuchle, Vyskočilka; Wenlock, Homerian, *C. lundgreni* Zone, latest *T. testis* Subzone; Motol Formation; L 38727. • A – lateral view. • B – ventral view. • C – apertural view. • D – cross section of the body chamber. × 1.4.

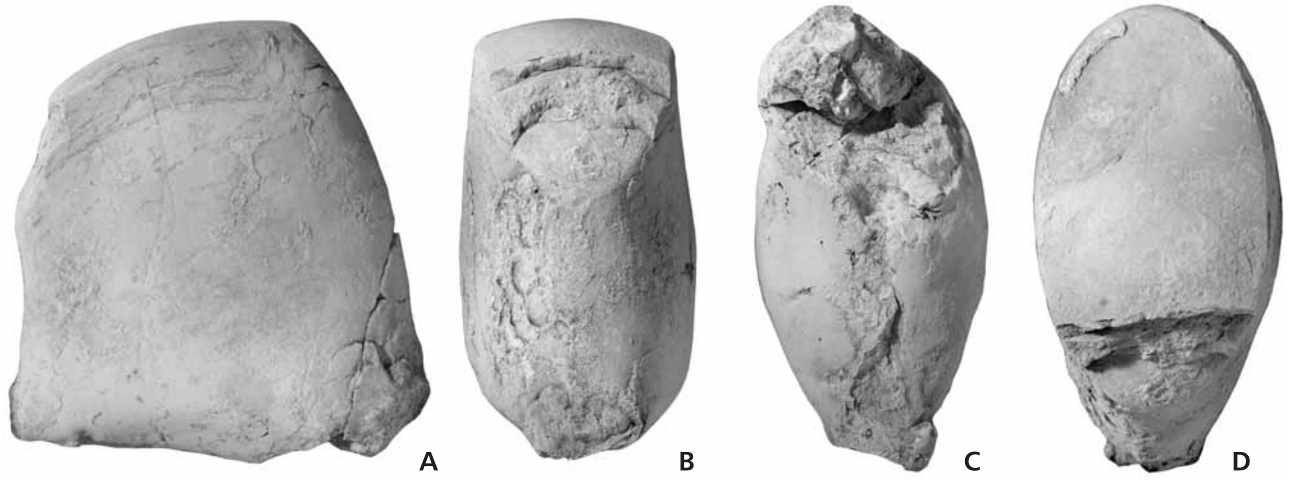

Figure 6. *Phragmoceras* cf. *undulatum* Hedström, 1917; Lištice, exact site unknown; Wenlock, Homerian, *C. lundgreni* Zone, *T. testis* Subzone; L 38729. • A – lateral view. • B – ventral view. • C – apertural view. • D – cross section of the body chamber. × 1.2.

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-

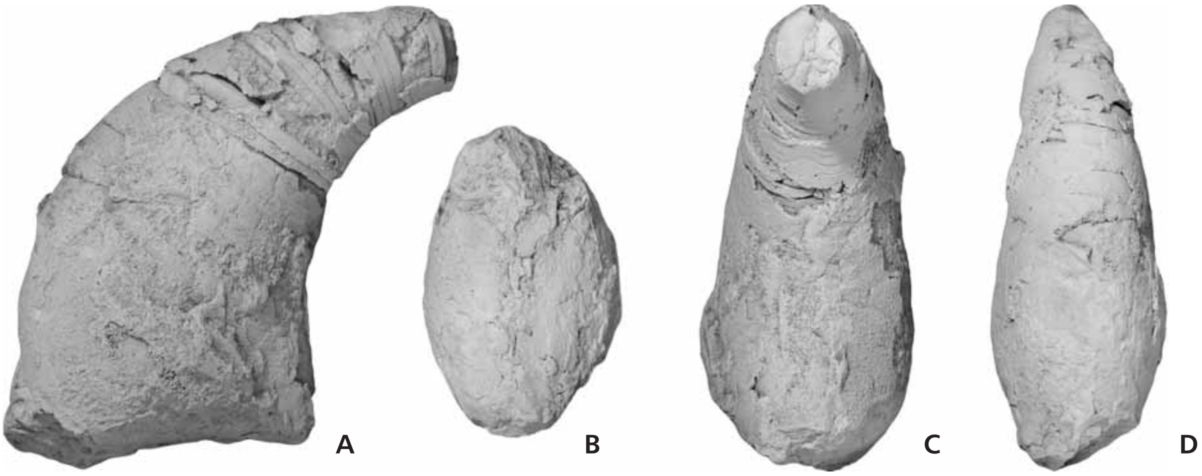

Figure 8. *Phragmoceras koneprusensis* sp. nov.; Koněprusy, Velký vrch Hill; Ludlow, Ludfordian, upper *S. linearis* Zone; SM 75. • A – lateral view. • B – apertural view. • C – ventral view. • D – dorsal view. × 0.7.

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).

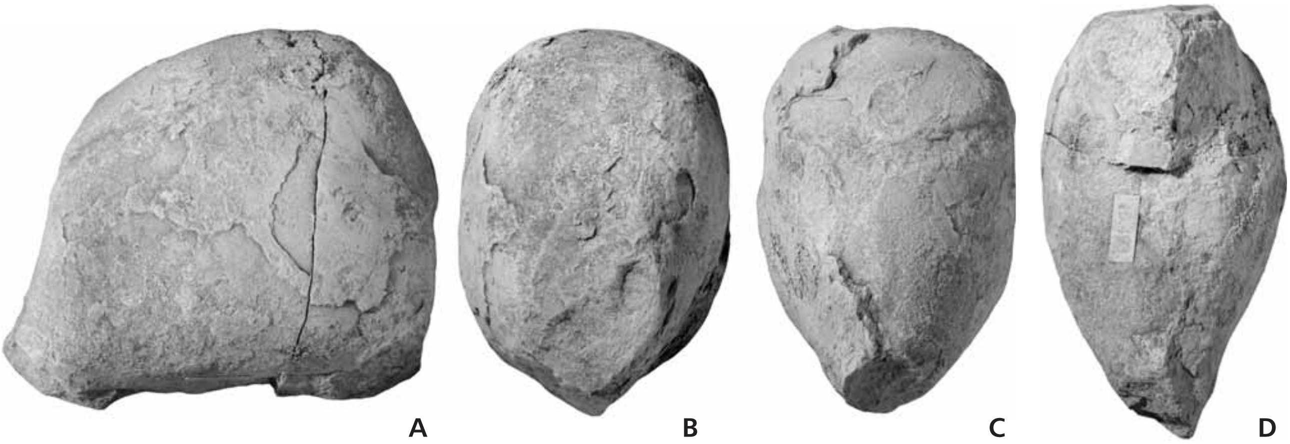

Figure 9. *Tubiferoceras proboscoideum* (Hedström, 1917); Svatý Jan pod Skalou, U Elektrárny Section; Wenlock, Sheinwoodian, *M. belophorus* Zone; FNS 15.493. • A – lateral view. • B – dorsal view. • C – ventral view. • D – apertural view. × 1.6.

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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PŘÍLOHA 3

Publikovaná práce

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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 Armoricano 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 developed at 14 stratigraphical levels and characterized by the Bivalvia dominated benthic communities (Ferretti, 1988; Kříž, 1991, 1998; Kříž 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, Kříž, 1991), see Fig. 1.

Fauna of the Silurian cephalopod limestone biofacies contains mainly bivalves and cephalopods adapted to this biofacies (Kříž, 1984, Kříž, 1999a). Progressive changes

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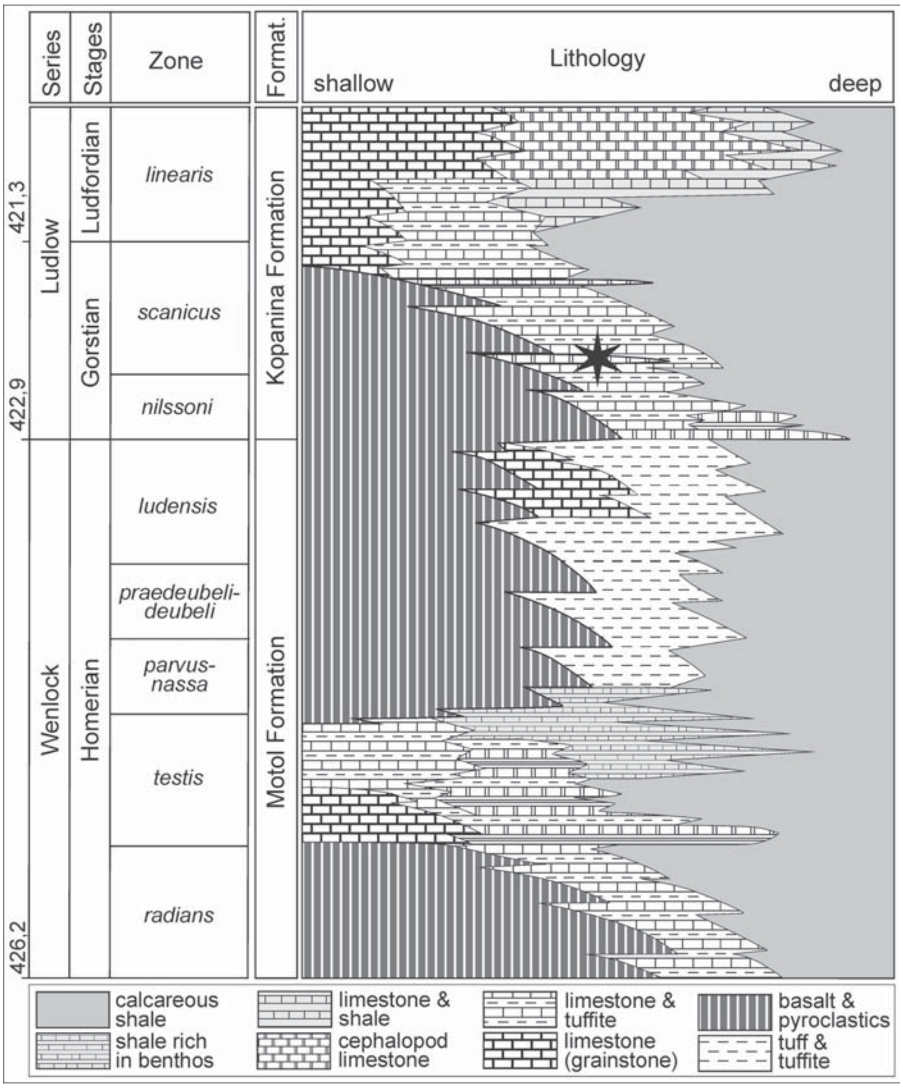

Fig. 1 - Homerian, Gorstian and early Ludfordian stratigraphy and lithostratigraphy of the Prague Basin (after Kříž, 1991, modified). Asterisk shows position of the studied section. Timescale after Gradstein et al. (2004).

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. Wyskočilka 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 Wyskočilka 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 Barrande´s Rock (Bouček 1941; Kříž, 1999d; Frýda & Manda, 1997). The early Lochkovian bivalves were marked Wyskočilka 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 bohemica*, and *Manulicula manulia*.

The section continues by 150 cm thick grey-green hyaloclastite (bed no. 1) overlain by 10-25 cm thick compact, grey finely laminated calcareous shale (bed no.

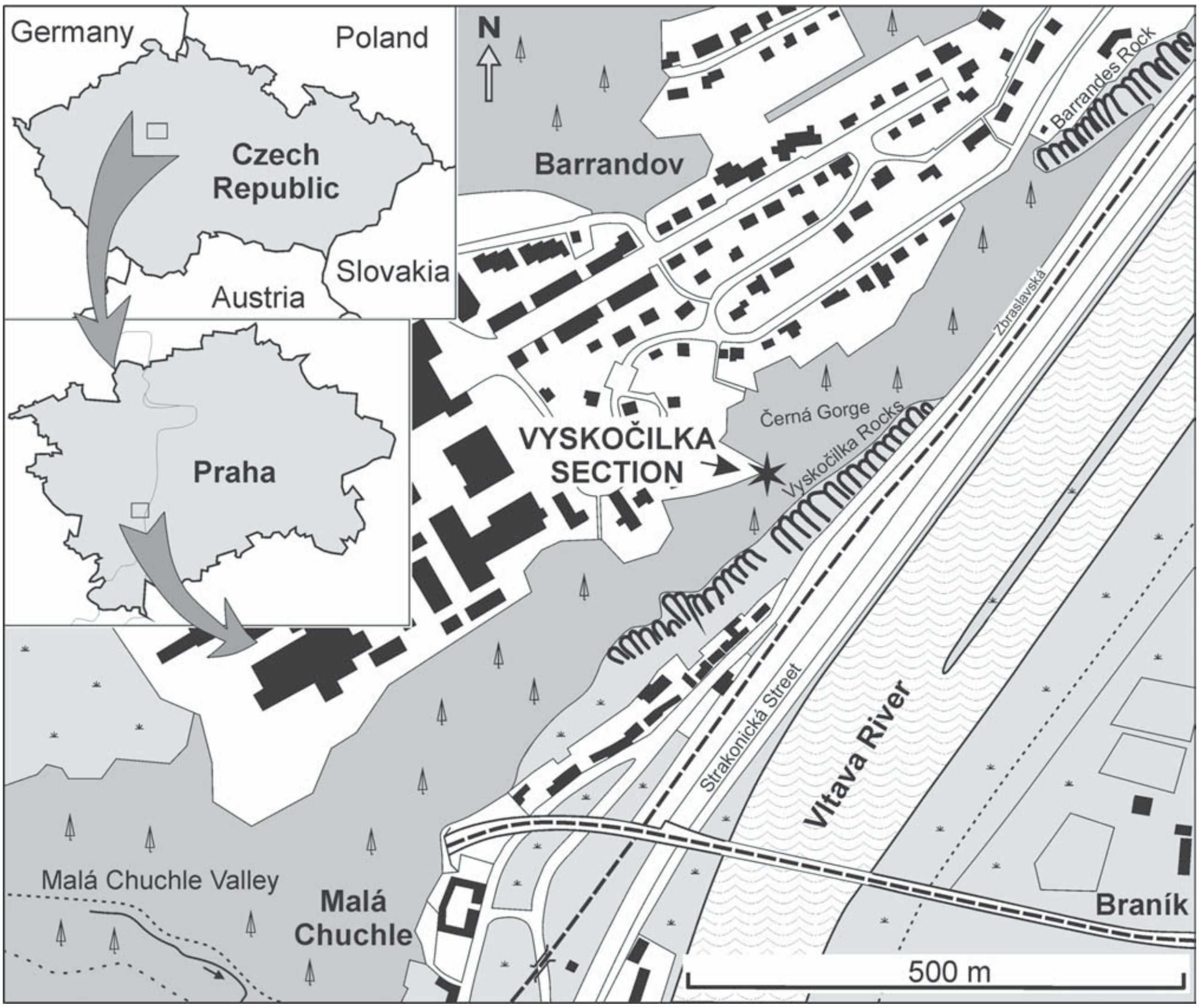

Fig. 2 - Position of the Vyskočilka Section.

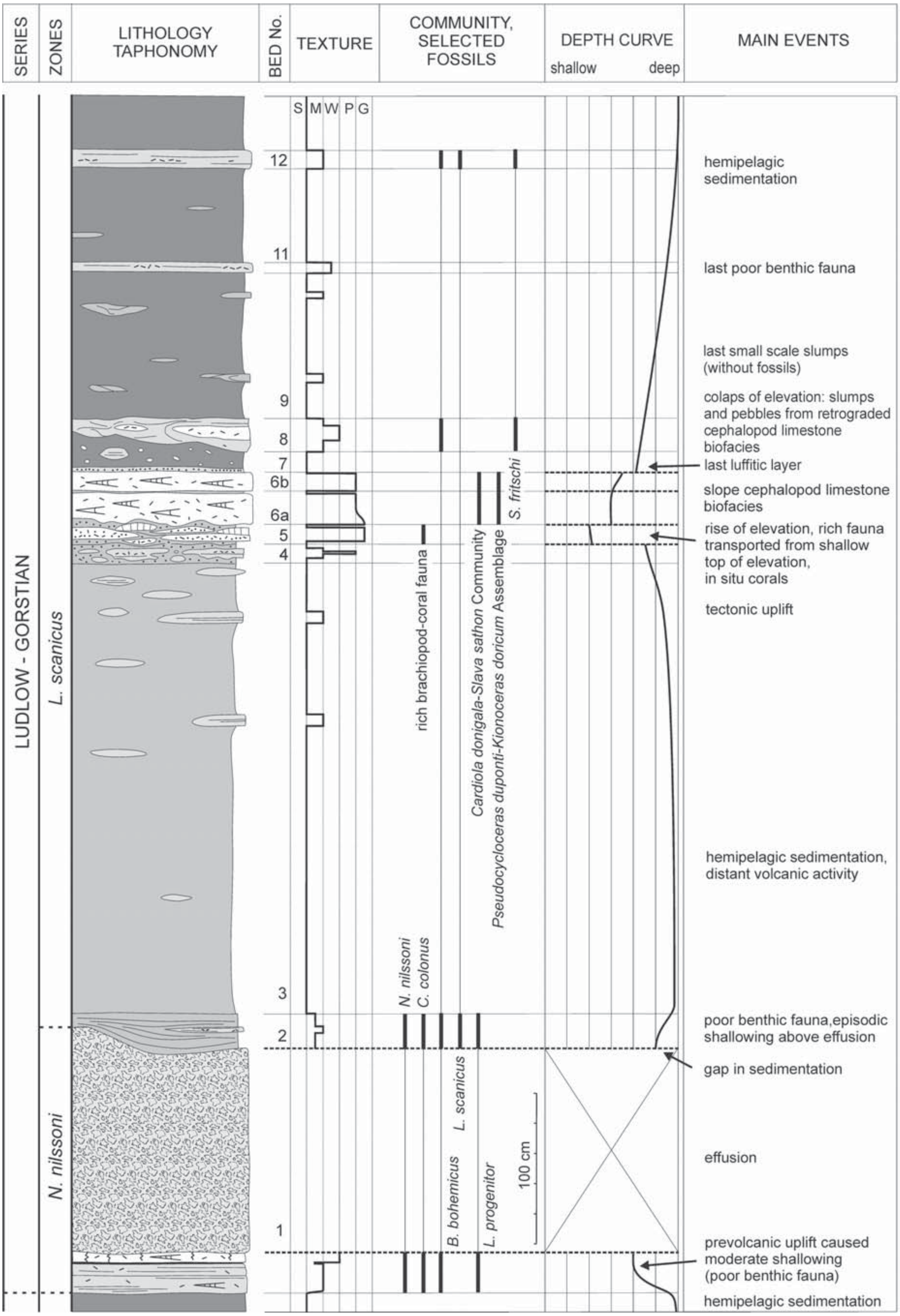

Fig. 3 - Vyskočilka Section showing lithologies, ranges of selected fossils, bivalve community, cephalopod assemblage and summary of main depositional events in the measured section. The colours used for lithology expression are stepped from white for limestone to dark grey for calcareous shale. Simple 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.

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, Neodiversograptus 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 *Pachytheca* 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 Břekvici 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, sometime 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.

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

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 cyrtocone 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 shell of pelagic orthocerids produced the majority of free cephalopod bioclasts

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

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 břekvici 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 Homerian (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 cycles (Arethusinová Gorege Section, Na břekvici

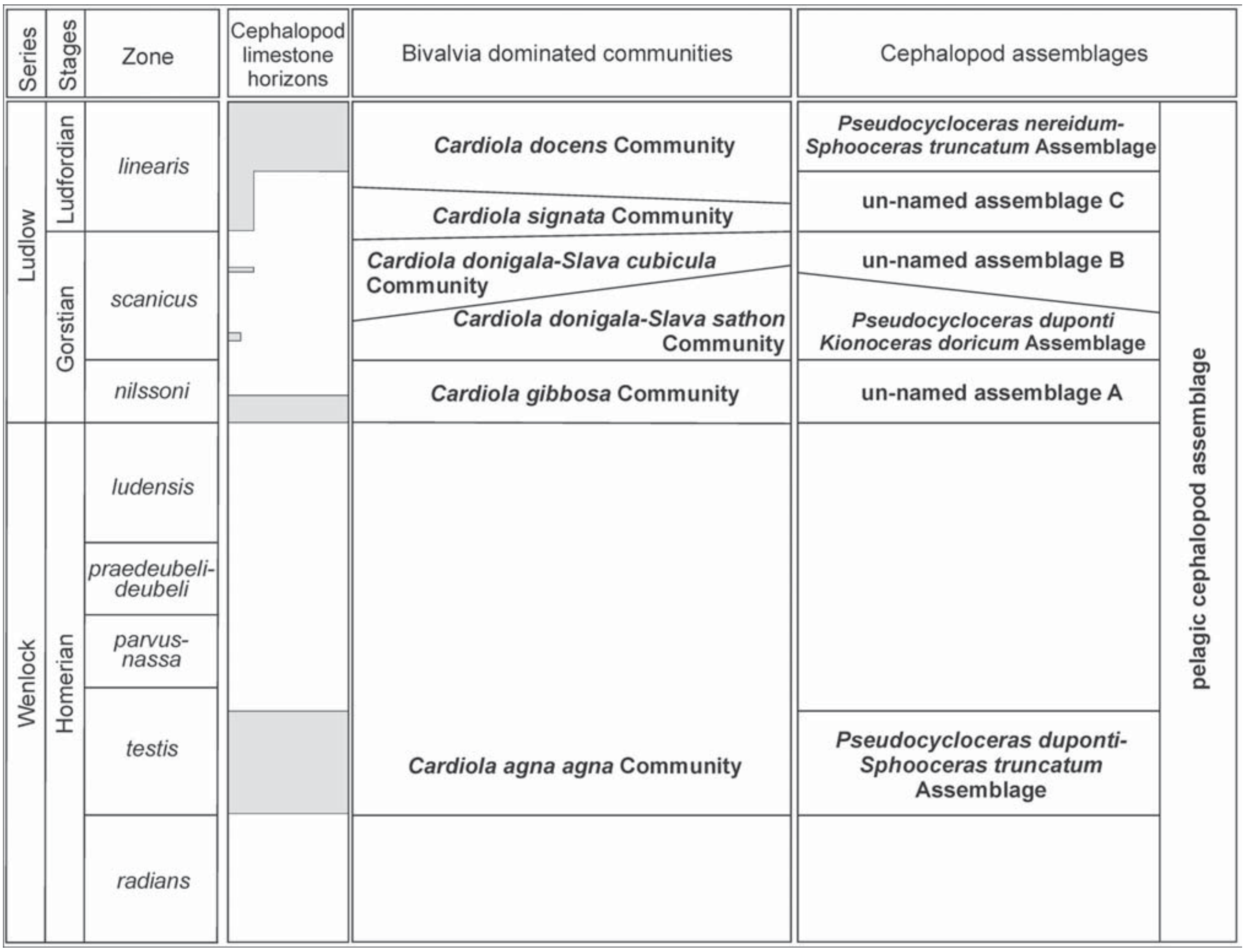

Fig. 6 - Distribution of bivalve communities (Kříž, 1999a, c) and cephalopod assemblages (Manda, 2003) in the Prague Basin during late Wenlock and early Ludlow.

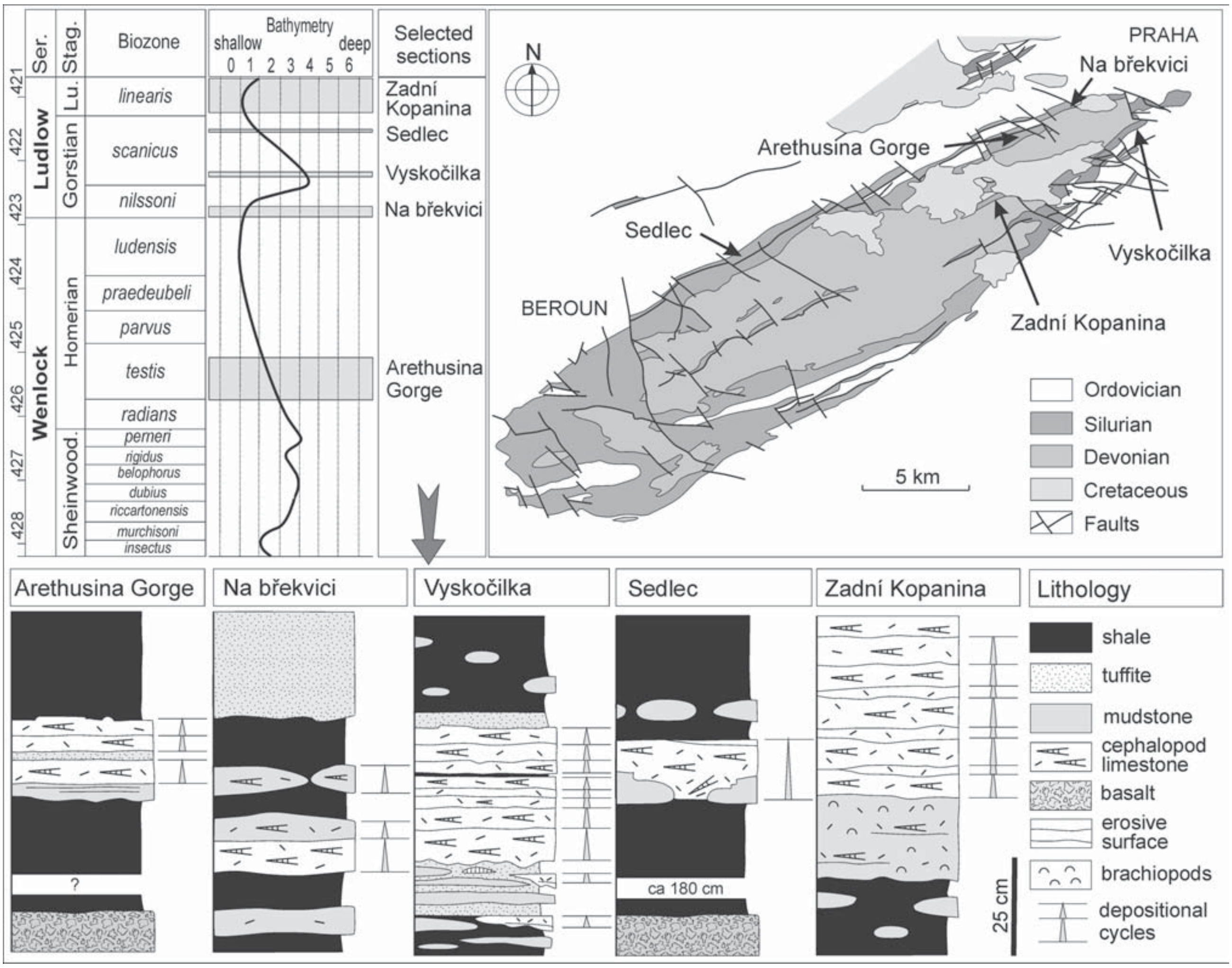

Fig. 7 - Position of the cephalopod limestone horizons (indicated by grey colour) plotted against global eustatic curve of Johnson et al. (1996) and selected sections showing changes in the cephalopod limestone framework during the late Wenlock (Homerian) and the Ludlow (Gorstian-early Ludfordian). The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

Section, Vyskočilka Section and Sedlec Section). They correspond to the relatively short-term existence of the surface current above the locally shallow and than rapidly quickly subsidising 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 stabile 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 cubicula* 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 cardiolids 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

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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* Počta, 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 cubicula Kříž, 1985
S. sathon Kříž, 1985
Slavinka acuta (Barrande, 1881)
Slava bohemica 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.
Lyecoceras 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)
Rizosceras 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.
Pachytheca sp.

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PŘÍLOHA 4

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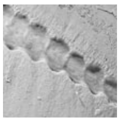
Palaeoecology and palaeogeographic relations of the Silurian phragmoceratids (Nautiloidea, Cephalopoda) of the Prague Basin (Bohemia)

Štěpán Manda



Phragmoceras and *Tubiferoceras* are discosorid nautiloid genera with endogastric cyrtoconic to orthoconic breviconic shells possessing a contracted aperture. Because of the constricted aperture phragmoceratids have usually been considered as microphages. The constriction of the aperture appears during the late ephebic stage. Preceding ontogenetic stages possessed a brevicone shell with an open aperture, usually considered to be indicative of nectobenthic predatory lifestyle. The apertural constriction probably improved hydrodynamic control and served as protection for the soft body. Attachment sites for distinct retractor muscles suggest evidence of potentially fast movement of the head-arm complex out of the aperture with consequent capture of larger prey. Phragmoceratids are a characteristic component of Silurian nautiloid faunas, which inhabited the mainly tropical carbonate platforms of Baltica and Laurentia. Phragmoceratids closely related to those of the Baltic and Avalonia occasionally appeared in the Prague Basin, which was located in the temperate zone at the northern margin of peri-Gondwana. The distribution pattern of phragmoceratids suggests that immigration into the Prague Basin occurred in three stages: (1) first appeared stray immigrants (or occasional visitors) from warmer seas, this stage of immigration reflecting activation of sea currents after the early Silurian widespread anoxia in peri-Gondwana (latest Llandovery-early Wenlock); (2) appearance of small endemic palaeo-populations of migrants (with evidence of local hatching of phragmocerids) that persisted only briefly during the early Homerian and early Gorstian low stands; (3) stable palaeo-populations appeared in the Early Ludfordian, with occurrence of endemic taxa related to the forms known from Baltica-Avalonia, suggesting stable conditions for nautiloid evolution. The Middle Ludfordian Kozlowskii Event caused the extinction of the last phragmocerid taxa in the Prague Basin as elsewhere. Nautiloid immigration to the Prague Basin (Perunica microplate) indicates that Perunica, in contrast to peri-Gondwanan areas, was within reach of the South Tropical Current since the latest Llandovery. Many other nautiloid families show a similar migration pattern although timing of the immigrations do not necessarily correlate. Thus the nautiloids provide useful data for palaeobiogeographic and climate reconstruction, such analysis can be made precise by comparison of nautiloid clades. • Key words: Silurian, Nautiloidea, *Phragmoceras*, migration, palaeoecology, peri-Gondwana, Perunica, Prague Basin.

Manda, Š. 2008. Palaeoecology and palaeogeographic relations of the Silurian phragmoceratids (Nautiloidea, Cephalopoda) of the Prague Basin (Bohemia). *Bulletin of Geosciences 83(1), 39–62*. Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received November 7, 2007; accepted in revised form February 26, 2008, issued March 31, 2008.

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A rich Silurian cephalopod fauna in the Prague Basin consisting of several hundreds of taxa has been known since Barrande's famous work (1865–1877). Here, cephalopods became abundant during the Wenlock as the successions of the Prague Basin changed from anoxic shales to calcareous shales and limestones. Therefore the majority of cephalopods that were described came from the Ludlow and Přídolí cephalopod limestones (Fig. 1). "Orthocerids" with longicone shells predominate whereas more diverse forms of nautiloids (oncocerids, discosorids, barrandeocerids and tarphycerids) rarely occur. The distribution pattern of these nautiloids is poorly known as the majority of them were collected during Barrande's time, and there are only a few examples that may facilitate a case study of nautiloid distribution patterns; namely tarphycerids (Turek 1976, Stridsberg & Turek 1997) and phragmoceratids. Amongst these taxa, the fossil record of phragmoceratids seems to be the best known in terms of biostratigraphic controls.

The Silurian family Phragmoceratidae Miller, 1877 (*i.e.* phragmoceratids) consists of two genera: *Phragmoceras* Broderip, 1839 (*in* Murchison 1839) and *Tubiferoceras* Hedström, 1917 (Discosorida Flower, 1940). Phragmoceratids possess a cyrtoconic or rarely orthoconic

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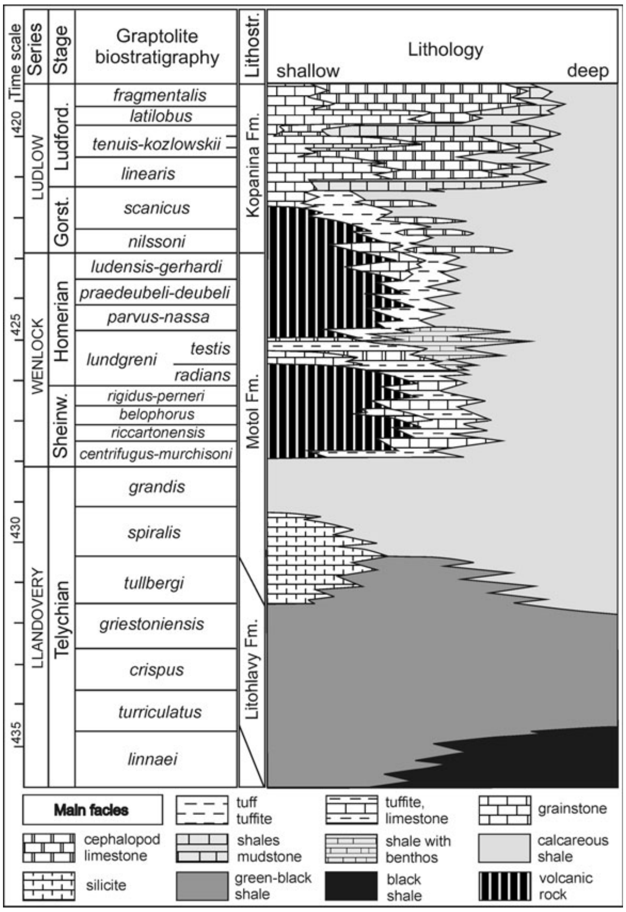

Figure 1. Llandovery, Wenlock and Ludlow stratigraphy and lithostratigraphy of the Prague Basin (adapted after Kříž 1991, 1992).

or coiled breviconic endogastric shell, with a more or less modified T-shaped contracted aperture. The siphuncle has broadly expanded and thick connecting rings (Flower & Teichert 1957, Dzik 1984). *Phragmoceras* represented a characteristic component of Silurian nautiloid faunas, appearing just after the beginning of the Silurian boundary and survived into the middle Ludfordian of the Ludlow Series. Several species have been described from Gotland, Estonia, Podolia in Ukraine, North Ural, Siberia, Severnaya Zemlya, Inner Mongolia, Tian Shan, Illinois, Indiana, New York, Ohio, Ontario, Quebec, Wisconsin, Scotland, Wales and the Welsh Borderland, Ireland, Sardinia and Bohemia (for summary see Manda 2007). The genus *Tubiferoceras* Hedström, 1917 ranges from the middle Llandovery to the Wenlock, with a few species known from Gotland, Scotland, Indiana, Wisconsin, Siberia, and Bohemia (see Manda 2007).

Phragmoceratids inhabited mainly tropical carbonate platforms of Baltica and Laurentia. Their occurrence in shallow carbonate platforms close to the reefs should be compared with the distribution pattern and ecologic requirements of the living *Nautilus* Linné, 1758 representing a model animal in palaeobiologic studies of fossil nautiloids. Nevertheless, diverse nautiloids including phragmoceratids also occurred in the Prague Basin (Perunica), located during the Silurian in the temperate zone. A few nautiloids, including phragmoceratids also occurred in other peri-Gondwanan terranes, including some located in the cool zone.

With the exception of the Ludfordian *Phragmoceras broderipi*, which is represented in many collections and also commonly figured as an example of the genus (*e.g.*, Koken 1896, Gürich 1908, Basse 1952, Prantl 1952, Dzik 1984), in the Prague Basin, phragmoceratids usually occur rarely in thin horizons at a few localities. *Phragmoceras broderipi* is very common at certain levels at some of Barrande's localities (*e.g.*, Kovářovic mez Section; Lochkov, App. loc. 10) and represents one of most common nautiloids in the Prague Basin.

The present study deals with palaeoecology, mode of life and geographic and stratigraphic distribution patterns of phragmoceratids in the Prague Basin (Perunica) and peri-Gondwana. The mode of life of nautiloids with constricted aperture remains poorly understood. New material collected during the last decade makes possible a new evaluation of earlier published interpretations of the palaeoecology. The distribution pattern of phragmoceratids is compared with other nautiloid families as well as recent *Nautilus*. The other questions addressed in this paper are: How did colonisation of the submarine highs by nautiloid immigrants proceed after the early Silurian anoxic episode in the Perunica and peri-Gondwana? What factors invoked the survival and further evolution of the nautiloid immigrants of Perunica and peri-Gondwana?

Material

Barrande's collection is housed in the National Museum, Prague (prefix L). Other material is deposited in collections of the Czech Geological Survey, Prague. Material collected by the author is deposited in the author's collection at the Czech Geological Survey, Prague (prefix SM). An index of mentioned localities is given in the Appendix and their geographic positions are shown in Fig. 2.

Taxonomic remarks: What is meant by "nautiloid"?

In the 1950, Flower & Kummel proposed a classification of cephalopods in which the subclass Nautiloidea Agassiz, 1847 included the orders Ellesmeroceratida Flower, 1950, Orthocerida Kuhn, 1940, Discosorida Flower, 1940, Oncocerida Flower, 1950, Barrandeocerida Flo-

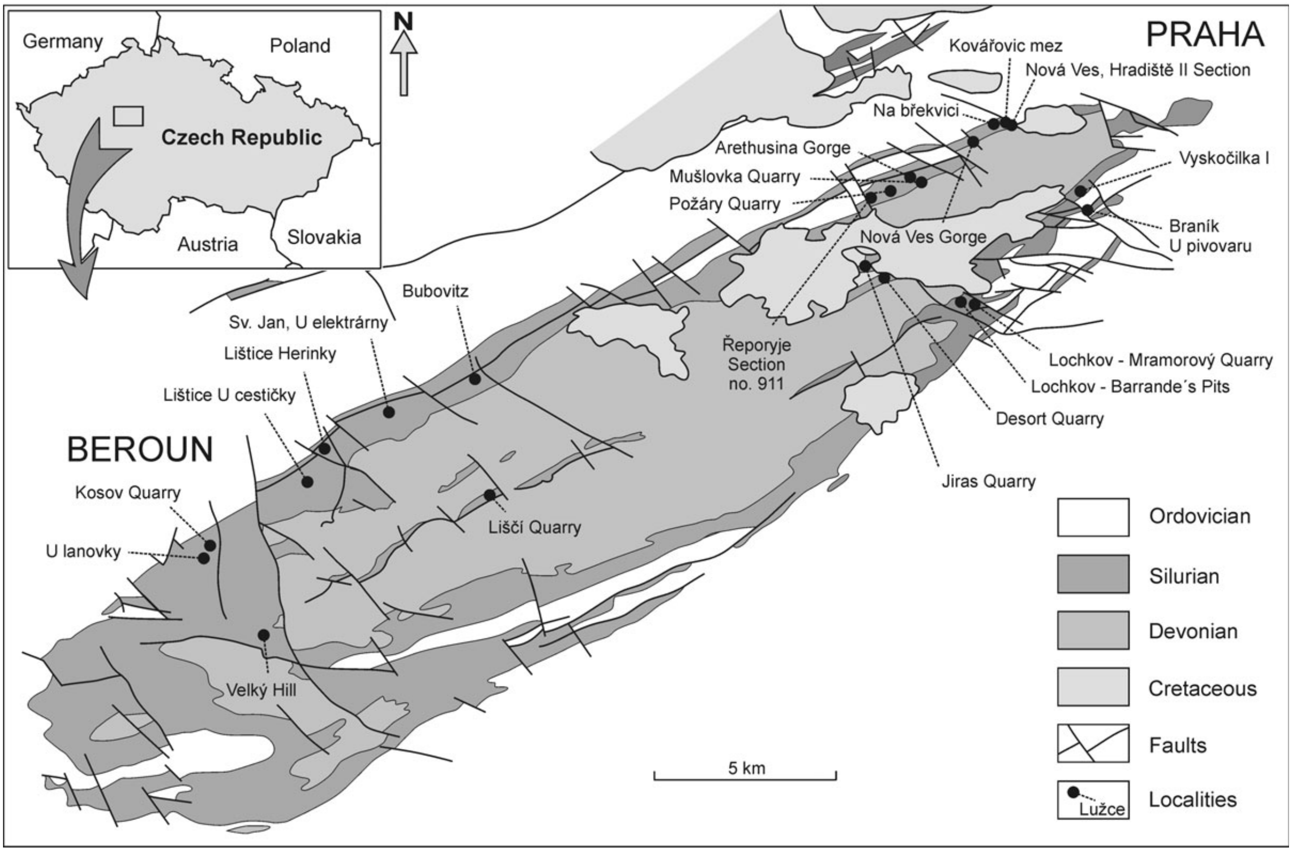

Figure 2. Distribution of Silurian rocks in the Prague Basin and the location of the sections discussed in the text (adapted after Kříž 1991, 1992 and Röhlich 2007).

wer, 1950, Tarphycerida Flower, 1950 and Nautilida Agassiz, 1847. This classification was generally adopted in the *Osnovy Paleontologyi* (Ruzhencev 1962) as well as in the *Treatise on Invertebrate Paleontology* (Moore 1964) and has been commonly used until now. Herein, author follows Teichert's (1988) classification, in which subclass Nautiloidea contains orders Discosorida, Oncocerida, Barrandeocerida, Tarphycerida and Nautilida. Whilst the former "Nautiloidea" grouped together cephalopods with different life strategies, the Nautiloidea as defined by Teichert (1988) contains cephalopods with similar general morphologies, embryonic development, life cycle and ecologic requirements comparable with Recent *Nautilus*, thereby providing the term 'nautiloids' with a useful sense in relation to palaeoecologic and palaeogeographic studies.

Phragmoceratids from the Prague Basin

Up to now, 14 species of *Phragmoceras* were described from the Prague Basin and each of them is briefly introduced below. The history of investigations on the Bohemian phragmoceratids was summarised by Manda (2007).

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

Genus *Tubiferoceras* Hedström, 1917

Tubiferoceras proboscoideum Hedström, 1917. – The lectotype from the early Silurian strata of Gotland was designated by Foerste (1926) from a figure of Hedström (1917, pl. 1, figs 4, 5-2). Two specimens were described by Manda (2007) from the early Wenlock strata of the Prague Basin.

Phragmoceras Broderip, 1839 (*in* Murchison 1839)

Phragmoceras acuminatum Hedström, 1917. – A lectotype was designated by Kiselev (1986) from a figure of Hedström (1917, pl. 10, figs 5, 6), Wenlock, Visby Formation, Larbo Section, Gotland. This taxon also occurs in the late Wenlock of the Prague Basin (Manda 2007) and probably the early Wenlock of Podolia, Ukraine (Kiselev *et al.* 1987).

Phragmoceras biimpresum (Barrande, 1865). – Barrande (1865, pl. 60, figs 1–4) figured two specimens from Bubovitz e1 locality (App. loc. 3) from brachiopod packstones of early Homerian age.

Phragmoceras labiosum Barrande, 1865. – This taxon is based on several specimens from Hinter Kopanina e2 and Konieprus e2 (App. locs 5, 7) (Barrande 1865, pl. 50, figs 1–6, pp. 218, 219). An additional specimen was found in the early Ludfordian U lanovky Section (App. loc. 23). Gnoli (1993) reported a single specimen of *Phragmoceras labiosum* from the Ludlow of Sardinia. *Phragmoceras labiosum* is closely related to *Phragmoceras retortum* Hedström, 1917 from the Ludlow of Gotland (Holland & Stridsberg 2004).

Phragmoceras longum Barrande, 1865. – This species was erected for several specimens from Lochkov e2 and Hinter Kopanina e2 (App. locs 5, 14) (Barrande 1865, pp. 213, 214, pl. 59, figs 1–4). Additional new, mostly fragmentary, specimens were collected from the early Ludfordian cephalopod limestone at Desort Quarry, Zadní Kopanina (App. loc. 6). *Phragmoceras longum* is closely related to *Phragmoceras inflexum* Hedström, 1917 from Gotland. Both species have a distinctive, laterally compressed cyrtoconic shell.

Phragmoceras imbricatum Barrande, 1865. – A lectotype was designated by Holland & Stridsberg (2004) based on the specimen figured by Barrande (1865, pl. 46, figs 1–4). The type locality is Vyskočilka e2 near Prague (App. loc. 26). The lectotype probably came from the cephalopod limestone beds of the early *L. scanicus* Zone (Manda & Kříž 2007). Most of specimens figured by Barrande were found in the cephalopod limestones of the early Ludlow Series, Butovitz e1 locality (Butovice Na břekvici Section No. 584; App. loc. 4). Some additional specimens were found during recent field studies at other locations in the early Ludlow Series (Řeporyje Section No. 911; Kosov Quarry, "new quarry", SW wall; Liščí Quarry; App. locs 21, 8, 11). *Phragmoceras imbricatum* was also recently re-described by Holland & Stridsberg (2004). Outside the Prague Basin, *Phragmoceras imbricatum* occurs in the Wenlock and early Ludlow rocks of Britain and Gotland (Holland & Stridsberg 2004) and has been recovered from Polish erratic boulders (Noetling 1884).

Kiselev (1984) assigned specimens of *Phragmoceras imbricatum* having an open aperture (Barrande 1866, pl. 46, figs 1–12) to *Protophragmoceras butovitcenze* Kiselev, 1984, the lectotype of which came from the early Ludlow Series of the North Urals (Kiselev 1984, p. 52, pl. 10, fig. 1, pl. 11, fig. 1) but Kisselev's illustration does not provide sufficient information to evaluate if the specimens from the Prague Basin and the Urals are really conspecific. However, the Prague Basin specimens, considered to be *Protophragmoceras butovitcenze* by Kiselev (1984), represent an early stage of *Phragmoceras imbricatum*, as already noted correctly by Barrande (1866).

Phragmoceras sigmoideum Hedström, 1917. – The lectotype was designated by Kiselev (1984) from a figure by Hedström (1917, pl. 17, fig. 1) from the Wenlock Visby Formation, Larbro, Storugns, Gotland (Hedström 1917). The species also occurs outside the Wenlock of Gotland, in the early Ludlow of the North Urals (Kiselev 1984) and late Wenlock of the Prague Basin (Manda 2007).

Phragmoceras munthei Hedström, 1917. – The lectotype was designated by Holland & Stridsberg (2004) based on the specimen figured by Hedström (1917, pl. 25, figs 1–3) from the early Wenlock Visby Formation of Visby, Gotland. *Phragmoceras munthei* also occurs in the late Llandovery and Wenlock of Gotland (Holland & Stridsberg 2004), the Wenlock of Estonia (Kiselev *et al.* 1990), the latest Llandovery and earlier Wenlock of the Prague Basin, and probably the latest Llandovery of Ireland (Manda 2007).

Phragmoceras cf. *undulatum* Hedström, 1917. – A single body chamber similar to that of *Phragmoceras undulatum* (Wenlock of Gotland) was recently described from the Prague Basin by Manda (2007).

Phragmoceras cf. *venticosum* Sowerby, 1839 *in* Murchison (1839). – Three specimens similar to *Phragmoceras venticosum* were described by Manda (2007) from the late Wenlock of the Prague Basin. *Phragmoceras venticosum* occurs in the Wenlock and early Ludlow of Wales and the Welsh Borderland (see Holland & Stridsberg 2004).

Phragmoceras koneprusensis Manda, 2007. – This species was described based on a single shell from the early Ludfordian strata of the Velký Hill Section (App. loc. 24).

Whereas the above-mentioned Bohemian taxa represent rather distantly related species of *Phragmoceras*, the Ludfordian *Phragmoceras broderipi sublaeve, Phragmoceras broderipi broderipi*, and *Phragmoceras beaumonti* are closely related and are considered to belong a single evolutionary lineage of phragmoceratids in the Prague Basin (Fig. 3). These taxa are known only from the Prague Basin. Taxa similar to the Ludfordian *Phragmoceras broderipi* occur in Wenlock and Ludlow strata of Gotland (Holland & Stridsberg 2004).

Phragmoceras beaumonti (Barrande, 1865). – The lectotype designated by Flower & Teichert (1957) is the specimen figured by Barrande (1865, pl. 165, figs 1–5) as *Cyrto-*

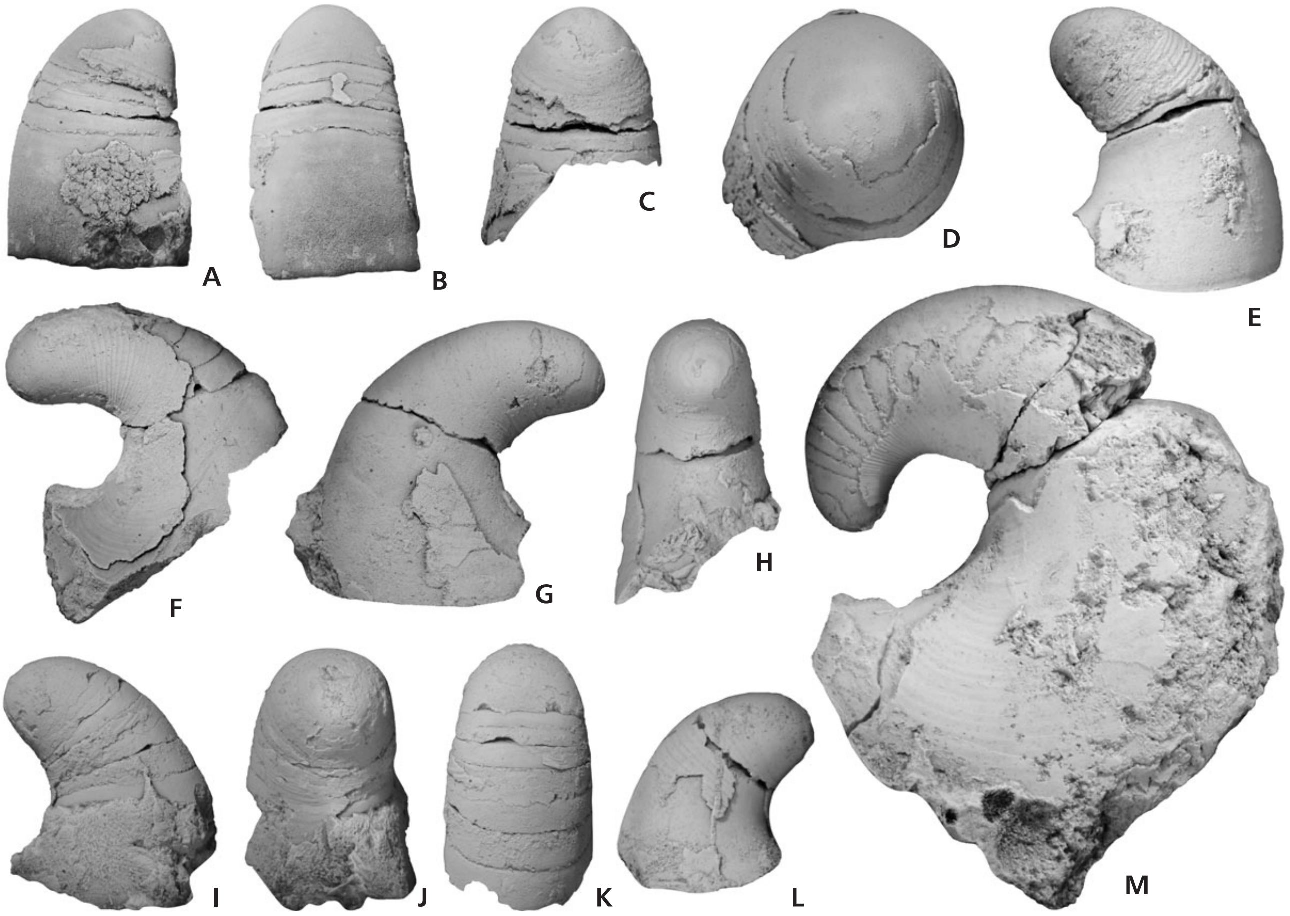

Figure 3. Embryonic chambers of phragmoceratids, early post-hatching specimens (A–L). • A–D – *Phragmoceras* cf. *ventricosum* Sowerby, 1839, Lištice U cestičky Section No. 759, Wenlock, Homerian, *T. testis* Zone; CGS SM 74; lateral (A), dorsal (B), ventral (C), × 2, apical view (D), × 3. • E – *Phragmoceras beaumonti* (Barrande, 1866), Mramorový Quarry Section no. 357, Ludlow, Ludfordian, uppermost *N. kozlowskii* Zone; CGS SM 99; lateral view, × 1.4. • F – *Phragmoceras beaumonti* (Barrande, 1866), Nová Ves, Hradiště II Section, bed No. 9; Ludlow, Ludfordian, *N. kozlowskii* Zone; CGS SM 73; lateral view, × 1.1. • G, H – *Phragmoceras broderipi sublaeve* Barrande, 1865, Velký Hill Section; Ludlow, Ludfordian, *S. linearis* Zone; CGS SM 98; lateral (G) and ventral (H) view, × 1.5. • I–K – *Phragmoceras broderipi broderipi* Barrande, 1865, Kovářovic mez Section; Ludlow, Ludfordian, *S. inexpectatus* Zone; CGS SM 55; lateral (I), ventral (J) and dorsal (K) view, × 1.9. • L – *Phragmoceras beaumonti* (Barrande, 1866), Nová Ves, Hradiště II Section; Ludlow, Ludfordian, *N. kozlowskii* Zone; CGS SM 62; lateral view, × 1.8. • M – *Phragmoceras beaumonti* (Barrande, 1866), Nová Ves, Hradiště II Section; Ludlow, Ludfordian, *N. kozlowskii* Zone; CGS SM 61; lateral view, × 1.3.

ceras beaumonti (Lochkov e2; App. loc. 14). Flower & Teichert (1957) regarded *Cyrtoceras beaumonti* to belong to the *Protophragmoceras* Hyatt, 1900. The latter genus differs from *Phragmoceras* in its slender cyrtocone shell and thinner siphonal tube. Dzik (1984) considered *Cyrtoceras beaumonti* to represent a juvenile stage of *Phragmoceras broderipi*. However, *Phragmoceras beaumonti* is a distinct species, which did not close its aperture in the adult stage and also has a smaller more coiled shell than *Phragmoceras broderipi broderipi*. New material of *Phragmoceras beaumonti* was collected recently from many localities in the late early Ludfordian strata of the Prague Basin.

Phragmoceras broderipi (Barrande, 1865). – *Phragmoceras broderipi* consists of two subspecies: *Phragmoceras broderipi sublaeve* (Barrande 1865, pl. 57, fig. 7, pl. 98, figs 1–4) and *Phragmoceras broderipi broderipi* (Barrande 1865, pls 56–58, 99). The subspecies differ mainly in sculpture. The first has a smooth shell or gently developed growth lines and the latter shows prominent growth lines sometimes forming irregular walls. New material of both subspecies was obtained recently from many sections in the early Ludfordian strata of the Prague Basin.

Ontogeny and mode of life of the *Phragmoceras*

The contracted aperture of adult phragmoceratids may be suggestive of a microphagous habit with reduced arms, as assumed by Abel (1916). Prell (1921) compared phragmoceratids with the Recent gastropod *Cypraea* and suggested that the body of *Phragmoceras* could flow out of the "extremely" restricted aperture. Further, he concluded that swimming using the hyponome was impossible in phragmoceratids and so assumed a life as bottom dwellers. Pia (1923) agreed with the proposal of a microphagous habit, but postulated active swimming behaviour. Flower (1957) considered that active swimming was too difficult and regarded phragmoceratids as benthic crawlers.

Holland (1984, p. 157), in his summary of Silurian cephalopod palaeoecology, agreed with Abel (1916) when he wrote: "It is difficult to see such a form other than as microphagous." Hewitt & Watkins (1980, p. 106) even suggested that phragmoceratids "might conceivably have had vegetarian habits". Westermann (1998, p. 281, fig. 20.13) made a reconstruction of *Phragmoceras* and suggested that the hyponome was at the height of the dynamic centre and thus *Phragmoceras* could be seen as a moderately good forward swimmer above a shallow substrate after brachiopod prey. Westermann (1998, p. 292) also commented on the lamellar subdivision of the siphuncle, indicating that it was "presumably for improved buoyancy regulation, permitting either for vertical migrations or hiding on the sea during storms". Whilst agreeing that phragmoceratids were active swimmers, Holland & Stridsberg (2004) assumed that the downward orientation of the apertural opening limited the ability of phragmoceratids to orient themselves. Nevertheless, Recent *Nautilus* is able to orient itself using not only visual cues, but also the use of chemical signals, and a similar mode of orientation can be assumed for fossil nautiloids (Basil *et al.* 2000).

Consideration of the deficiencies in the palaeoecologic interpretation of *Phragmoceras* should focus on the late ontogenetic stage where a contracted aperture is present. However, the contracted aperture only appeared as a modification of the mature animal at the end of shell growth. Phragmoceratids spent a major proportion of their life with a brevicone shell and open aperture.

Embryonic stage and hatching time of phragmoceratids

The embryonic shell of *Phragmoceras* is cup-like and slightly curved on the ventral side with an elliptical cicatrix. The diameter of the first chamber varies from 6.3 mm up to 10 mm with its height ranging from 5.6 mm up to 6.9 mm. The distance between the following septa usually continually increases. In some specimens, up to two shallow camerae are developed (Fig. 3J–L). Growth lines appear on the embryonic chamber around the field of the cicatrix or at the first camera, and their distance usually increases slightly but continuously (Barrande 1867, Hedström 1917, Manda 2007; see Fig. 3).

Due to the absence of a distinctive change in morphology, the recognition of the hatching time in *Phragmoceras* (as well as other early Palaeozoic nautiloids) is uncertain. Hatching time of nautilids is clearly marked by a nepionic constriction (*i.e.*, constriction of the shell) and is usually accompanied by changes in ornament and distance between septa (*e.g.*, Teichert 1964, Ward 1987, Chirat & Rioult 1998). Changes in ornament and spacing of septa are concentrated between the embryonic chamber and the 3rd septum in phragmoceratids (Fig. 3). Turek (2007) observed a similar early ontogenetic pattern in the Early Devonian oncocerids *Ptenoceras proximum* Barrande, 1865 and *Hercoceras mirum* Barrande, 1865. Thus, the hatching size of the Silurian phragmoceratid and Devonian hercoceratids was rather lower than that of post-Triassic nautilids (see Chirat & Rioult 1998).

A hatching site can be identified in the fossil record by the presence of specimens that died shortly after hatching (*i.e.*, as a consequence of a mass kill), because the embryonic shell is present throughout life. The majority of embryonic portions are found attached to part of the adult phragmocone, which was broken off from the rest of the shell during post-mortem processes, and thus a deposit with such remains does not indicate hatching place.

The Silurian early post-hatching nautiloids occur together where the density of adult-populations was at their greatest, *e.g.*, *Phragmoceras imbricatum*, Butovice Na břekvici Section No. 584 (see Barrande 1866, pl. 46; App. Loc. 4). At the margins of these populations, the early post-hatching stage is missing, *i.e.*, in deeper water environments (see Fig. 13). Silurian phragmoceratids hatched in relatively shallow environments below wave-base. A similar distribution pattern has been observed for several Silurian oncocerids (unpublished data). Thus the Silurian nautiloids do not exhibit the segregation of adult and early post-hatching individuals described in post-Triassic taxa (Ward 1987, Chirat & Rioult 1998).

Neanic and early ephebic stages of phragmoceratids with open aperture

The majority of phragmoceratids have a relatively rapidly expanding and endogastric shell (Figs 4, 5). The siphuncle is positioned on the shorter ventral side. With increasing diameter, the width of siphonal tube increases with a slight allometry. The cylindrical connecting rings are relatively thick. The body-chamber is usually relatively long relative to the phragmocone. The hyponomic sinus is generally shallow and relatively narrow. Stridsberg (1985) pointed out that an endogastric breviconic shell is more suitable for swimming than an exogastric. Silurian brevicones with a slightly curved shell are usually endogastric. In contrast, brevicones with cyrtoconic shell are mostly exogastric. *Phragmoceras* is virtually the only Si-

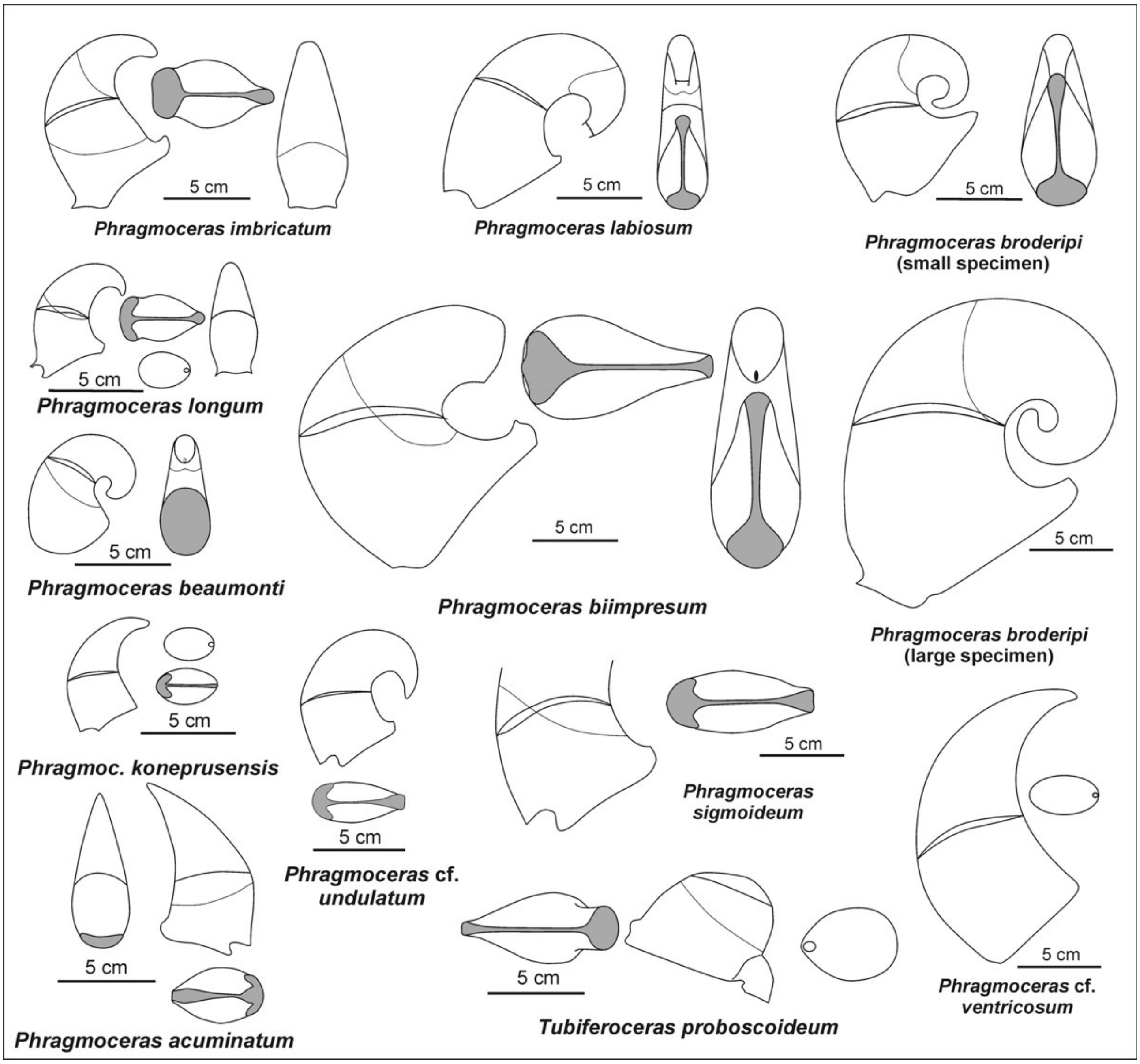

Figure 4. General morphology of Silurian phragmoceratids from the Prague Basin. Diagram showing presumed life position.

lurian nautiloid with an endogastric and cyrtoconic shell. Constructional constraints might possibly explain the relative rarity of endogastric cyrtoconic shells because the siphuncule is placed on the shorter side and thus provides a lower effective surface. The rapidly expanding siphuncle in phragmoceratids probably balanced this constructional handicap. Early phragmoceratids possessing an open aperture probably lived close to the bottom as nectobenthic predators.

An interesting feature is that the height and width of the aperture was much larger just in front of the aperture closure than after. This suggests that the head and arms were dorsally placed (*i.e.* in around the broad, shallow saddle of the aperture) and did not fill the whole aperture as in nautilids or tarphycerids (Fig. 5). This conclusion fits well with observations made by Kröger (2007) on the earliest Ordovician ellesmeroceratids; he suggested that the dorsally placed (in conventional terminology) head-arm complex and associated multiple-paired retractor muscles represent the basal body plan for nautiloids. Recently, Shigeno *et al.* (2008) reported embryological evidence for the morphological development of the head complex of the unique assembly of multiple archetypal molluscan body parts in *Nautilus*. The commonly developed constriction of the aperture of some oncocerids and discosorids should provide additional evidence for a dorsally placed head-arm complex because in such cases the constriction of the aperture limited the head-arm complex less than was previously thought.

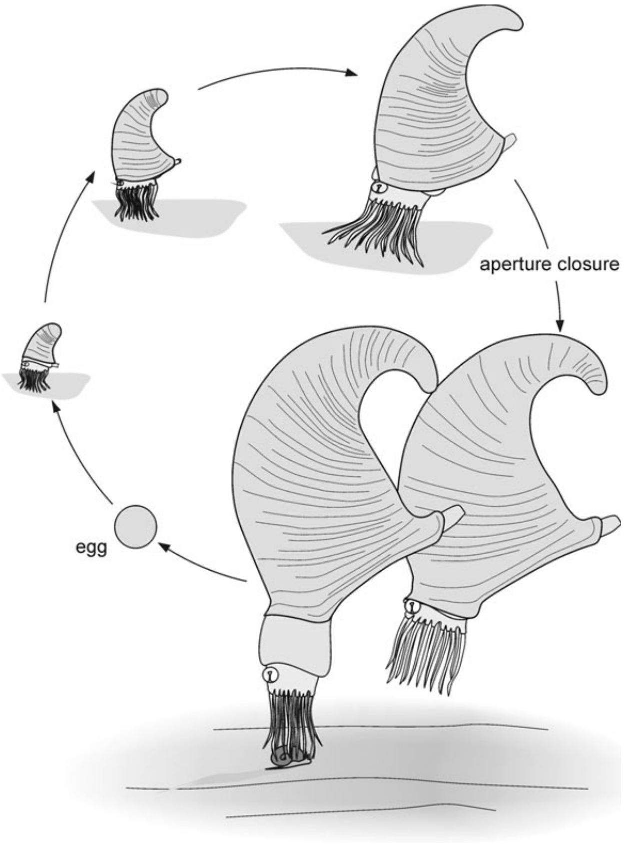

Figure 5. General morphology, ontogeny and mode of life of *Phragmoceras imbricatum*. Diagram shows change in mode of life during aperture closure in the late ephebic stage.

Late ephebic stage of phragmoceratids with contracted aperture

The constriction of the aperture in *Phragmoceras* corresponds to the cessation of shell growth in the long axis. The high frequency of growth lines at the constriction of the body-chamber indicate a decrease in shell growth rate, as reported in brevicone oncocerids (Stridsberg 1985). The shape of the contracted aperture in phragmoceratids is variable. The apertural opening faces downward or is dorsally oriented. The shape is also variable: circular to elliptical, sometimes with lobes developed or surrounded by a collar (*e.g.*, *Phragmoceras imbricatum*, Figs 4, 5). The hyponomic sinus is narrow and is terminated by a protruding hyponomic opening. A few species (*e.g.*, *Phragmoceras labiosum*, Fig. 4) have a T-shaped contracted aperture with a narrow apertural opening. One or two very shallow camerae may have been precipitated after the closure of the aperture. In addition, after apertural closure shell growth continued around the apertural opening and a more or less protruding collar developed. The highly variable thickness of the shell at the aperture and anterior part of the body chamber suggests that the shell continually thickened after apertural closure, *e.g.*, in *Phragmoceras broderipi* the shell thickness at the hyponomic opening varies from 2 mm to 9 mm.

The contraction of the aperture probably improved swimming as well as passive floating by providing a more hydrodynamically efficient shell-shape with a fixed and protruding hyponomic opening supporting the hyponome. This idea supports the phragmocerid distribution pattern; the specimens with an open aperture were restricted to shallower areas whereas specimens with a contracted aperture were widely distributed across the slope, even if the size of their shells differs only slightly. The presence of a similar distribution pattern in other nautiloids with contracted aperture cannot be tested because those early stages with open aperture are missing from the fossil record, *i.e.*, those cephalopods had a very low mortality before the stage during which the aperture became constricted (*e.g.*, Hemiphragmoceratidae Foerste, 1936).

The contracted aperture and collar lining the apertural opening probably also improved protection of the soft body against predators (Teichert 1964, Stridsberg 1985). On the other hand, the constriction of the aperture limited the size of the buccal mass and thus complicated food capture. There appears to be adaptive conflict: protection/improved buoyancy versus sufficient food intake.

Muscle scars of *Phragmoceras*: Implications for the mode of life of an ephebic phragmocerid possessing a contracted aperture

A further possible function of the contracted aperture might be the support of the soft body within the shell (Teichert 1964). Nevertheless, phragmoceratid shells commonly exhibit well-developed muscle scars. Why then are prominent retractor muscles developed in combination with a constricted aperture? The frequent preservation of muscle scars in phragmoceratids can be attributed to their relatively thick shells, because muscle scars are more frequently preserved in thick-shelled molluscs (*e.g.*, Stanley 1970). However, some Silurian nautiloids with a similar shell shape and shell thickness to those of phragmoceratids exhibit the preservation of muscle scars less frequently, *e.g.*, *Rizoceras* Hyatt, 1884 and *Protophragmoceras* Hyatt, 1900 with a breviconic shell and open aperture, or even *Octameroceras* Hyatt, 1900 with a breviconic shell and contracted aperture. Thus the frequent preservation of muscle scars in phragmoceratids reflects rather well-developed muscles. Well-preserved muscle scars were found in three species as described below.

The annular elevation of *Phragmoceras imbricatum* (Fig. 6C, D, G) is relatively low, 3 mm wide with elliptical longitudinally elongated muscle scars. On the ventral side, the annular elevation is reduced in width and a pair of me-

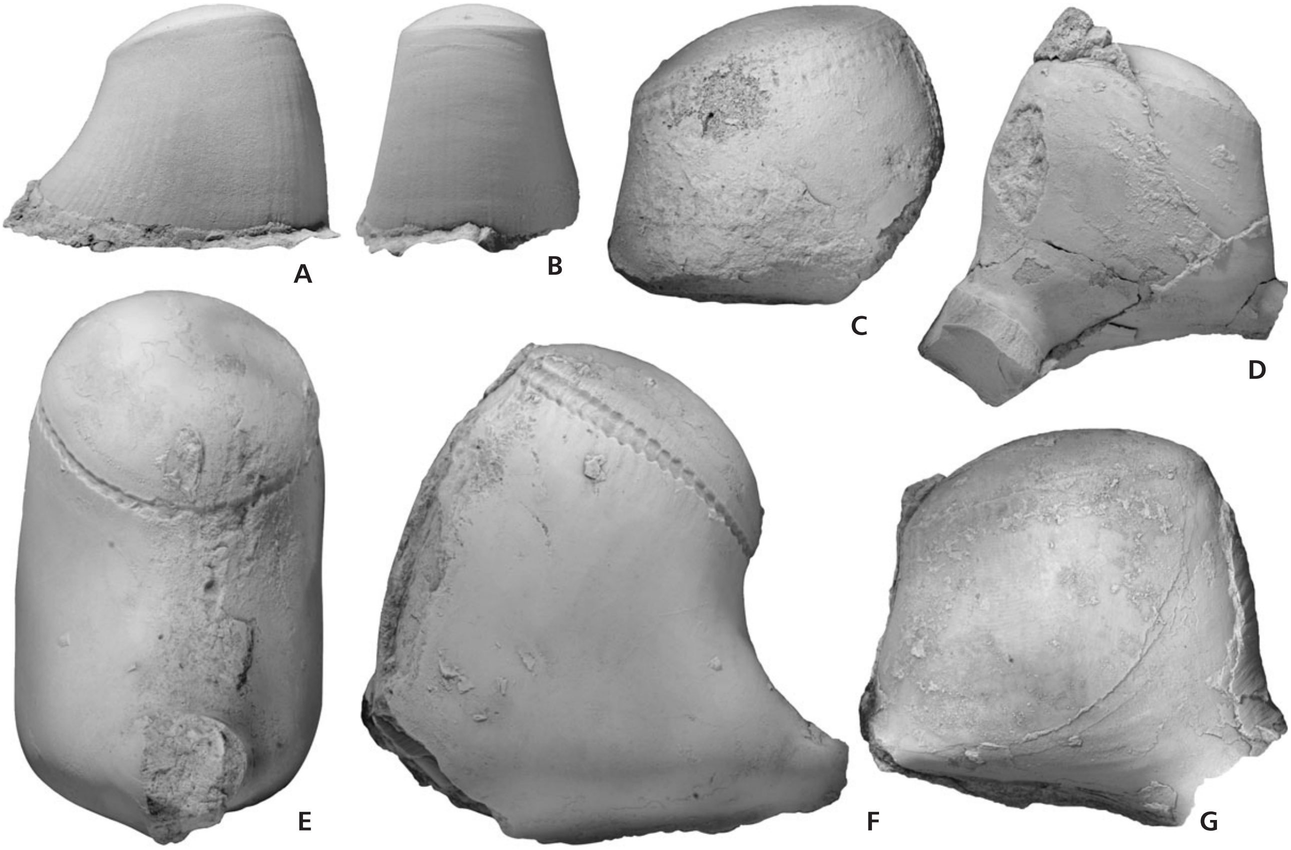

Figure 6. Muscle scars in *Phragmoceras*. • A, B – *Phragmoceras acuminatum* Hedström, 1917, Arethusina Gorge Section No. 687; Wenlock, Homerian, *T. testis* Zone; leg. J. Kříž; CGS SM 78 lateral (A) and dorsal (B) view, × 1.8. • C – *Phragmoceras imbricatum* Barrande, 1865, Kosov Quarry, "new quarry", SW wall; Ludlow, Gorstian, *S. chimaera* Zone; CGS SM 57; lateral view, × 0.8. • D – *Phragmoceras imbricatum* Barrande, 1865, Butovice Na břekvici Section No. 584; Ludlow, Gorstian, *C. colonus* Zone; Barrande's collection NM L40299; lateral view, × 0.7. • E, F – *Phragmoceras broderipi broderipi* Barrande, 1865; Kosov Quarry, "old quarry"; Ludlow, Ludfordian, *S. inexpectatus* Zone; CGS SM 70; ventral (E) and lateral (F) view, × 0.8. • G – *Phragmoceras imbricatum* Barrande, 1865, Butovice Na břekvici Section No. 584; Ludlow, Gorstian, *C. colonus* Zone; leg. J. Kříž and R. Horný; CGS SM 92; lateral view, × 1.

dially elongated muscle scars is developed (Fig. 8B, CGS SM 80). On the distal part of the last septum, imprints of the pallioviscerall ligament may be seen. More or less straight, longitudinal ridges directed parallel to the apertural opening are developed below the annular elevation.

Specimens of *Phragmoceras broderipi broderipi* (Fig. 6E, I) possessing contracted apertures exhibit annular elevations that are segmented into 23 pairs of muscle scars. The width of the elevation increases from 2 mm on the ventral side to 5 mm on the lateral side; on the dorsal side, the width of the elevation decreases slightly again. The muscle scars close to the ventral side are trapezoidal in shape, whereas close to the dorsal side they are longitudinally elongated with a medial ridge. The ad-oral margin of the annular elevation is sinusoidal, whereas the opposite margin is formed in asymmetrical waves. The imprint of the pallioviscerall ligament is preserved on the terminal part of the last septum. A zone with longitudinal and slightly ventrally curved ridges is developed below the annular elevation. The width of the zone increases from 5 mm on the ventral side up to 12 mm on the dorsal side of the specimen. The width of the zone with longitudinal ridges of the specimen figured by Barrande (1865) on pl. 99 as fig. 1, increases from 12 mm on the ventral side up to 18 mm on the dorsal side and the anterior termination forms a fine elevation.

The muscle scars described above occur in specimens with a contracted aperture. Early stages with open aperture exhibit a simple narrow annular elevation. For example, the early stage of *Phragmoceras acuminatum* with an open aperture (Fig. 6A, B) shows a 1 mm-wide annular elevation parallel with the suture. The width of the annular elevation decreases slightly on the ventral side. Gently longitudinal ridges that terminate close to the aperture are developed below the elevation. The distance between the ridges is about 1 mm, and dorsally this distance is doubled (Fig. 6B).

These serial muscle scars are shared by oncocerids and discosorids, and were grouped by Mutvei (1964) as Oncoceratomorphs. Between seven and 25 pairs of muscle attachment scars can be present, with the ventral pair being the largest (Kröger & Mutvei 2005). Such a prominent and

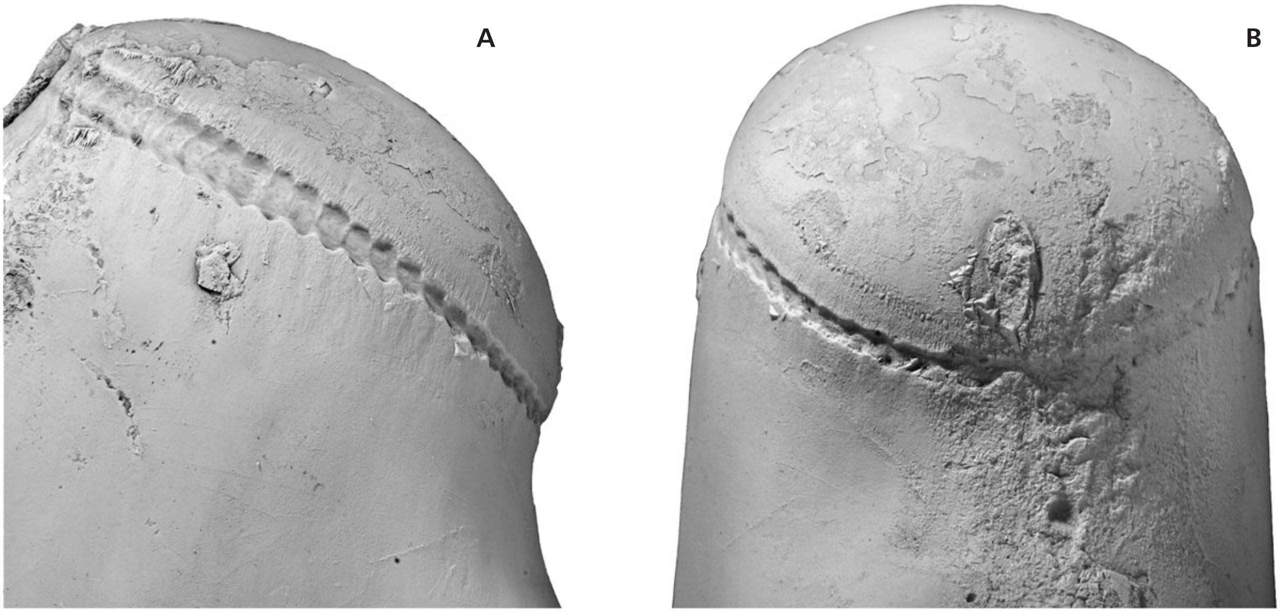

Figure 7. A, B – *Phragmoceras broderipi broderipi* Barrande, 1865 – detail of annular elevation; Kosov Quarry, "old quarry"; Ludlow, Ludfordian, *S. inexpectatus* Zone; CGS SM 70; lateral (A) and ventral (F) view, × 1.6.

laterally elongated ventral muscle scar pair was described by Sweet (1959) from the late Ordovician *Parryoceras euchari* Sweet & Miller, 1957 (Fig. 8A) belonging to the family Cyrtogomphoceratidae (from which the Phragmoceratidae are thought to have diverged in the Silurian, see Flower & Teichert 1957). *Phragmoceras* is distinctive amongst discosorids in its reduced area (*P. imbricatum*) or even absence (*P. broderipi*) of the ventral pair of differentiated muscle attachment scars (Fig. 8). In contrast, the width of the annular elevation and its segmentation increases on the lateral surfaces. The inferred reduction of the ventral pair of muscles in phragmoceratids suggests a high degree of evolutionary plasticity in the musculature driven by adaptive changes in the form of the shell.

The recognition of the imprints of the palliovisceral ligament as similar to those described in Recent *Nautilus* and post-Palaeozoic nautilids (Deecke 1913, Klug & Lehmkuhl 2004) is notable.

The longitudinal ridges below the annular elevation in early-post hatching *Phragmoceras acuminatum* indicates the early segmentation of the muscles although this has not yet been exhibited by muscle attachment scars on the annular elevation. The longitudinal ridges correspond to the elongated muscle attachment scars on the annular elevation and are oriented toward the apertural opening. Following Mutvei (1964), the longitudinal ridges on the inner shell indicate a shallow mantle cavity on each side of the central foot. The segmentation of the annular elevation becomes distinctive as the aperture becomes constricted.

In comparing the morphologies of a shell with an open aperture and one with a contracted aperture, the first comparison characterizes phragmoceratids as nectobenthic predators and the second as microphages, and so the question is raised as to whether such a change was possible during the ephebic stage? Is a microphagous habit really the only possible interpretation of phragmoceratids with a contracted aperture?

Phragmoceras beaumonti is a phragmocerid in which the constricted aperture is not developed, which may suggest that sexual maturity in phragmoceratids preceded the closure of the aperture. Thus the closure of the aperture may be considered to be a special adaptation to improve active swimming and protect the organs (*i.e.* a mature modification). Phragmoceratids with contracted apertures swam or floated in currents above the sea-floor searching for prey below. The prominent muscle attachment scars combined with the morphology of the apertural opening suggests that the head was normally protected within the shell, but during predation it could shoot out of the apertural opening by using the well-segmented muscles (Fig. 5). The wide siphuncle not only improved buoyancy regulation but probably also accelerated the vertical migration of phragmoceratids during food capture (*cf.* Westermann 1998, see p. 49).

Nature of fossil nautiloid assemblages

Each study in the past dealing with cephalopod palaeoecology and distribution patterns started with a crucial question – How much are fossil cephalopod assemblages affected by long-term post-mortem drift of the cephalopod shells? Two contradictory approaches have been presen-

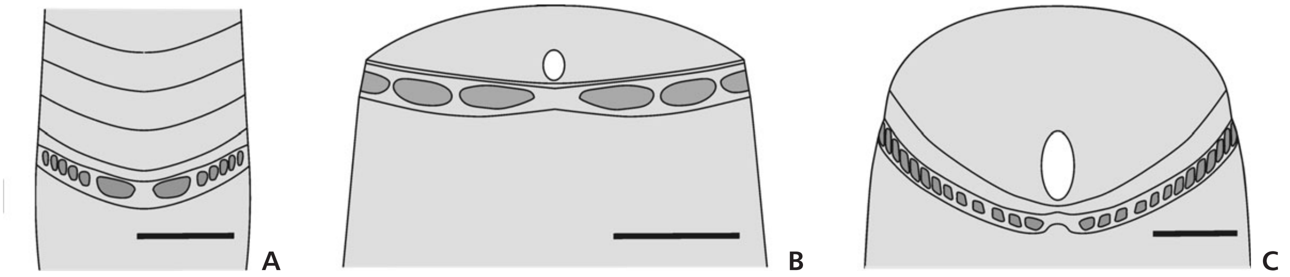

Figure 8. Idealized muscle scar shapes at *Parryoceras euchari* Sweet & Miller, 1957 (A), *Phragmoceras imbricatum* Barrande, 1865 (B) and *Phragmoceras broderipi broderipi* Barrande, 1865 (C). Ventral view. Scale bar equal 10 mm.

ted. In the first, fossil cephalopod assemblages have been considered to be essentially natural and thus only slightly affected by post-mortem drift of the shells (Flower 1957 and previous references therein). The second approach suggests that there is a large proportion of long-term drifted shells in the fossil assemblages (Miller & Furnish 1937, Miller & Youngquist 1949, Tasch 1955, Reyment 1958 and others). The latter opinion seems to be supported by observation of long-term drift by surface currents in recent *Nautilus* shells, as described and interpreted by Reyment (1958), Stenzel (1964), and Teichert (1970).

However, Collins & Minton (1967) showed that water permeability of the connecting rings in *Nautilus* makes long-term drift of the shells problematic (see Turek 1974). Subsequently, Chamberlain *et al.* (1981) studied post-mortem behaviour of *Nautilus* shells and pointed out that extensive post-mortem drift of the shell is a relatively rare event. Palaeozoic cephalopods usually have uncoiled and commonly rapidly expanding shells. This type of shell geometry is less suitable for post-mortem drift than that in *Nautilus* (Turek 1974).

Flower's earlier suggestion (1957) that the fossil record of Palaeozoic cephalopods would not seem to be compatible with the concept of extensive post-mortem transport was later confirmed by detailed analysis of the Late Ordovician cephalopod assemblages of the Cincinnati area (Frey 1989) and of the Silurian cephalopod assemblages of Wales (Hewitt & Watkins 1980). A similar conclusion provided the present study of the cephalopod assemblages in the Prague Basin. The distribution pattern of cephalopod assemblages generally respects benthic communities in the Prague Basin. Detailed analysis showed that some cephalopod taxa are restricted to a specific benthic community even if more than one community is present within one facies. In addition, deep-related cephalopod assemblages across the slope were observed whereas different cephalopod assemblages occur in shallow water environments above wave base and in the middle slope and lower slope settings.

In summary, the Palaeozoic cephalopod assemblages keep the original structure of former communities, which were affected only slightly by local transport and subsequent taphonomic processes. Although the long-term post-mortem transport of cephalopod shells cannot be excluded, it represents a mere confusion in the fossil record. Sedimentary processes such as storm events might cause transport of shells from shallower to deeper environments or even re-deposition of still older buried shells but shells from such deposits should be omitted from palaeoecologic studies aimed at understanding living communities.

Distribution of phragmoceratids in the Prague Basin

The replacement of black, anoxic graptolitic shales by laminated calcareous shales reflects the activation of surface currents during the latest Llandovery *O. spiralis* Zone (Fig. 1). These weak currents occasionally ventilated the bottom in shallower parts of the eastern Central and Pankrác segments of the Prague Basin (Kříž 1991) and thus a pioneer community accompanied by pelagic orthocerids and *Phragmoceras munthei* appeared there (for details see Manda 2007). The low-density population of *Phragmoceras munthei* consists mainly of ephebic shells with an open aperture whilst neanic stages and ephebic shells possessing contracted apertures are rare (Fig. 9). Phragmoceratids probably migrated to deeper water environments from a distant shallow-water environment and persisted with the coeval pioneer community for a short period (note that a coeval shallow-water facies is not present in the Prague Basin).

Large fragments (up to 8 cm wide) of *Phragmoceras munthei* cover the upper bedding plane of a single mudstone unit in an early Wenlock *C. murchisoni* Zone shale sequence in the eastern part of the Central Segment (Manda 2007). The mudstone unit reflects a depositional event in a deeper water setting dominated by shale sedimentation. Mud deposition was followed by the short-lived influence of currents that ventilated the anoxic sea floor as indicated by the appearance of a pioneer benthic community. Phragmoceratid shells, which are normally preserved as fragments suggest a relatively high-energy environment. There are two possible explanations of the phragmocerid

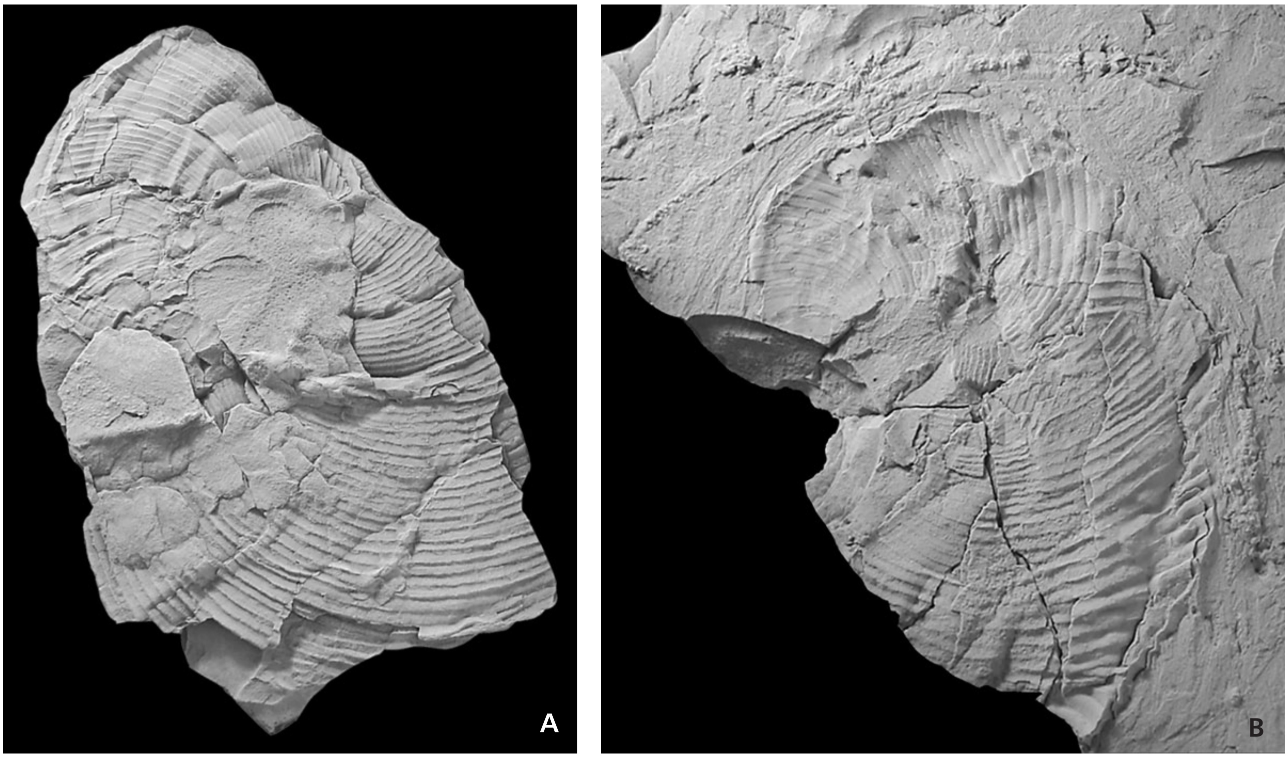

Figure 9. *Phragmoceras munthei* Hedström, 1917, Llandovery, Telychian, *O. spiralis* Zone. • A – Novoveská Gorge Section; CGS SM 82a; lateral view, × 1.1. • B – Braník U pivovaru Section; CGS SM 86; lateral view, × 1.3.

accumulation: 1) the phragmoceratid shells were transported post-mortem to the deeper environment by currents; however, there is no other transported shallow-water shell material present; and, 2) the shell deposit reflects a selective mass immigration of phragmoceratids into a deeper biofacies due to an event that affected the shallow water environment hosting the phragmoceratid population.

In the late *C. murchisoni* Zone, submarine elevations of the Svatý Jan and Řeporyje volcanic centres (Kříž 1991) had originated and these extended further during the Sheinwoodian (Fig. 1). The floors of these elevations were colonised by incoming benthic communities (Havlíček & Štorch 1990) with a rich brachiopod and trilobite fauna accompanied by the nectobenthic orthocerid *Dawsonoceras annulatum* (Sowerby, 1816). The phragmoceratid *Tubiferoceras proboscoideum,* together with four other nautiloid taxa, appear in limestones containing the *Leptaena rugalita* Community (Havlíček & Štorch 1990), reflecting local shallowing in the *M. belophorus* Zone on the upper slope of the Svatý Jan Volcano (U elektrárny Section, Fig. 2: App. loc. 22). The coeval Sheinwoodian nautiloid faunas of Baltica and Avalonia are much more diversified than those in the Prague Basin. Low current activity accompanying the Sheinwoodian high-stand probably confined more cephalopod immigrations (Fig. 12) to the submarine elevations of the Prague Basin. An additional reason might have been the small area of shallow sea-floor in the region.

A rich cephalopod fauna, including many nautiloids (oncocerids, discosorids, barrandeocerids) and longiconic forms (orthocerids, pseudorthocerids, actinocerids) appeared in the early Homerian *T. testis* Zone. This sudden onset of a diverse cephalopod fauna indicates the first large-scale cephalopod immigration to the Prague Basin. Cephalopods are common in thin limestone beds just above thick basalt effusions. The cephalopod immigration coincides with shallowing and a low-stand reflected in the extension of the shallow-water carbonates surrounding the volcanic elevations (Kříž 1991). Carbonate sedimentation and faunal radiation reflected a break in volcanic activity after the large earlier Homerian basalt effusions, *i.e.*, volcanic activity gave rise to the submarine elevations and the subsequent break in volcanic activity permitted colonisation of these basin highs. Further evolution of nautiloid immigrants, *e.g.*, *Phragmoceras* (Fig. 12) on the volcanic elevations was limited by recurrent volcanic activity and the deposition of pyroclasts (pyroclastic confined biofacies of Havlíček 1995) and by global changes related to the Lundgreni Event (Melechin *et al.* 1998).

Five taxa of phragmoceratids occur in the *T. testis* Zone. Whilst *Phragmoceras sigmoideum* and *Phragmoceras* cf. *undulatum* are closely related (Manda 2007), the other species differ in shell shape and represent separate branches of *Phragmoceras*. As a rule phragmoceratids are rather rare, but they occur in different environmental settings and communities, and each ontogenetic stage is present (Figs 12, 13). The relatively thick-shelled *Phragmoceras* cf. *ventricosum* occurs in shallow water sediments considered to have been deposited above wave base and close to the feeder channel of the Svatý Jan Volcano (Lištice U cestičky Section No. 759, Fig. 2: App. loc. 13). A similar environment was occupied by *Phragmoceras* cf. *undulatum* (Lištice, exact site unknown) and by *Phragmoceras biimpresum* (Bubovitz e1: App. loc. 3). *Phragmoceras acuminatum* with a thinner and smaller shell occurred commonly in the slightly deeper high-energy environment of the upper slope of the Svatý Jan Volcanic elevation (Lištice Herinky, Fig. 2: App. loc. 12). A single specimen of *Phragmoceras acuminatum* was found in the cephalopod limestone reflecting brief surface current activity above the basaltic deposits of the Řeporyje Volcanic Centre (Arethusinová Gorge Section No. 687, Fig. 2: App. loc. 1).

During the latest Wenlock (*i.e.* between the Lundgreni Event and the base of the Ludlow), nautiloids are missing. A diverse cephalopod fauna including nautiloids (oncocerids, discosorids, barrandeocerids, tarphycerids and ascocerids) suddenly reappeared in the early *N. nilsonni* Zone with the reappearance of the cephalopod limestone biofacies. This second large-scale cephalopod immigration and radiation coincides with a low-stand and break in volcanic activity. While in the Wenlock phragmoceratids occurred mostly in the shallow-water brachiopod limestone, the earlier Ludlow *Phragmoceras imbricatum* is preserved in a cephalopod limestone deposited on the upper slope of Nová Ves Volcanic centre elevation (Butovice Na břekvici Section No. 584, fig. 2; Barrande 1865, Kříž 1992: App. loc. 4). All ontogenetic stages are present there; specimens with open aperture prevail slightly over shells with a contracted aperture.

The earlier Ludlow low-stand was terminated by the middle Gorstian high-stand, which caused the retrogression of the cephalopod limestone biofacies (Manda & Kříž 2007). In shallow-water facies, the fauna was restricted by an increased pyroclastic input. These changes caused the extinction of many nautiloids. *Phragmoceras imbricatum* is one of the few nautiloids surviving from the early *N. nilsonni* Zone into the early *L. scanicus* Zone. It occurs rarely in a local bed of cephalopod limestone at Vyskočilka e1 locality (Barrande 1865: App. loc. 25) and of coral-gastropod limestone (Řeporyje Section 911, Liščí Quarry, and Kosov, "new quarry", SW wall: App. locs 21, 8).

A third cephalopod immigration-radiation coincided with the low-stand and extension of the shallow areas over elevations in the *S. linearis* Zone (Fig. 1). The extension of carbonate sedimentation and faunal radiation was also related to the lack of volcanic activity.

Four species of *Phragmoceras* appeared; these taxa are morphologically distinct from each other and represent separate branches within the genus. *Phragmoceras labiosum*, *Phragmoceras longum* and *Phragmoceras koneprusensis* are rare whilst *Phragmoceras broderipi sublaeve* is relatively common.

Phragmoceras labiosum with a small shell (Fig. 4) occurs in cephalopod wacke-packstones (Hinter Kopanina e2, Konieprus e2, Barrande 1865: App. locs 5, 7) and brachiopod-cephalopod grainstones (U lanovky Section: App. loc. 23). *Phragmoceras longum* (Fig. 4) with a larger and more cyrtoconic shell occurs in cephalopod wacke-packstones (Lochkov e2, Hinter Kopanina e2, Barrande 1865; Horní Desort Quarry near Zadní Kopanina: App. locs 5, 6, 14). A single shell belonging to *Phragmoceras koneprusensis* was found in a cephalopod grainstone in the Velký Hill Section near Koněprusy: App. loc. 24 (Fig. 2).

Phragmoceras broderipi sublaeve, with a relatively large and coiled shell occurs commonly at several localities; most commonly in cephalopod wacke-packstones, but also in deeper water mudstones as well as shallow-water fine-grained trilobite-brachiopod grainstones. *Phragmoceras broderipi sublaeve* is the only phragmoceratid taxon to appear in the late *S. linearis* Zone, and which survived the deepening in the *B. bohemicus tenuis* Zone persisting into the *N. inexpectatus* Zone (*e.g.*, Kosov Quarry – "old quarry", Lochkov-Barrande's pits, Velký Hill Section, and Zadní Kopanina Jiras Quarry, Mušlovka Quarry: App. locs 9, 15, 17, 24, 27).

The closely related *Phragmoceras broderipi broderipi* first appeared in the *N. inexpectatus* Zone. It was most common in this zone when shallow-water brachiopod limestones extended over the elevated parts of the basin during the low-stand (Fig. 11). Later, the species occurred mainly in brachiopod pack-grainstones, and less commonly in cephalopod limestones (Fig. 10). A decrease in numbers took place in the duration of the overlying *N. kozlowskii* Zone when the brachiopod limestone facies was replaced by cephalopod limestones during and in the subsequent high-stand (*e.g.*, Kovářovic mez – Butovice, Nová Ves Hradiště II Section and Lochkov – Barrande's pits: App. locs 10, 15, 18).

The last phragmocerid recorded from the Prague Basin is *Phragmoceras beaumonti* (Figs 12, 13), which appeared in the cephalopod wackestones of the *N. kozlowskii* Zone (Kříž 1998, Manda & Kříž 2006), *e.g.*, in Mušlovka and Požáry quarries at Řeporyje, Nová Ves-Hradiště and Lochkov-Barrande's pits: App. locs 15, 17, 18, 20 (Figs 2, 11). *Phragmoceras beaumonti* is evidently derived from the *Phragmoceras broderipi broderipi*, and both later taxa occur together in the early *N. kozlowskii* Zone.

Phragmoceras broderipi broderipi became less abundant during the deepening in the *N. kozlowskii* Zone. Some individuals reached maturity, but the overall size of the shell was smaller, whilst the shells of immature individuals

Figure 10. Polished slab of Silurian cephalopod limestone showing two specimens of *Phragmoceras broderipi broderipi* Barrande, 1865. Most probably from the middle Ludfordian, of Zadní Kopanina, Jiras Quarry, × 0.4. Facing stone in the entrance of the Ministry of Finance of the Czech Republic, Letenská Street, Malá Strana, Praha.

make up a larger proportion of the population, suggesting a high mortality rate. Shells similar to immature specimens of *Phragmoceras broderipi broderipi* (*i.e.*, with open aperture), with more strongly coiled shells but lacking the distinctive annulations, appeared simultaneously with the decline of *Phragmoceras broderipi broderipi*. These smaller shells are here regarded as *Phragmoceras beaumonti*. Within the late *N. kozlowskii* Zone, only those specimens with an open aperture and more strongly coiled shells have been found. Thus *Phragmoceras beaumonti* should be considered as a distinctive species. The loss of the contracted aperture and the small size of later species probably reflect adaptation to deeper water and a less ventilated environment during the high-stand of the *N. kozlowskii* Zone (Figs 12, 13).

Extinction of phragmoceratids

In the Prague Basin the last phragmocerid record, that of *Phragmoceras beaumonti* is from the uppermost *N. kozlowskii* Zone, *i.e.*, just below the Kozlowskii Event (Figs 12, 13). In Gotland, the last phragmoceratid record is from the Hemse Beds, the uppermost part of which can be correlated with the *N. kozlowskii* Zone (Jeppsson & Aldridge 2000, Manda & Kříž 2006). Holland & Stridsberg (2004, p. 302) did not assume the extinction of *Phragmoceras* at this level, but attributed the lack of *Phragmoceras* in the beds overlying the Hemse Beds to the fact that the majority of these units comprise a regressive succession unsuitable for nautiloids. Outside the Prague Basin and Gotland phragmoceratids disappeared even earlier: during the Gorstian and earlier Ludfordian, respectively. The Kozlowskii Event reflects changes in global oceanic circulation, causing rapid deepening and shallowing cycles, climatic changes including cooling (*e.g.*, Melechin *et al.* 1998, Manda & Kříž 2006, Lehnert *et al.* 2007), and most probably was the cause of the worldwide extinction of *Phragmoceras*.

Migration of the *Phragmoceras*

Mode of dispersion of the phragmoceratids

The Silurian phragmoceratids show features characteristic of a K-selected cephalopods: slow growth rate, long life, large protoconch, large shell, absence of a pelagic stage and low juvenile mortality. The majority of phragmoceratids inhabited stable, warm, well-ventilated, shallow-water environments extending across the Silurian carbonate platforms of Laurentia and Baltica, which had been evolutionary centres for nautiloids.

Fossil nautiloids are usually compared with the Recent *Nautilus*, for which dispersion limiting factors are well known, water temperature and the local condition of the sea-floor being the most important (Ward 1987). A nectobenthic mode of life and similar morphology of the shell at all ontogenetic stages is another limiting factor (Chirat & Rioult 1998). Earlier nautiloids generally exhibit similar restrictions to *Nautilus*. Here it should be noted that Silurian nautiloids commonly exhibited relatively large geographic dispersions by comparison with Ordovician and post-Silurian nautiloids. Amongst Silurian nautiloids, *Phragmoceras* exhibits one of the most dispersed taxa; occurring in all low-latitude palaeocontinents with the exception of China. By comparison, the morphologically convergent Devonian oncocerids (*e.g.*, *Metaphragmoceras* Flower, 1938) exhibit a restricted distribution and narrow range.

There are two modes of nautiloid dispersion: along shelves and by warm surface currents (see Chirat & Rioult 1998). Transport by currents was common among cosmopolitan 'orthocerids' with small pelagic post-hatching stages, but was rare among nautiloids, which thus exhibited a restricted dispersion. By comparison with the currents

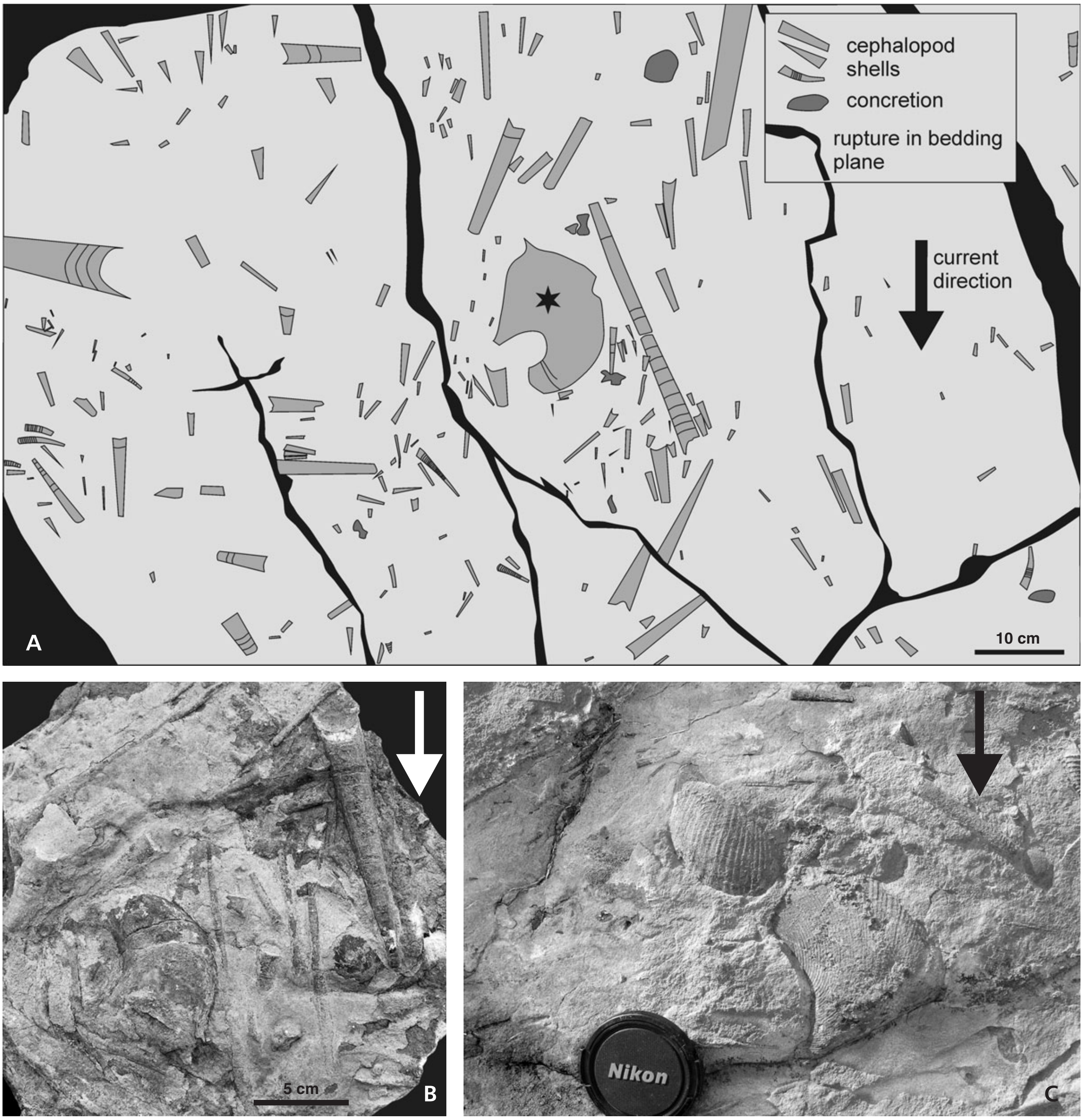

Figure 11. Mode of preservation of *Phragmoceras broderipi broderipi* in the cephalopod limestone, upper bedding plane of the bed No. 10, Kosov Section No. 782 (see Kříž 1992), Ludlow, Ludfordian, upper *N. inexpectatus* Zone. About 33 m^2 of the bedding plane was recovered during spring 2007. Eight specimens of *Phragmoceras broderipi broderipi* were observed: four shells with contracted aperture (A, C), two shells with open aperture (B) and two large fragments (C). Each phragmoceratid shell was oriented toward current by anterior or posterior side (see also Fig. 9). After unpublished data collected by J. Kříž and Š. Manda. • A – A line drawing showing arrangement of the cephalopod shells, *Phragmoceras broderipi broderipi* indicated by asterisk. • B – a shell of *Phragmoceras broderipi broderipi* with open aperture, field photograph. • C – two specimens of *Phragmoceras broderipi broderipi*, fragment of the lateral part of the shell and body chamber with part of the phragmocone, field photograph. Current direction indicated by arrow.

that passively transported and dispersed 'orthocerids', adult nautiloids dispersed through active swimming. The evidence of colonisation of submarine elevations by adult immigrants can be seen in their rare finds together with common juvenile 'orthocerids' in basin shales.

Closely related Silurian nautiloid faunas occur in Baltica, Avalonia and Laurentia where the shelves provided favourable conditions for nautiloid dispersion (Fig. 14). There are many common genera and even species originally described under different names from England,

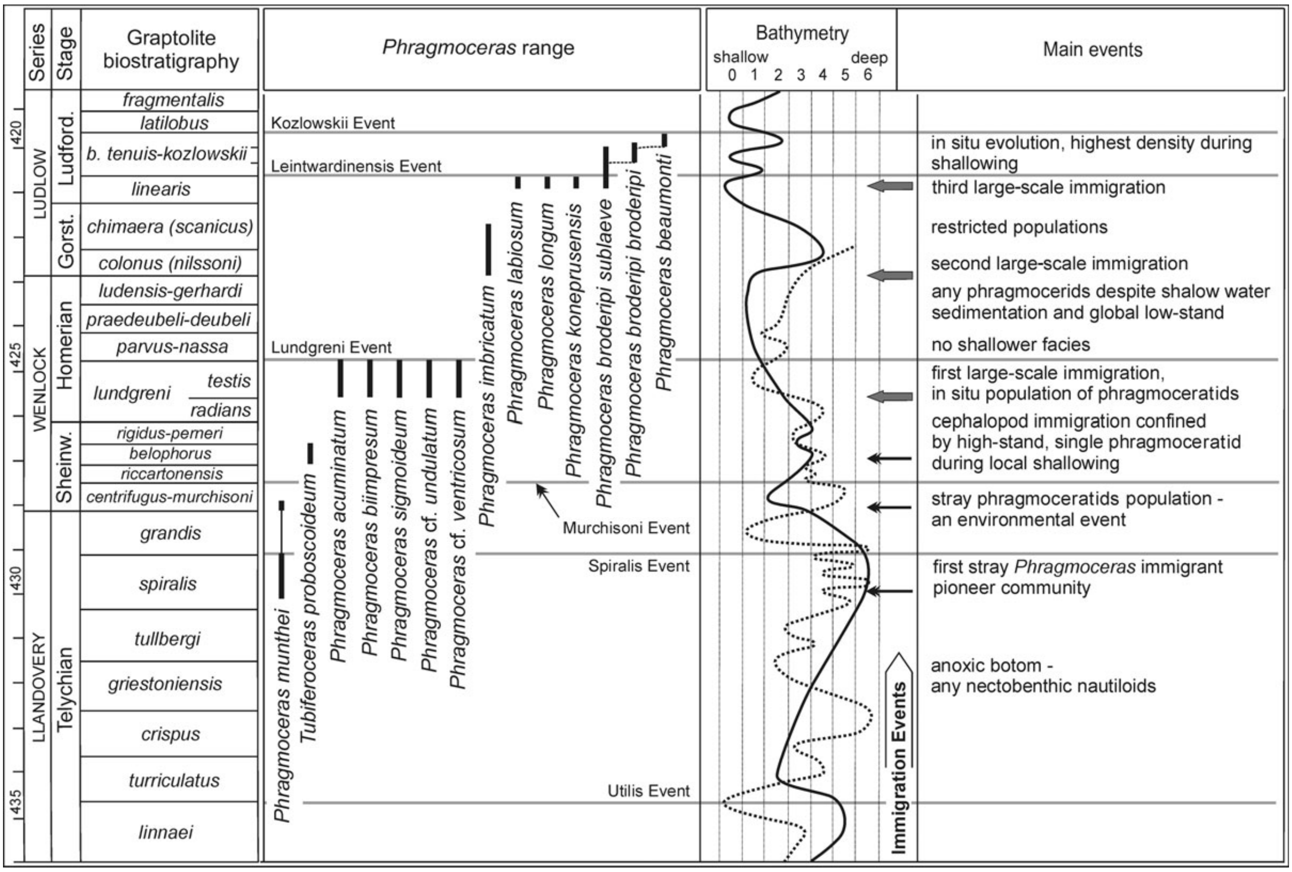

Figure 12. The stratigraphic range of phragmoceratids, immigration events, eustatic oscillations and main events of the phragmocerid succession in the Prague Basin. First eustatic curve (solid line) after Johnson *et al.* (1998) for the Llandovery-early Ludlow and Manda & Kříž (2006) for the Ludfordian; second curve after Loydell (1998).

North America, Gotland and Bohemia (Stridsberg 1985, Stridsberg & Turek 1997, Holland & Stridsberg 2004).

Nautiloids of the same genera (rarely species) also occur in the carbonate platforms of Kazakhstania and Siberia (Kiselev *et al.* 1993, Kiselev 1998), which were located within warm water masses to the north of the contemporary equator (Wilde *et al.* 1991) and separated from Laurentia, Baltica and Avalonia by great oceanic depths (Fig. 14). In this case, nautiloid immigrations via a north tropical current (Wilde *et al.* 1991) are presumed.

Stages of immigration to the Prague Basin

Closely related nautiloid faunas occurred in the Prague Basin, located in the temperate zone and separated from Baltica-Avalonia by the Rheic Ocean (Figs 14, 15). During the Silurian, the Prague Basin was situated on the microplate Perunica (Fig. 13), close to the northern margin of peri-Gondwana shifting toward to the equator (Havlíček *et al.* 1994, Krs *et al.* 2001, Cocks & Torsvik 2002). Widespread anoxia in the peri-Gondwanan basins during the earliest Silurian limited the distribution of nectobenthic cephalopods, which needed a well-oxygenated water column. Thus nautiloid immigration was not initiated until the late Llandovery. Three stages of nautiloid immigration into the Prague Basin are recognised: stray immigrants; in situ populations of immigrants; and their progenitors (Figs 12, 13).

1) Stray immigrants. – The early immigration of *Phragmoceras* into the Prague Basin can be compared with the immigration of Recent adult living *Nautilus* by currents from the main populations, *e.g.*, from the Philippines to Kyushu Island, Japan (Hamada *et al.* 1980). Reproduction of *Nautilus* in Japan is limited by low temperature. The latest Llandovery-early Wenlock phragmoceratids represent such ancient stray immigrants of Baltic-Avalonian origin. The early Wenlock accumulation of *Phragmoceras munthei* in a single bed suggests a "stray population" reflecting an environmental event. There is no correlation between eustatic oscillation and immigrations (see Fig. 12).

2) In situ populations. – The majority of late Wenlock phragmoceratids occurred in shallow-water brachiopod li-

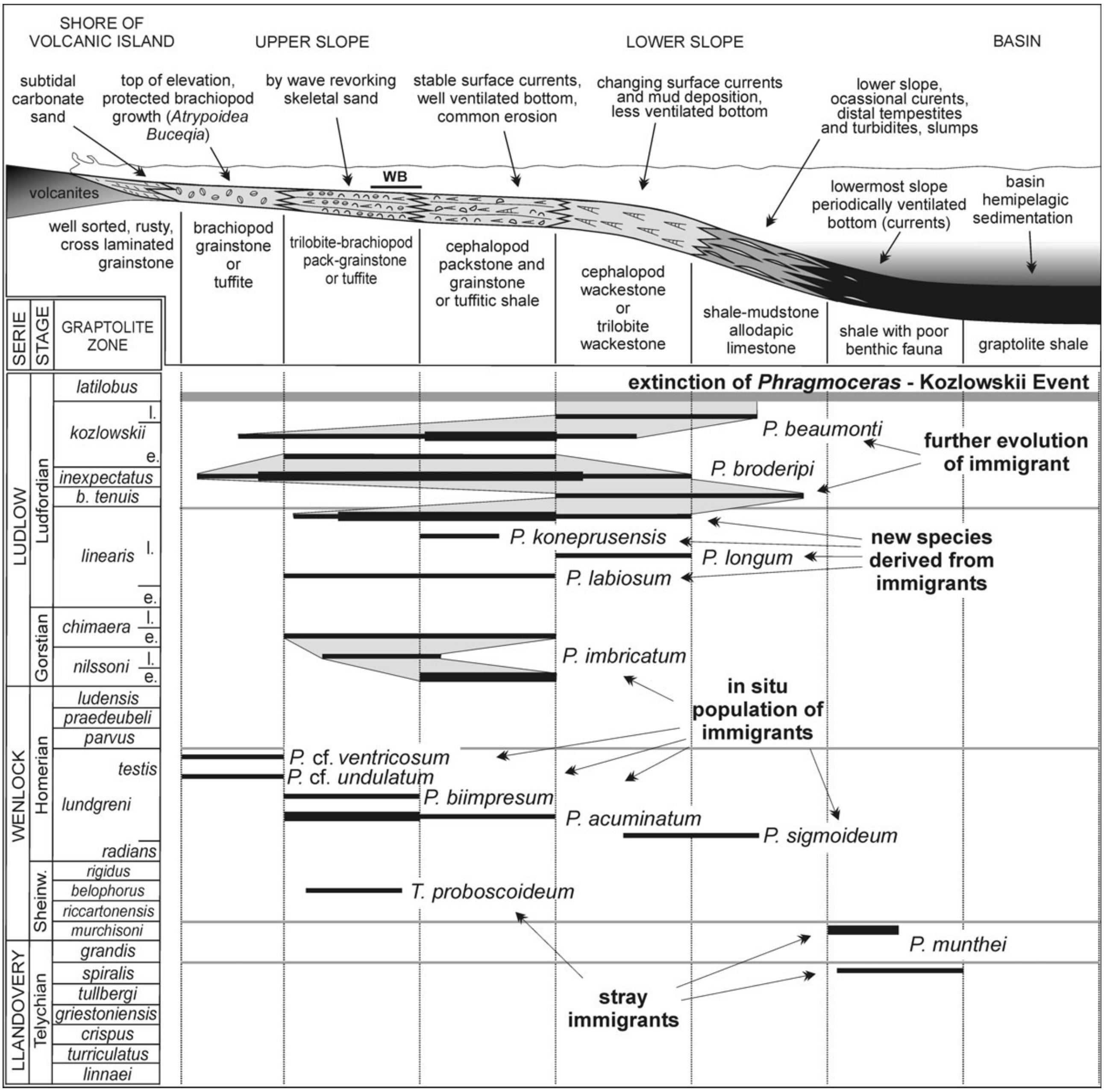

Figure 13. Distribution of Silurian phragmoceratids of the Prague Basin in relation to the facies (depth) zones. Not to a time scale. Grey areas indicate continual evolution of a species. The distribution of phragmoceratids is compared with the global eustatic curve (Fig. 12) and the lithostratigraphy of the Prague Basin (Fig. 1). Abbreviation: WB – wave base.

mestones, whereas in the early Ludlow the majority of them are to be found in the cephalopod limestone biofacies (Fig. 13), representing deeper-water environments. In situ populations of immigrants appeared during low-stands (*T. testis, N. nilsoni* zones), but did not survive the subsequent deepening (Fig. 13). The presence of each ontogenetic stage including early post-hatching specimens during the late Wenlock and later permits their interpretation as *in situ* populations of phragmoceratid immigrants on submarine volcanic elevations in the Prague Basin. All pragmocerid immigrants are of Baltic or Avalonian origin and form small populations on these submarine elevations.

The presence of post-hatching specimens is worthy of comment. Recent *Nautilus* embryos live in water at temperatures of 22–24 °C with a long incubation period, 9.5–14 months in aquaria (Ward 1987). Jurassic nautilids hatched in slightly cooler water with a lower limit of 19.5 °C (Chirat & Rioult 1998). The size of the shell and protoconch of *Phragmoceras* is similar to that of *Nautilus*. Thus the recognition of early post-hatching specimens and

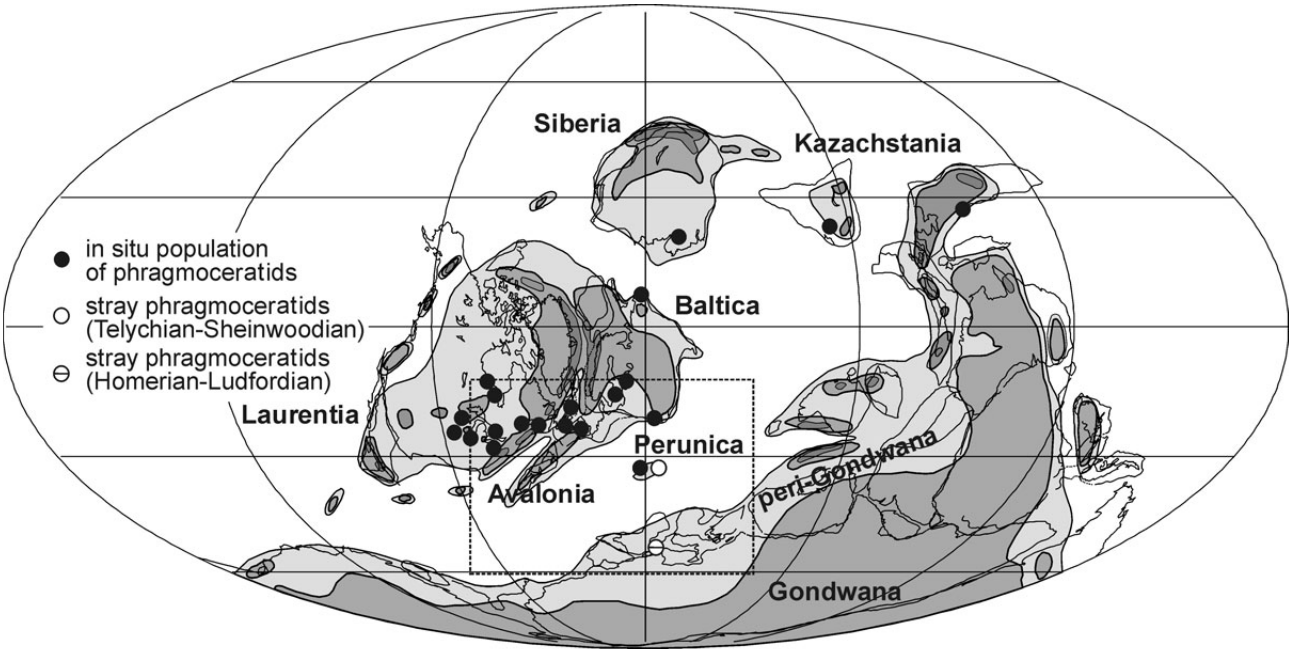

Figure 14. Distribution of phragmoceratids. Wenlock palaeogeographic reconstruction based on the Paleomap Project of C.R. Scotese; Perunica microplate position after Krs *et al.* (2001) and Cocks & Torsvik (2002). Data set: Prague Basin (Manda 2007), Gotland (Hedström 1917, Holland & Stridsberg 2004), Estonia (Kiselev *et al.* 1990), Podolia in Ukraine (Kiselev 1986, Kiselev *et al.* 1987), North Ural (Kiselev 1984), Siberia (Kiselev 1998), Severnaya Zemlya (Bogolepova *et al.* 2000), Inner Mongolia (Zou 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 1988; Gnoli 1990, 1993).

local populations suggests relatively temperate water in the Prague Basin during the late Wenlock.

Nevertheless, the temperature of water could not have been as high as in the subtropical and tropical waters enabling the incubation of *Nautilus* and post-Triassic nautilids. This is indicated by the absence of warm-water carbonates and associated biota. It can be presumed that phragmoceratids in the Prague Basin as well as accompanying nautiloids, including the ancestors of *Nautilus*, were able to reproduce in temperate waters.

3) Further evolution of immigrants. – The early Ludfordian phragmoceratids are represented by local taxa, whilst allied taxa have been described from Baltica. This suggests further evolution (peripatric speciation) of immigrants during the early Ludfordian low-stand (*S. linearis* Zone) and thus the presence of more stable conditions needed by nautiloids. Only one of four phragmoceratids described from the *S. linearis* Zone survived the deepening event in the *B. tenuis* Zone and continued to evolve up to the Kozlowskii Event (Figs 12, 13). The Ludfordian phragmoceratids occur mainly in the cephalopod limestone biofacies. The adaptation of immigrants to the deeper-water cephalopod limestone biofacies with intense surface currents and a less stable environment is of note during the Wenlock-Ludlow in the Prague Basin (Fig. 13).

Nautiloid immigrations to the others peri-Gondwanan terrains

Two phragmoceratids were described from the cephalopod limestones of Sardinia (Figs 14, 15); the late Wenlock *Phragmoceras* sp. (*Phragmoceras broderipi sublaeve* in Gnoli 1990) and the Ludfordian *Phragmoceras labiosum* (Gnoli 1993). Both species are based upon a single mature shell and probably represent stray immigrants from warmer seas, as suggested by Stridsberg (1988). *Phragmoceras labiosum* indicates faunal links with the Prague Basin as do the majority of the cephalopod assemblage(s) (Gnoli 1993).

In the Prague Basin, stray immigrants appeared in the late Llandovery and then after the late Wenlock, only endemic populations were present. In Sardinia, located further to the south, stray immigrants appeared very late in the Wenlock and there is no evidence of *in situ* phragmoceratid populations during the Silurian. A similar migration pattern is exhibited by other nautiloids of Sardinia and the Carnic Alps (*e.g.*, Gnoli 1990, 2003). Nautiloid dispersion in peri-Gondwana (except Perunica) was probably limited by low water temperature. The distribution of nautiloid assemblages confirms the distinctive position of the Perunica microplate in northern peri-Gondwana, within reach of warm currents (Fig. 15).

Comparison of phragmocerid palaeo-population from Gotland and Prague Basin

As noted above, the phragmoceratids of the Prague Basin are immigrants from warm water carbonates platforms or represent closely related species that evolved from these immigrant ancestors. In total 14 phragmocerid taxa are reported from the Prague Basin. This is the second most diversified local fauna of phragmoceratids after Gotland, where 24 taxa are known (Holland & Stridsberg 2004). Amongst these, probably six species are in common to both places. Certain other species are closely related to taxa that occur in Gotland or Britain. Are there some differences in the structure of the palaeo-populations from Gotland and the Prague Basin (*i.e.*, between warm and temperate water, respectively)? The majority of phragmoceratids from Gotland occurred in very shallow-water environments close to reefs; in the Prague Basin they generally inhabited deeper-water environments lacking reefs. In the Prague Basin, the majority of phragmoceratids occur in cephalopod limestones, in which common juvenile bivalves indicate occasional anoxic conditions in the lowermost part of the water column (see Ferretti & Kříž 1995, Kříž 1998). Locally common pelagic cephalopods document current instabilities in the water column, which caused mass mortality of pelagic cephalopod para-larvae.

Compared with the number of phragmocerid specimens known from Gotland, the phragmoceratids of the Prague Basin are usually rarer. Exceptions to this are the Ludfordian *Phragmoceras broderipi* and *Phragmoceras beaumonti*, which represent an endemically evolved clade. In addition, the phragmoceratid populations of the Prague Basin commonly contain specimens with open apertures. During the latest Llandovery, Wenlock and early Ludlow the early stages with an open aperture form a significant portion of fossil samples. It can thus be concluded that phragmocerid palaeo-populations in the Prague Basin were subjected to relatively high mortality rates. By contrast, phragmoceratids from Gotland exhibited fairly low mortality rates; only a single specimen with an open aperture (*i.e.*, died before maturity and aperture closure) is present amongst several specimens with contracted aperture, figured by Hedström (1917).

Another interesting difference is shape variation. Phragmoceratids from the Prague Basin exhibit fairly low shape variability when compared with those from Gotland. The difference is expressed by well-defined and discreet morphologies in the Prague Basin, whereas in Gotland only "a few specimens are really identical" (Holland & Stridsberg 2004, p. 302). Thus the phragmoceratids that migrated to the Prague Basin carried only a small part of the phenotypic variability of Gotland's population and thus morphological variability was lower. The lower variability of phragmoceratids in the Prague Basin may indirectly suggest that a relatively small number of migrants were involved.

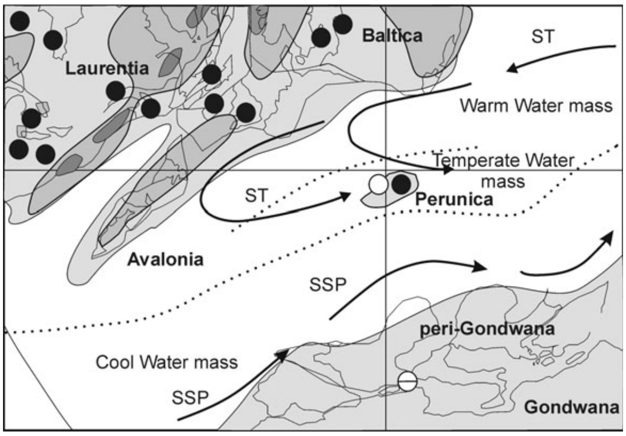

Figure 15. Phragmoceratid distribution around the early Silurian Rheic Ocean and adjacent areas (detail of map given as Fig. 8) showing reconstruction of oceanic currents (Wilde *et al.* 1991) and distribution of warm and cool water masses. Abbreviations: ST – South Tropical Current, SSP – South Subpolar Current.

In summary, the low density, high mortality, and small range of morphological variations of the phragmoceratids is considered to reflect less suitable environmental conditions for and higher adaptive pressure of nautiloids in the Prague Basin.

Why immigrations coincided with low stands?

The appearance of nautiloids during the late Llandovery suggests that the Perunica was reached via a South Tropical Current directed along the southern margin of Baltica-Avalonia and across the Rheic Ocean (Kříž 1979, Wilde *et al.* 1991, here Fig. 14). Latest Llandovery and Early Wenlock nautiloid immigrations to the Prague Basin (Fig. 9) show features reflecting an ecosystem recovery after the early Silurian anoxia event (post-extinction stage boundary of Jablonski 2001). It is notable that these early immigrations were initiated after short-lived glaciations followed by global warming (Caputo 1998).

The subsequent migrations (Figs 12, 13) of nautiloids coincided with low-stand episodes. Chirat & Rioult (1998) assumed that low stands allowed nautiloids to swim along the sea floor, which were previously below their implosion depths. The great depth of the Rheic Ocean (*i.e.*, between Baltica and Perunica) must have persisted despite eustatic oscillations. The correlation between migrations and low stands requires another explanation. For example the retreat of carbonate sedimentation, and the emergence of carbonate platforms during low stands accompanied by a decrease in the area of shallow seas (*e.g.*, Jeppsson 1990) along Baltica could have pressed nautiloids to search for new living places. Such new eco-space might have been offered by sites on northern peri-Gondwana located in temperate zone, where during low-stands submarine elevations ventilated by currents were extended in area. Increasing migration and the subsequent endemic evolution of phragmoceratids is reflected in a stepwise decrease in distance between Baltica-Avalonia and Perunica (*i.e.*, closure of the Rheic Ocean) as well as warming caused by the shift of Perunica (peri-Gondwana) toward to the equator and accentuated by global warming during the Silurian (Frakes *et al.* 1992).

Comparison of distribution pattern of phragmoceratids and other nautiloids: is the size of embryonic stage a limiting factor to dispersion?

Many other Silurian nautiloids exhibit similar distribution and migration patterns to the phragmoceratids; *e.g.*, *Euryrizoceras* Foerste, 1930 (Sheinwoodian-Přídolí), *Octameroceras* Hyatt, 1884 (Homerian-Přídolí), *Oonoceras* Hyatt, 1900 (Sheinwoodian-Lochkovian) and *Peismoceras* Hyatt, 1884 (Sheinwoodian-Přídolí, Turek 1976); and whereas *Phragmoceras* disappeared during the Late Ludfordian Kozlowskii Event, other nautiloids continued to evolve during the latest Silurian. The morphological contrasts between the phragmoceratids and the nautiloids that survived after the phragmoceratid extinction generally are based on few differences. The nautiloid clades that survived the Kozlowskii Event have smaller embryonic shells. Furthermore, nautiloids with a smaller embryonic stage exhibited a higher rate of speciation and commonly composed a larger and more stable palaeo-population than phragmoceratids in the Prague Basin. It is possible that the difference in ontogenetic pattern, *i.e.*, size of embryonic shell, of the nautiloid families was linked to different reactions to rapid environmental abrupt change such was the late Ludfordian Kozlowskii Event.

In general, the large eggs of present cephalopods have a rather longer incubation time than smaller eggs (*e.g.*, Boletzky 1994). If this were also true of Palaeozoic nautiloids, the eggs of those with large apices and hatching size (*e.g.*, *Phragmoceras*) offered a longer time for predators and changing environment. An inverse correlation between temperature and duration of embryonic development (*e.g.*, Boletzky 1994) is another important factor relevant to cephalopod dispersion in the past. This suggests that embryos developed in temperate water (*e.g.*, Prague Basin) longer than on tropical platforms. Embryonic life extension left eggs open to changing environment and predators for more times. In addition, the seasonal fluctuations accompanying especially icehouse climate would have affected populations of nautiloids; effect of these on coleoid cephalopods was summarised by Leporati *et al.* (2007).

In summary, nautiloids with a large embryonic chamber and hatching size were under higher evolutionary pressure especially during any period of rapid environmental change. An example might be the extinction of *Phragmoceras* at the Kozlowskii Event during which the green house climate passed into icehouse climate (Lehnert *et al.* 2007).

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Appendix – List of referred sections

1. Arethusina Gorge Section No. 687 (Praha, Velká Ohrada). Location: See Kříž (1992), fig. 71. Motol Formation. Wenlock, Homerian, *T. testis* Zone: Bouček (1937), Kříž (1992), Kříž *et al.* (1993).

2. Braník U pivovaru Section (Praha, Braník). Location: see Kříž (1999), figure on p. 215. Motol Formation. Llandovery, Telychian, *O. spiralis* Zone: Kříž (1999).

3. Bubovitz e1. Barrande's locality, Czech modern name Bubovice. Type locality of *Phragmoceras biimpresum.* Location: exact site unknown. Motol Formation. Wenlock, Homerian, *T. testis* Zone (determined based on known fossils in Barrande's collection).

4. Butovice Na břekvici Section No. 584 (Praha, Butovice). Location: Kříž (1992), fig. 65. Kopanina Formation. Ludlow, Gorstian, early *C. colonus* Zone: Kříž (1992), Kříž *et al.* (1993).

5. Hinter Kopanina e2. Barrande's locality from which type material of *Phragmoceras labiosum* Barrande, 1865 and *Phragmoceras longum* Barrande, 1865 came. Exact sites unknown, one of them was probably in the Jiras Quarry area (see below).

6. Horní Desort Quarry (Praha, Zadní Kopanina). Location: locality No. 13, geological map 1 : 25 000, sheet Rudná 12-412 (Kovanda ed. 1984). Kopanina Formation. Ludlow, Ludfordian: Svoboda & Prantl (1948), Kříž (1999).

7. Konieprus e2. Barrande's locality. See Velký Hill Section.

8. Kosov Quarry, "new quarry", SW wall. Location: SW wall of the Kosov Quarry. Kopanina Formation. Ludlow, Gorstian, early *S. chimaera* Zone: Manda (unpublished data).

9. Kosov Quarry, "old quarry" (Beroun). Location. Kříž (1992), fig 28. Kopanina Formation. Ludlow, Ludfordian: Horný (1955), Kříž (1992).

10. Kovářovic mez Section (Praha, Butovice). Location: see Kříž (1992), fig. 65. Kopanina Formation. Ludlow, lower-middle Ludfordian: Kříž (1992, 1999).

11. Liščí Quarry (Mořina). Location: Havlíček & Štorch (1990), fig. 6. Kopanina Formation. Ludlow, Gorstian, *S. chimaera* Zone: Horný (1955), Havlíček & Štorch (1990).

12. Lištice Herinky (Lištice). Location: Havlíček & Štorch (1990), fig. 6. Motol Formation. Wenlock, Homerian, *T. testis* Zone: Havlíček & Štorch (1990), Manda (1996).

13. Lištice U cestičky Section No. 759 (Lištice). Location: Kříž (1992), fig. 48. Motol Formation. Wenlock, Homerian, *T. testis* Zone: Kříž (1992), Kříž *et al.* (1993), Manda (1996).

14. Lochkov e2. Barrande's locality. See below, Lochkov, Barrande's pit.

15. Lochkov, Barrande's pits (Praha, Lochkov). Barrande's locality Lochkov e2. Location: Kříž (1999), figure on p. 106. Kopanina Formation. Ludlow, Ludfordian: Kříž (1999). Remarks: old pits of fossil collectors, actually still covered with debris.

16. Mramorový Quarry Section No. 357 (Praha, Lochkov). Location: Kříž (1992), p. 90. Kopanina and Požáry formations. Ludlow, Ludfordian-Přídolí: Kříž (1992).

17. Mušlovka Quarry (Praha, Řeporyje). Location: Kříž (1992), fig. 71. Kopanina and Požáry formations. Ludlow-Přídolí: Bouček (1937), Kříž (1992, 1999), Manda & Budil (2007).

18. Nová Ves, Hradiště II Section (Praha, Nová Ves). Location: Manda & Kříž (2006), fig. 1. Ludlow, Ludfordian, *N. kozlowskii* and *M. latilobus* Zone: Manda (unpublished data), simplified section was published by Manda & Budil (2007), fig. 20.

19. Nová Ves Gorge Section (Praha, Nová Ves). Location: see Bouček (1938). Motol Formation. Llandovery, Telychian, *O. spiralis* Zone: Bouček (1938). Remarks: inaccessible, studied fauna was obtained during sinking of well.

20. Požáry Quarry (Praha, Řeporyje). Location: Kříž (1992), fig. 71. Kopanina and Požáry formations. Ludlow-Přídolí: Kříž (1992, 1999), Carls *et al.* (2007).

21. Řeporyje Section No. 911 (Praha, Řeporyje). Location: see Bouček (1937), p. 9. Kopanina Formation. Ludlow, Ludfordian, lowermost *L. scanicus* Zone: briefly mentioned by Bouček (1937) and unpublished data (Kříž & Manda 2006).

22. U elektrárny Section (Svatý Jan pod Skalou). Location: locality No. 14, geological map 1 : 25 000, sheet Beroun 12-411 (Havlíček 1987). Motol Formation. Wenlock, Sheinwoodian, *M. belophorus* Zone: Havlíček & Štorch (1990).

23. U lanovky Section (near to the town of Beroun). Location: Horný (1955), p. 349. Kopanina Formation. Ludlow, Ludfordian, *S. linearis* Zone: Horný (1955).

24. Velký Hill Section (Koněprusy). Location: locality No. 16, geological map 1 : 25 000, sheet Králův Dvůr 12-413 (Chlupáč 1987). Kopanina Formation. Ludlow, Ludfordian, *S. linearis* Zone: Horný (1955).

25. Vyskočilka e1 Section. Location: see Manda & Kříž (2007), fig. 2. Kopanina Formation. Ludlow, Gorstian, early *L. scanicus* Zone.

26. Vyskočilka e2. Barrande's locality. Type locality of *Phragmoceras imbricatum*. See 25.

27. Zadní Kopanina, Jiras Quarry (Praha, Zadní Kopanina). Location: see Kříž (1999), figure on p. 242. Kopanina Formation. Ludlow, Ludfordian: Kříž (1999).

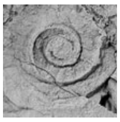
PŘÍLOHA 5

Publikovaná práce

Manda, Š. 2008b. Trocholites Conrad, 1838 (Nautiloidea, Tarphycerida) in the Middle Ordovician of the Prague Basin and its palaeobiogeographical significance. Bulletin of Geosciences 83, 327−334.

Trocholites Conrad, 1838 (Nautiloidea, Tarphycerida) in the Middle Ordovician of the Prague Basin and its palaeobiogeographical significance

ŠTĚPÁN MANDA



Nautiloids of the order Tarphycerida are a characteristic component of warm-water Ordovician faunas of Baltica and Laurentia but are usually absent from the cooler high latitude marine environments. The presence of the tarphycerid *Trocholites,* reported from the Middle Ordovician, Dobrotivian (late Darriwilian) strata of the Iberian Chain and Armorican Massif (peri-Gondwanan Europe), provide an exception. *Lituites primulus* Barrande, 1865, represented by a single poorly-preserved individual was reported from coeval strata in the Prague Basin (Perunica) and doubtfully assigned to *Curtoceras* or *Trocholites*. New biostratigraphicaly well-constrained specimens of *Trocholites* described and discussed from the early Dobrotivian of the Prague Basin, are conspecific with *Trocholites fugax* previously described from the Iberian Chain and Armorican Massif. The contemporaneous presence of *Trocholites fugax* in Perunica and peri-Gondwanan terranes is additional evidence for faunal connections between these microcontinents during the Dobrotivian. By comparison with the preceding Llanvirnian (early Darriwilian) fauna, the low diversity Dobrotivian cephalopod fauna of the Prague Basin suggests an increasing faunal separation between Perunica and Baltica. The occurrence of *Trocholites* in early Dobrotivian strata of Perunica, the Iberian Chain and Armorican Massif reflects an unusual dispersion event of tarphycerids into lower latitude seas coinciding with a distinct climate perturbation during the Ordovician. • Key words: Middle Ordovician, Dobrotivian, Darriwilian, Cephalopoda, Tarphycerida, taxonomy, Prague Basin.

MANDA, Š. 2008. *Trocholites* Conrad, 1838 (Nautiloidea, Tarphycerida) in the Middle Ordovician of the Prague Basin and its palaeobiogeographical significance. *Bulletin of Geosciences 83(3)*, 327–334 (4 figures, 1 table). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received August 11, 2008; accepted in revised form September 1, 2008, issued September 30, 2008.

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The Ordovician cephalopod fauna of the Prague Basin was described by J. Barrande in his classic *"Système silurien du Centre de la Bohême"* (1865–1877). Barrande erected 35 species of *Orthoceras* Bruguière, 1789, two species of *Bathmoceras* Barrande, 1867, three species of *Endoceras* Hall, 1847, and a single species each of *Tretoceras* Salter, 1858, *Bactrites* Sandberger, 1843, *Gomphoceras* Sowerby, 1839 (*in* Murchison 1939), and *Lituites* Bertrand, 1763. Despite continual and intensive research on the Ordovician strata of the Prague Basin since Barrande's time, only a single new cephalopod species has been added (Marek 1999). This suggests that our knowledge of the Ordovician cephalopod fauna of the Prague Basin is relatively complete. Dzik (1981) synonymized *Tretoceras parvulum* Barrande, 1868 with *Bactroceras sandbergeri* (Barrande, 1868); see also Hewitt & Stait (1985) and Evans (2005). Marek (1999) suggested that *Bathmoceras complexum* (Barrande, 1856) is conspecific with *Bathomoceras praeposterum* Barrande, 1867. Many researches have provided information about the stratigraphic ranges of Barrande's species (for example Prantl 1952; Havlíček & Vaněk 1966; Mergl 1978; Kraft & Kraft 1990, 1993, 1994; Budil 1999), although the identity of certain taxa is in need of revision. The last short summary of cephalopod distribution in the Ordovician of the Prague Basin was published by Marek (1999).

As a rule, cephalopods are rather uncommon in the Ordovician of the Prague Basin. The fauna usually consists of one species or a few taxa of orthocone cephalopods belonging to the orders Orthocerida and Pseudorthocerida (and where unrevised, commonly referred to the genus *Orthoceras*). Ellesmerocerids are known from the Klabava Formation (Arenigian; Dapingian–earliest Darriwilian), the Šárka Formation (early Darriwilian; latest Arenigian-Llanvirnian) and the Králův Dvůr Formation (Kralodvorian; early Hirnantian). Endocerids and a single actinocerid are restricted to the Šárka Formation. A single oncocerid shell has been described from the Králův Dvůr Formation (see Marek 1999).

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Tarphyceratids are known only from the Dobrotivá Formation (Dobrotivian, late Darriwilian). Barrande (1865) described a single poorly-preserved shell, assigning it to "*Lituites*" *primulus*. Klouček (1909), Vaněk (1999), and Marek (1999) all referred to the presence of "*Lituites*" *primulus* or *Curtoceras*, respectively, but without providing descriptions. This paper describes a suite of newly-collected specimens regarded as belonging to *Trocholites fugax* Babin & Gutiérrez-Marco, 1992. The occurrence of tarphycerids in the low diversity cephalopod fauna of the early Dobrotivian is of palaeobiogeographic significance because they are only known from Perunica and peri-Gondwanan Europe during Dobrotivian time (*e.g.*, Babin *et al.* 1996, Bogolepova 1999).

The order Tarphycerida Flower, 1950 includes nautiloids with a bilaterally symmetrical, evolute or convolute shell and a relatively thick siphonal tube. Lithuitids originally grouped together with tarphyceratids (see Flower 1950, Furnish & Glenister 1964) in fact comprise an independent clade "Lituitina" Dzik, 1984 within the Orthoceratoidea Khun, 1940 (see Dzik 1981, 1984). In addition, some authors considered the order Barrandeocerida Flower, 1950 as a suborder within the Tarphycerida (see Turek 2008), but more data concerning early ontogeny and structure of the siphuncle are needed. Tarphyceratids appeared during the latest early Ordovician and their diversity rapidly reached its maximum just before the Middle Ordovician (Frey *et al.* 2004). During the Ordovician tarphycerids inhabited shallow and warm seas of carbonate platforms, *e.g.*, Baltica, Laurentia, and Kazakhstania. The end-Ordovician extinction event reduced the diversity of the Tarphycerida, and the few surviving clades became extinct during the Silurian (for summary see Dzik 1984, Stridsberg & Turek 1997). The tightly-coiled nautiliconic shell of tarphyceratids suggests that they might have been active swimmers (see Westermann 1998).

Cephalopod distribution in the Middle Ordovician of the Prague Basin

The Middle Ordovician sequence of the Prague Basin is divided into the Klabava, Šárka and Dobrotivá formations. In the classic concept (for summary see Havlíček 1998), the Klabava Formation corresponds with the Arenigian–earliest Llanvirnian, the Šárka Formation with the Llanvirnian and the Dobrotivá Formation with the Dobrotivian. The recent international division of the Middle Ordovician does not fit well with the British and Mediterranean stages and the correlation of Bohemian to international remains unclear. Following the concept of P. Kraft and O. Fatka and presented by various authors (see Kraft & Fatka 1999), the Middle Ordovician is here taken to have started within the Klabava Formation and ended close to the boundary between the Dobrotivá and Libeň formations.

Klabava Formation: Arenigian-earliest Llanvirnian (Dapingian–earliest Darriwilian)

Cephalopods appear in the Prague Basin at the beginning of the Middle Ordovician in the upper part of the Klabava Formation, which consists mainly of yellow-grey and reddish shales. Two indeterminable species of orthocone cephalopods and the ellesmerocerid *Bathmoceras complexum* (Barrande, 1856) have been reported from the shales of the *Holograptus tardibrachiatus* Zone, Arenigian, Dapingian (Kraft & Kraft 1993, Marek 1999). The ellesmerocerid *Bactroceras* cf. *sandbergeri* (Barrande, 1867), and lituitid *Rhynchorthoceras* cf. *angelini* (Boll, 1857) occur rarely in the shales and tuffites of the succeeding *Azygograptus ellesi–Tetragraptus reclinatus abbreviatus* Zone (Kraft & Kraft 1994, Marek 1999). The appearance of ellesmerocerid and lituitid genera in the upper Klabava Formation is considered to be a refection of the initiation of communication between Perunica and Baltica during the late Arenigian (Frýda 1988, Mergl 1991, Frýda & Rohr 1999). Dzik (1983) pointed out that the conodont fauna of the late Klabava Formation contains some Baltic taxa although diversity is low in comparison with Baltica probably due to cold water conditions (see also Zusková 1993). The same distribution pattern is exhibited amongst trilobite and gastropod faunas as well as cephalopod faunas.

Šárka Formation: Llanvirnian (early Darriwilian)

The Šárka Formation (Llanvirnian; early Dariwillian) consists mainly of dark shales and contains the most diverse cephalopod fauna in the Ordovician of the Prague Basin. Cephalopods have been collected mainly from siliceous nodules in the Rokycany and Praha town areas. The most common material consists of orthoconic cephalopods belonging to the orders Orthocerida and Pseudorthocerida, which need to be revised. The ellesmerocerids *Bactroceras sandbergeri* (Barrande, 1867) (including *Tretoceras parvulum* Barrande, 1868, see Dzik 1984) and *Bathmoceras complexum* (Barrande, 1856) (including *Bathmoceras praeposterum* Barrande, 1867, see Marek 1999) are less common. Endocerids are represented by three rare species: *Vaginoceras novator* (Barrande, 1870), *Cameroceras peregrinum* (Barrande, 1870) and "*Endoceras*" *conquassatum* Barrande, 1870 (see Marek 1999). The single actinocerid species "*Orthoceras*" *bonum* is also rare (Marek 1999). The presence of ellesmerocerids, endocerids and actinocerids reflects a period of enhanced faunal exchange between Baltica and Perunica during the Llanvirnian (Marek 1999). The cephalopod fauna of the Šárka Formation exhibits the strongest affinity within the Ordovician sequence of the Prague Basin with Baltic cephalopod faunas (*e.g.*, Holm 1899a, b; Balashov 1968). By contrast, the

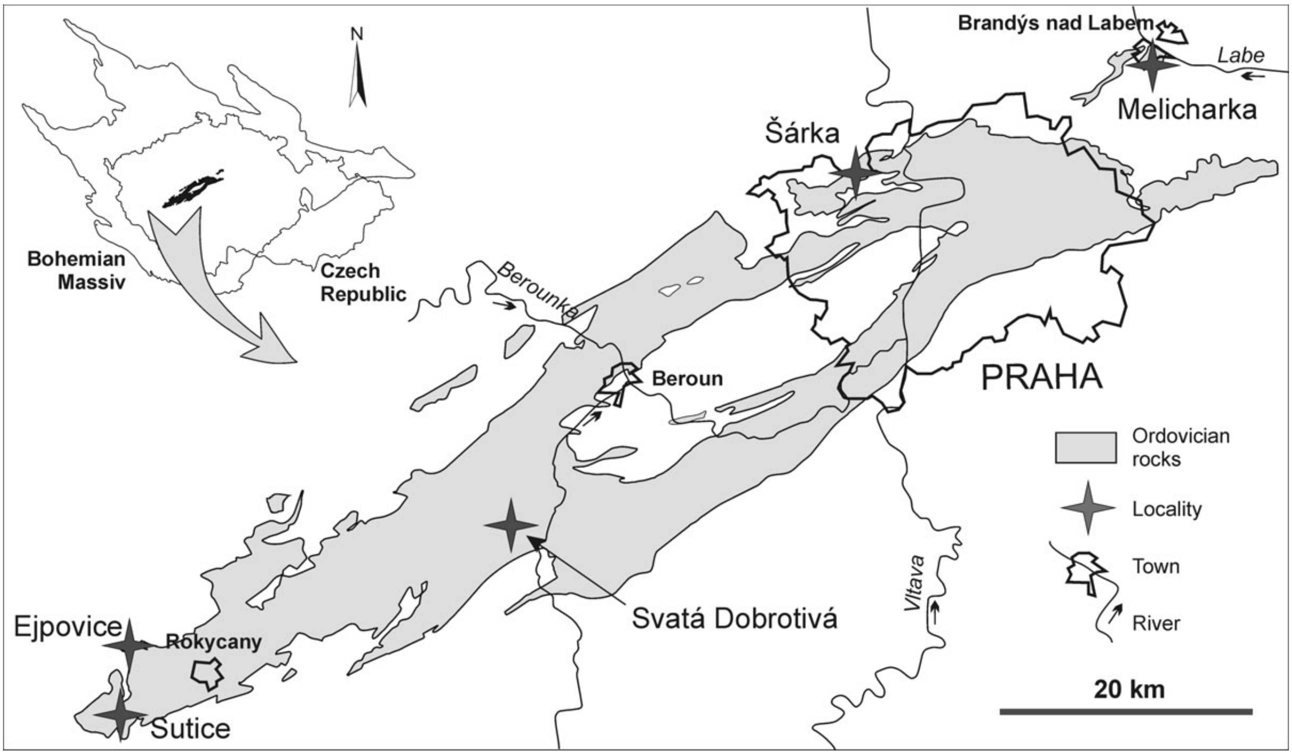

Figure 1. Distribution of the Ordovician rocks in the Prague Basin, Czech Republic and the location of *Trocholites*-bearing localities.

benthic fauna that consists of trilobites and brachiopods shows only weak affinities with Baltic assemblages (Havlíček *et al.* 1994).

Dobrotivá Formation: Dobrotivian (late Darriwilian)

The Dobrotivá Formation is developed as black shales similar to those of the underlying Šárka Formation. The two formations differ in the nature of their faunal communities rather than facies. The cephalopod fauna of the Dobrotivá Formation is reduced in diversity by comprison with the Šárka Formation. The Baltic genera represented in the Šárka Formation are missing from the Dobrotivá Formation. Three rare species of longiconic orthocerids occur in siliceous nodules and more rarely in shale (Klouček 1909, Havlíček & Vaněk 1966). In addition, Barrande (1865) described a poorly-preserved portion of a coiled shell from the Svatá Dobrotivá (Sancta Benigna) locality as *Lituites primulus* Barrande, 1865 (see Fig. 2). Klouček (1909) also reported *Lituites primulus* from the Šárecké Valley at Praha and Vaněk (1999) listed "*Lituites*" *primulus* from siliceous nodules from the lower part of the Dobrotivá Formation at locality Melicharka in Brandýs nad Labem Town. An additional specimen was reported by Mergl (1996) from a shale of the *Hustedograptus teretiusculus* Zone at Ejpovice Village (Fig. 1).

Palaeobiogeographical significance of *Trocholites*

Tarphycerid nautiloids originated in the late Early Ordovician and form a characteristic component of Middle to Upper Ordovician cephalopod faunas, inhabiting warm-water carbonate platforms (for summary see Furnish & Glenister 1964, Dzik 1984). Thus tarphycerids may be considered as an indicator of warm-water masses or might suggest connections with such water bodies. *Trocholites* Conrad, 1838 including 42 species is widely distributed in Middle and Upper Ordovician strata of Baltica, South and North China, Tibet, Laurentia, and Australia (for summary see Schröder 1891, Whiteaves 1904, Chen & Liu 1976, Dzik 1984, Stait *et al.* 1985, Babin & Gutiérrez-Marco 1992 and Guo 1998).

Havlíček *et al.* (1994, p. 37) emphasized the "absolute difference in benthic and necto-benthic association" between Baltica and Perunica during the Dobrotivian. According to Havlíček *et al.* (1994), Tornquist's Ocean "functioned as an effective barrier" during Dobrotivian times. Kraft & Kraft (1990) and Fatka *et al.* (1998) described a single specimen of the Baltic graptolite *Gymnograptus linnarsoni* (Moberg, 1896) from the *Hustedograptus teretiusculus* Zone of the Prague Basin. The presence of *Trocholites* in the Prague Basin further suggests a degree of connection with Baltica during the *Hustedograptus teretiusculus* Zone. The presence of *Trocholites* in early Dobrotivian contrasts with the absence of any other

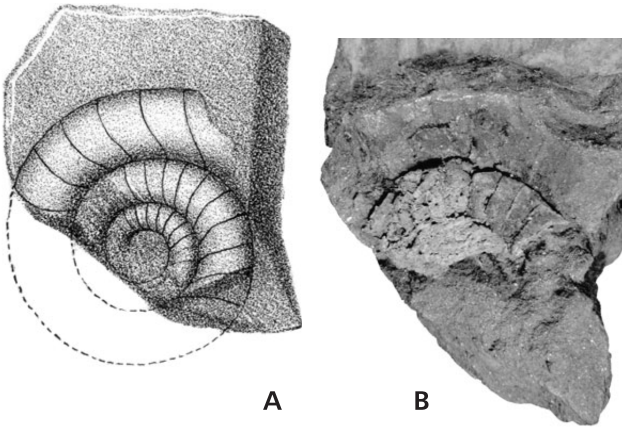

Figure 2. "*Lituites primulus*" Barrande, 1865; holotype by monotypy. Svatá Dobrotivá (Sancta Benigna) d1 locality. Most probably Middle Ordovician, lower Dobrotivian, Dobrotivá Formation. • A – reproduction of a specimen illustrated by Barrande (1865) on pl. 99 as fig. 12, × 1.2. • B – the same specimen, lateral view, × 1.2. National Museum, L 40460.

cephalopod genus shared with Baltica during this time as well as the absence of tarphycerids in the underlying Llanvirnian where five Baltic genera are present.

Trocholites fugax was described by Babin & Gutiérrez-Marco (1992) from the early Dobrotivian of Spain. Babin *et al.* (1996) described the same species from the Dobrotivian of the Armorican Massif. Thus the presence of *Trocholites fugax* in the Prague Basin, Iberian Chain and Armorican Massif are coeval, suggesting that faunal exchange took place between these areas during the early Dobrotivian, which is in agreement with the conclusions of Havlíček *et al.* (1994). More recently Ausich *et al.* (2002) described a Dobrotivian echinoderm fauna from the Iberian Chain and suggested that there was faunal isolation between peri-Gondwana and Perunica. In addition, Evans (2000) noted the presence of *Trocholites* even in the Middle Ordovician of Bolivia, Northwestern Gondwana, but this material has not yet been described nor figured.

Conclusions

The appearance of the coiled tarphycerid *Trocholites fugax* in the early Dobrotivian of Perunica and peri-Gondwana seem to reflects an unusual dispersion event of tarphycerids to higher latitudes (Fig. 4). It suggests that isolation between Baltica and Perunica was not absolute, as was previously stated. Havlíček *et al.* (1994) explained the isolation between the Prague Basin and Baltica through enhanced surface currents of Tornquist's Sea. However, there is no reason why such currents should have confined faunal exchange. Contrarily, faunal isolation would be more likely where surface current activity is low, leading to prolonged transport of invertebrate larvae and the higher probability of their mortality. With more occasional instability common in weak currents, this would cause mass mortality of the larvae. Babin & Gutiérrez-Marco (1992) proposed that the presence of *Trocholites* in Spain during the early Dobrotivian might be explained by a prolonged period of climatic disturbance in which storm systems that developed in temperate palaeolatitudes in the vicinity of Baltica, transferred bodies of water carrying planktic and nektonic animals southward onto peri-Gondwana.

The nektonic habit of *Trocholites* is clearly suggested by its small nautiliconic shell (see Westerman 1998). In addition, the very small size of the embryonic shell of *Trocholites* might indicate the planktotrophy of the early post-hatching stage. Evans (2000) studied an Ordovician cephalopod fauna from Saudi Arabia that included warm-water elements, *i.e.* northern shelf of Gondwana, using the hypothesis of Babin & Gutiérrez-Marco (1992) to explain their presence there. The occurrence of *Trocholites fugax* in the Prague Basin also appears to support this hypothesis.

Systematic palaeontology

Subclass Nautiloidea Agassiz, 1847
Order Tarphycerida Flower, 1950 (*in* Flower & Kummel 1950)
Family Trocholitidae Chapman, 1857

Genus *Trocholites* Conrad, 1838

Type species. – *Trocholites ammoinius* Conrad, 1838.

Trocholites fugax Babin & Gutiérrez-Marco, 1992

Figure 3A–E

?1865 *Lituites primulus* Barr.; Barrande, pl. 99, fig. 12.
1992 *Trocholites fugax* n. sp.; Babin & Gutiérrez-Marco, pp. 530–534, figs 3a–h, 4a–f. See for further synonymy of Spanish material.
?1992 *Lituites primulus*. – Babin & Gutiérrez-Marco, p. 534.
1996 *Trocholites fugax*. – Babin *et al.*, p. 107, pl. 1, figs 1–3.
1996 "cyrtokonní nautiloid". – Mergl, p. 32.
1999 "*Lituites*" *primulus* Barrande. – Vaněk, p. 8.
?1999 *Curtoceras primulus*. – Marek, pp. 415, 416.

Holotype. – Specimen No. NE VII 2639 (Museo GeoMinero, Madrid) designated by Babin & Gutiérrez-Marco (1992) and figured by them as fig. 3D. Middle Ordovician, early Dobrotivian. Navas de Estena, Massif Hesperian, Spain.

Material. – Seven more or less flattened shells preserved in shale: specimens No. 11484, 11518, 11521, 11560, 11664,

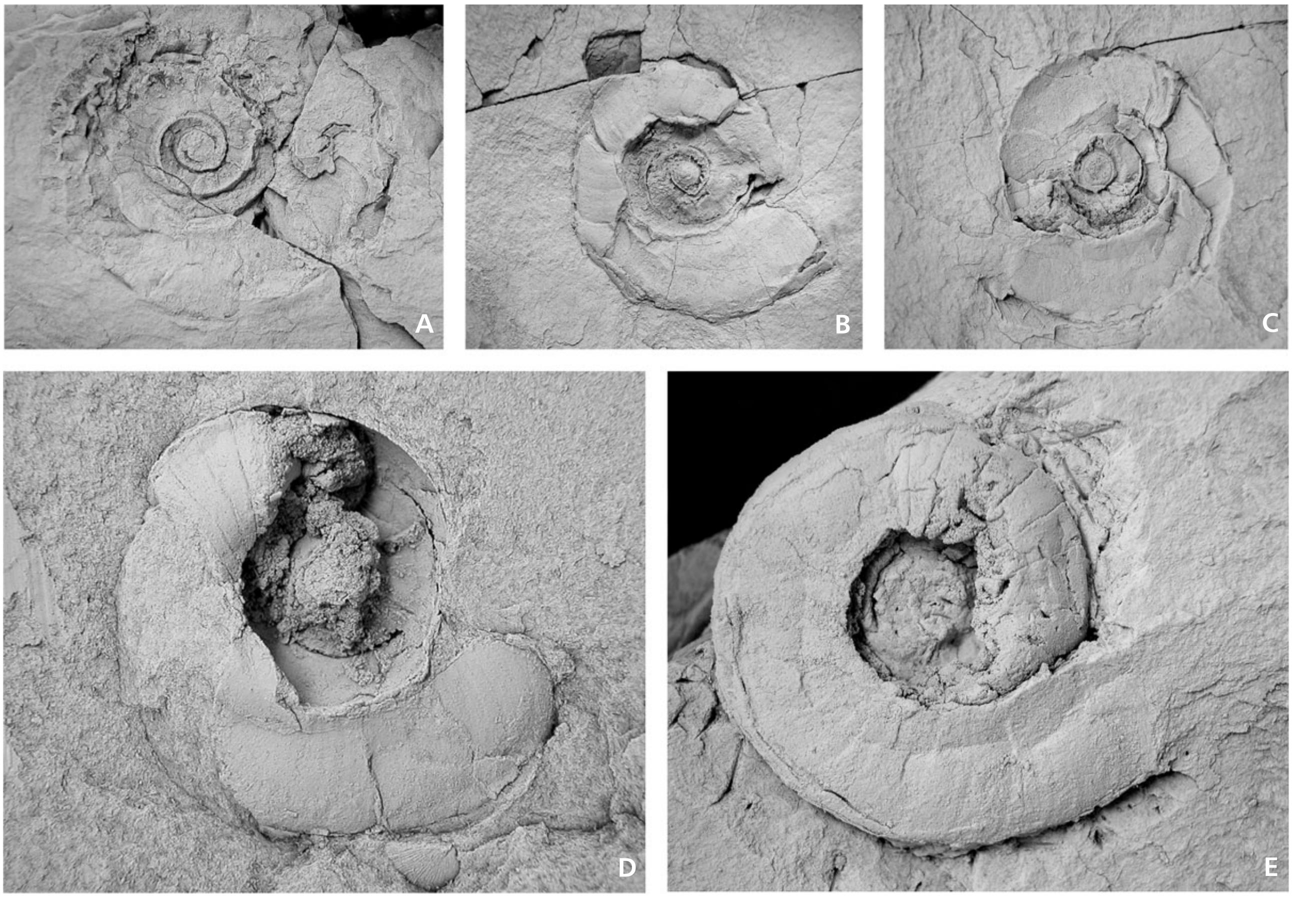

Figure 3. *Trocholites fugax* Babin & Gutiérrez-Marco, 1992. Prague Basin, Ordovician, Middle Ordovician, lower Dobrotivian. Dobrotivá Formation. • A – Tymákov, Sutice 1, western slope, lateral view, × 1.4, specimen No. 11675, collection of M. Mergl, Museum of Doctor Bohuslav Horák, Rokycany. • B – Tymákov, Sutice 1, western slope, lateral view, × 1.3, specimen No. 11518, collection of M. Mergl, Museum of Doctor Bohuslav Horák, Rokycany. • C – Tymákov, Sutice 1, western slope, lateral view, × 1.2, specimen No. 11484, collection of M. Mergl, Museum of Doctor Bohuslav Horák, Rokycany. • D – Ejpovice, Ejpovice, northern slope of Čilina Hill, lateral view, × 1.8, CGS MM 517a. • E – Tymákov, Sutice 1, western slope, lateral view, × 2.3, specimen No. 11521, collection of M. Mergl, Museum of Doctor Bohuslav Horák, Rokycany. All specimens are coated with ammonium chloride.

11675 are housed in the Museum of Doctor Bohuslav Horák in Town of Rokycan, West Bohemia; specimen MM 517a, b is deposited in the Czech Geological Survey, Praha, Collection of M. Mergl. Two additional unnumbered specimens are housed in the private collection of O. Karoušek.

Description of the Bohemian material. – Gradually expanding exogastric convolutedly coiled shells. Whorl cross section depressed and rounded across the venter and flanks. Siphuncle dorsal and submarginal, its diameter is about 0.5 mm where the lateral diameter of the shell is about 6 mm. Body chamber long, about two-thirds of a volution. Cameral depth is about 1/3–1/4 of the dorsoventral diameter of the whorl. Sutures are poorly preserved, probably almost straight with weak dorsal lobe. First three whorls exhibit almost straight, densely-packed growth lines that later become irregular and more distant. Hyponomic sinus is shallow and broad. Approximately five whorls are developed. Embryonic shell is not visible, but must be very small with a diameter less than 0.5 mm. Dimensions are giving in Table 1.

Discussion. – Barrande (1865, pl. 99 as fig. 12) first illustrated *Lituites primulus* as a new species (holotype by monotypy, see Fig. 2). This type specimen is a small part of a convolute phragmocone with three whorls preserved in a slightly flattened state in dark shale. As noted by Babin & Gutiérrez-Marco (1992), the preservation of the specimen figured by Barrande as *Lituites primulus* excludes a precise comparison with better-preserved specimens showing more diagnostic features. The mode of coiling and the depth of the camerae are similar to that of *Trocholites fugax.* The holotype of *Lituites primulus* came from the Svatá Dobrotivá – Sancta Benigna d1 locality, the exact site of which is unknown. However, the brachiopods and trilobites described by Barrande from this locality clearly suggest a Dobrotivian age, and the lithology of the matrix is similar

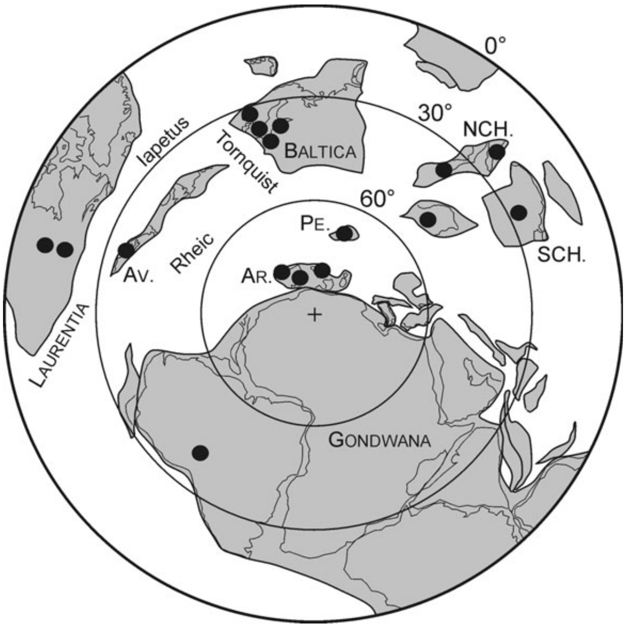

Figure 4. Distribution of *Trocholites* in the Middle Ordovician. Palaeogeographic reconstruction adopted from Cocks & Torsvik (2002). For data see Schröder (1891), Chen & Liu (1976), Dzik (1984), Babin & Gutiérrez-Marco (1992), Babin *et al.* (1996), and Frey (1995). Abbreviations: Ar. – Armorica, Av. – Avalonia, NCH. – North China, SCH. – South China, Pe. – Perunica.

Table 1. Dimensions of *Trocholites fugax*. Abbreviations: dv – diameter of shell (ventral), dd – diameter of shell (dorsal), wh – whorl height, uw – umbilical width (diameter of whorl), n – number of visible whorls. All measurements are in mm.

Specimen	dv	dd	wh	uw	n
MM 517	24	21	8	11.5	5
11484	30	25.5	10	12	5
11518	29	24	11	14	5
11521	27	21	8	10.5	4
11560	19	16	5	9	4
11664	13	12	4	8	4
11675	30.5	26.5	12	14	5

to that of the Dobrotivá Formation. This suggests that *Trocholites fugax* and *Lituites primulus* are coeval and probably conspecific, but the poor preservation of the holotype of the latter leaves some uncertainty as to this and therefore the type species is not proposed as a senior synonym of *Trocholites fugax*.

Occurrence. – Dobrotivian of Spain and the Armorican Massif, France (Babin & Gutiérrez-Marco 1992; Babin *et al.* 1996).

Prague Basin (Bohemia): Middle Ordovician, early Dobrotivian (early Llandeillan, late Darriwilian), *Hustedograptus teretiusculus* Zone. Lower Dobrotivá Formation.

1. Ejpovice, northern slope of Čilina Hill, W of Rokycany Town, West Bohemia; black shale with brachiopods, conularids, graptolites, bivalves, hyolithids, orthocone cephalopods, trilobites, machaerids, ostracods and echinoderms (for detail of fossil contents see Mergl 1996); single specimen was collected by M. Mergl.
2. Tymákov, Sutice 1, western slope, West Bohemia, dark grey shale with numerous trilobites and brachiopods (see Mergl 1978); all available specimens were collected by M. Mergl.
3. Melicharka, field at Melicharka factory, Brandýs nad Labem, Central Bohemia; shale with small siliceous nodules rich in trilobites, brachiopods, graptolites, orthocone cephalopods, conularids, bivalves and echinoderms (for detailed descriptions see Vaněk 1999); two specimens of *Trocholites* are present in private collection of O. Karoušek from Brandýs nad Labem.

Acknowledgments

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DOI 10.3140/bull.geosci.2008.02.141

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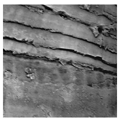
PŘÍLOHA 6

Publikovaná práce

Manda, Š., Turek, V. 2009a. A Silurian oncocerid with preserved colour pattern and muscle scars (Nautiloidea). Bulletin of Geosciences 84, 755–766.

A Silurian oncocerid with preserved colour pattern and muscle scars (Nautiloidea)

ŠTĚPÁN MANDA & VOJTĚCH TUREK



A new genus *Euryrizocerina* (Nautiloidea, Oncocerida, Oonoceratidae) from the late Silurian strata of Bohemia (Prague Basin) is established. Two species are included within the genus: the type species *E. normata* (Barrande, 1877) and *E. pulchra* sp. nov. The genus is striking for two features – the preservation of shell colouration and muscle attachment scars in the type species. These features are reliable for taxonomic and palaeoecological analysis of nautiloids, but due to their only occasional preservation in fossils, the evolutionary trends of these characters remain poorly understood. The colour pattern of *Euryrizocerina* consists of irregular pulsed transverse bands that clearly differ from the colour patterns known in other oncocerids where rather regular wave-like or zig-zag bands have been observed. It is questionable whether the new type of colouration represents a taxonomic or morphotypic feature, as *Euryrizocerina* is the first oncocerid to be recognised with a highly curved shell that retains colouration. Oncocerids exhibit multiple paired muscle scars and there is uncertainty whether these represent an original metamery, inherited from a cephalopod ancestor, or a derived feature. *Euryrizocerina* possesses four pairs of retractor muscle scars, but its ancestor "*Oonoceras*" *fraternum* and allied forms, possess multiple pairs of muscle scars around the base of the body-chamber, as do the majority of oncocerids. A similar reduction in the number of muscle scar pairs has been documented in Devonian rutoceratoids. The high evolutionary plasticity of muscle attachments patterns, as indicated by these examples, suggests that the muscle complex and its attachment to the shell was under adaptive control and is more likely to reflect the form of the shell and the mode of life of the organism. It seems likely that shell colouration and the pattern of attachment of the retractor muscles have a much more complex evolutionary history (including several convergences) than was previously supposed. •

Key words: Nautiloidea, Oncocerida, colour pattern, muscle scars, Silurian, Prague Basin, new taxa.

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The shell in nautiloids serves a hydrostatic, hydrodynamic and protective function. Final shell form reflects evolutionary interplay between both these functions. Disparity of shell form in nautiloids is striking and almost all geometrically possible forms evolved at some time during the Palaeozoic. The first classifications of cephalopods in the 19th, and in particular during the early 20th century, used morphotype as the main diagnostic feature. Hyatt (1883, 1994, 1900) and later Flower & Kummel (1950) adopted new systematic approaches emphasising the importance of the morphology of the siphonal tube. Subsequent studies of muscle scars (*e.g.*, Mutvei 1964, Evans 2005, Kröger & Mutvei 2005), embryonic development (*e.g.*, Manda 2008), and shell colouration (*e.g.*, Kobluk & Mapes 1989, Turek 2009) provided important additional data with significant implications in relation to the taxonomy and palaeoecology of nautiloids. Some of this data is not yet fully incorporated into concepts of classification and remain a matter of debate; for example, the significance of variation in the number of multiple paired muscle scars in oncocerids and discosorids.

Embryonic shells, muscle scars or shell colouration are rarely preserved in the fossil record, whilst precise data relating to age and locality are often missing in specimens from old collections. Therefore any additional material representing exceptionally preserved nautiloids may provide important data for a better understanding of nautiloid taxonomy and evolution. We follow Teichert (1988) in his concept of a subclass, Nautiloidea, which includes the orders Oncocerida, Discosorida, Tarphycerida and Nautilida.

A new oncocerid genus, *Euryrizocerina,* from the Silurian strata of Bohemia with preserved shell colouration and

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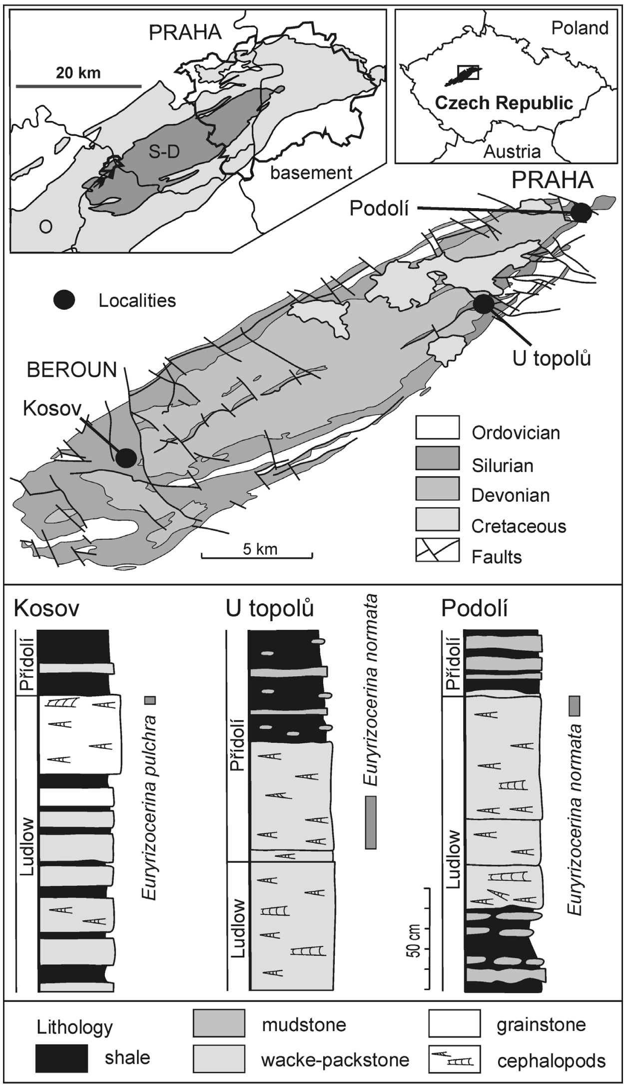

Figure 1. Position of Early Palaeozoic Prague Basin within the Czech Republic (A), Central Bohemia (B), respectively, and detailed map of Prague Synform with location of fossil bearing localities (C). Simplified stratigraphic and lithologic columns are given (B). Data sources: Kosov Quarry after Vokáč (1999), modified; U topolů (unpublished data, Zedník & Manda); and Podolí (Kříž & Manda, unpublished data).

muscle scars is described in this paper and its taxonomic assignment is discussed. Most of the specimens studied were collected during recent studies of selected sections within the Prague territory and from Kosov Quarry near Beroun, Prague Synform (Fig. 1). A marked change in the character of the muscle scars of *Euryrizocerina* and its ancestor over a short time interval suggests a high degree of plasticity in the evolution of muscle attachment patterns at least in the Oncocerida and Discosorida.

Terminology. – 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). Detailed parameters of the curved exogastric shell were not elaborated until now; some terms have been used intuitively. Figure 5 shows the basic parameters we used in descriptions.

The graptolite Zone is used as defined by Štorch (1994, 1995), Kříž (1998) and Manda & Kříž (2006).

Institutional abbreviations. – Studied specimens are deposited in the Czech Geological Survey, Prague, in the Š. Manda collections (prefix CGU SM); National Museum, Prague (prefix NM L); and Museum of Comparative Zoology, Harvard University, Cambridge (prefix MCZ). All specimens, except those figured in Figs 2 and 7F, were coated with ammonium chloride prior to photographing. Specimens with preserved colour pattern were photographed in alcohol.

Colour pattern in nautiloids

Colour pattern is known only in a small number of Early Palaeozoic nautiloid genera (Kobuk & Mapes 1989, Turek 2009 and further references herein). Colour patterning was described in the Ordovician tarphycerid *Trocholites* Conrad, 1838 from Germany (Schuh 1920), in the Silurian oncocerids *Octameroceras* Hyatt, 1900 from Gotland (Stritsberg 1985) and *Rizosceras* Hyatt, 1900 from Canada (Foerste & Savage 1927). Colour patterns in the Devonian *Cyrtoceratites* Goldfuss, 1833 from Germany were mentioned by Foord (1888) but not illustrated. Sweet & Leutze (1956) described a shell fragment of a presumed oncocerid with preserved colouration from the Silurian rocks of New York. All other nautiloids with preserved colour pattern are known from the Prague Basin, Bohemia. Several coloured shells were described and illustrated by Barrande (1865–1877) in the Silurian cumulative genera *Trochoceras* Barrande, 1848, *Orthoceras* Bruguière, 1792, *Cyrtoceras* Goldfuss, 1833, and *Phragmoceras* Broderip, 1839 (*in* Murchison 1839). Turek (1990, 2004) observed colour patterns in some other oncocerids and the discosorid *Phragmoceras imbricatum* Barrande, 1865, but these specimens have yet to be figured or described in detail. Turek (2009) described well-preserved colour patterns in the Devonian oncocerid *Ptenoceras* Hyatt, 1894 and Manda & Turek (2009a) in the Silurian oncocerid *Pomerantsoceras* Kröger, 2007a.

Almost all Bohemian nautiloid shells with traces of colouration have been obtained from cephalopod limestones that comprise the "condensed" dark grey cephalopod wacke-packstone (Braník type *sensu* Ferretti & Kříž 1995, Kříž 1998). Turek (2009) assumed that low oxygen level on and below the sea-floor, combined with rapid burial and cementation provided suitable conditions for the preservation of colour markings. However, although such

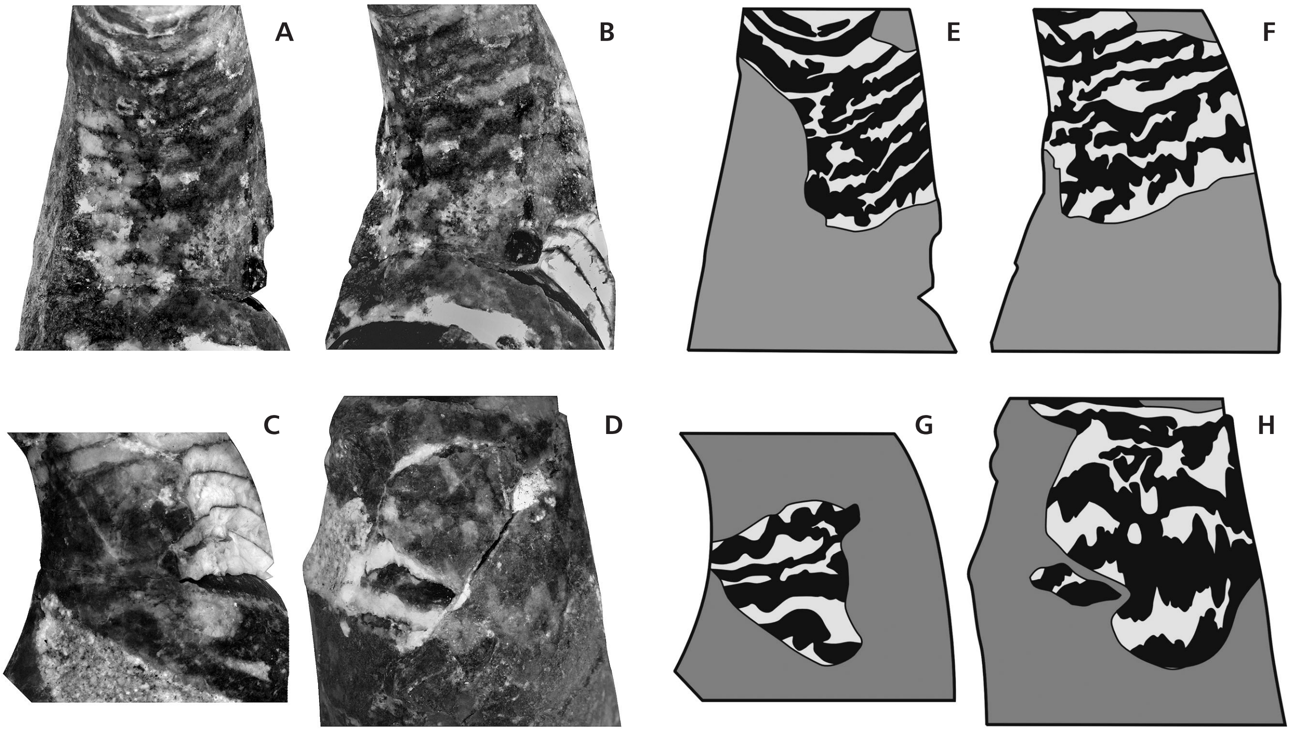

Figure 2. Colour pattern in *Euryrizocerina normata* sp. nov., photographs (on the left) and sketch drawings (on the right) of the same specimens from Lochkov, U topolů Section, earlier Přídolí, *Priastiograptus parultimus* Zone, Kopanina Formation. • A, B, E, F – CGS SM 379, dorsal and ventolateral views, × 2. • C, D, G, H – CGS SM 378, lateral and dorsal views, × 1.2.

conditions characterised the cephalopod limestones of the Braník type in general, coloured shells occur only in a few localities. For example, rich new material, comprising 12 coloured shells (including specimens described below), was obtained from a single bed and limited area in the U topolů Section. In other parts of the section, as well as in neighbouring sections (Nad ubikacemi, Hvížďalka sections), no coloured shell has been found. This indicates that there are additional factors controling colour preservation that have yet to be recognized.

It is generally accepted that shell colouration in present day *Nautilus* and *Allonautilus,* as well as in fossil nautiloids, serves as light screening and camouflage (Stenzel 1964, Cowen *et al.* 1973, Westermann 1998, Manda & Turek 2009). Details concerning the intraspecific variability of colour patterns and their evolution remain poorly understood. The exceptionally well-preserved cephalopods from Bohemia are an important source of material with which to resolve these questions, especially in oncocerids (tarphycerids and discosorids with preserved shell colouration are very rare). A further problem is that many of the taxa now thought likely to be oncocerids were originally assigned to *Orthoceras* and *Cyrtoceras* by Joachim Barrande (1865–1877). These taxa are poorly known and in need of revision.

Colour patterns in nautiloids take several forms. These include radial bands, transversal undulating lines, zig-zag lines, as well as combinations of these forms (Ruedeman 1921, Foerste 1930a, Teichert 1964, Stridsberg 1985, Kobuk & Mapes 1989, Turek 2009). High disparity in the pattern of shell colouration itself suggests an adaptive control of shell colouration. Links between shell morphotype, biofacies and colour pattern are poorly understood; although recently such an example was discussed by Manda & Turek (2009a).

Description of colour pattern in *Euryrizocerina* and its significance

Shell colouration is preserved in two specimens of *Euryrizocerina normata*. In CGS SM 378 (Fig. 2C, D, G, H) the colour pattern is preserved on the dorsal side and in particular the left lateral side of the phragmocone. The colour pattern consists of irregular transverse bands that vary in width between 2 and 4 mm. Neighbouring bands are occasionally connected by narrow longitudinal zones. The course of the bands approximately coincides with the direction of growth lines. In CGS SM 379 (Fig. 2A, B, E, F) the pattern of colouration is preserved in part on the ventral, right lateral, and in particular, the left lateral and dorsal sides of the shell. The colour pattern consists of transverse bands that vary strongly in width (2 to 5 mm). As with the specimen described previously, the bands are connected by narrow longitudinal or slightly oblique zones. In the holotype of *Euryrizocerina normata,* colouration is poor, but just visible.

Euryrizocerina is the first oncocerid known with a strongly curved shell in which the colour pattern is known. The irregular and pulsating colour bands differ markedly from colour patterns in other oncocerids. The colour pattern in breviconic oncocerids with straight or slightly curved shells (that do not reach the inflexion point, see Fig. 5) that resemble *Rizosceras* Hyatt, 1900 and *Metarizoceras* Foerste, 1930b (see Sweet 1964), usually consist of rather regular narrow wavey bands, or zig-zag structures, or a combination of the two (Barrande 1865–1877). *Rizosceras* and *Metarizoceras* are regarded as demersal nautiloids living close to the sea-floor with a more or less downwardly oriented aperture. By contrast, *Euryrizocerina,* with a slender and highly curved shell is interpreted as a nectobenthic, actively swimming nautiloid with a forwardly oriented aperture (see Westermann 1998). Consequently, the difference in the observed colour pattern may be linked to the shell morphotype and thus the mode of life of the organism. Another possibility is that this type of colour pattern is in keeping with the Oonoceratidae, but in actuality only one additional species with a colour pattern that certainly belongs to the latter family is known (mentioned by Turek 1990). The slightly curved "*Oonoceras*" *fraternum* (Barrande, 1866) from the late Silurian (late Ludfordian, upper *Monograptus latilobus* and *Monograptus fragmentalis* zones) of Bohemia shows similarly pulsating colour bands resembling those of *Euryzocerina,* but in this case, oblique to the growth lines. It is probable that the difference in the course of the colour bands reflect changes in shell flexure and thus the orientation of the life position of the shell, but a detailed study of "*Oonoceras*" *fraternum* is required.

In addition, the preservation of colour markings in three of the seven available specimens of *Euryrizocerina normata* which possess thin shell walls (max. 0.4 mm), suggests that shell thickness is not a significant agent responsible for the preservation of colour in the shells of Nautiloids (see discussion in Turek 2009, p. 500).

Muscle scars in *Euryrizocerina*: comparison with other Oonoceratidae

Mutvei (1957) published the first detailed study of muscle scars in Early Palaeozoic cephalopods and discussed muscle scars with regard to the anatomy of nautiloid soft parts and their taxonomic significance. Sweet (1959) described some additional attachment structures and discussed their taxonomic value. Later Mutvei (1964) distinguished three groups of fossil nautiloids on the basis of their shell morphology combined with the number and position of muscle scars – Oncoceratomorphi, Nautilomorphi and Orthoceratomorphi. The Oncoceratomorphi includes the orders Oncoceratida and Discosorida, where 7 to 25 pairs of retractor muscle scars may be developed, the ventral pair being the largest. Nautilomorphi and Orthoceratomorphi probably originated by reduction and further specialisation from cephalopods with multiple paired retractor muscles (compare discussion in Kröger 2007b). A study of muscle scars in *Phragmoceras* suggested that the number of muscle scar pairs may vary substantially within a clade, and the prominent ventral pair of muscle scars may even be reduced (Manda 2008). The evolution of multiple paired muscle attachments and their function is still poorly understood, but it seems likely to be a promising line of research in the study of the taxonomy and autecology of these groups (see Mutvei 2002, Evans 2005, Kröger & Mutvei 2005, Manda 2008).

Muscle scars in the Oonoceratidae Hyatt, 1884 are poorly known. Usually there is a narrow annular elevation around the base of the body-chamber with several transversally elongated muscle scars. The ventral pair of scars is usually only slightly larger than the other pairs. The annular elevation is thin on the dorsal side of the body-chamber. A ventral furrow is not known. For examples, see the shells of *Oonoceras acinaces* (Barrande, 1866) from the late Ludlow, Ludfordian, *Monograptus fragmentalis* Zone, and *Oonoceras* aff. *acinaces* (Barrande, 1866) from the late Přídolí, lower *Monograptus transgrediens* Zone, of Bohemia (Fig. 3A, B, E, F).

"*Oonoceras*" *fraternum* (Barrande, 1866) from the late Ludlow (Ludfordian) of Bohemia (*Monograptus latilobus* and *Monograptus fragmentalis* zones) is regarded as the ancestor of the *Euryrizocerina* line (see below), and exhibits muscle scars that differ from other members of the Oonoceratidae. As with *Oonoceras,* the annular elevation is situated around the base of the body-chamber, but its width increases from the dorsal to ventral side. Muscle scars are longitudinally elongated and the ventral pair is significantly larger than the others. The ventral furrow is usually well developed (Fig. 3C).

Specimen CGS SM 378 (*Euryrizocerina normata*) has well-preserved muscle scars (Figs 3D, G and 7C). These scars are rather weak in comparison with the muscle attachments seen in the taxa mentioned above. The annular elevation is shifted aperturally and is broadest on the ventral side but rapidly decreases in width laterally, and on the dorsal side is marked by only a fine ridge. Five pairs of longitudinally elongated muscle scars are developed, and the ventral pair is distinctly larger. The mid-ventral conchal furrow is developed between the ventral pair of muscle scars; its width is greatest at the position of the annular elevation.

The reduction in the width of the annular elevation in *Euryrizocerina* on the lateral and dorsal surfaces is accom-

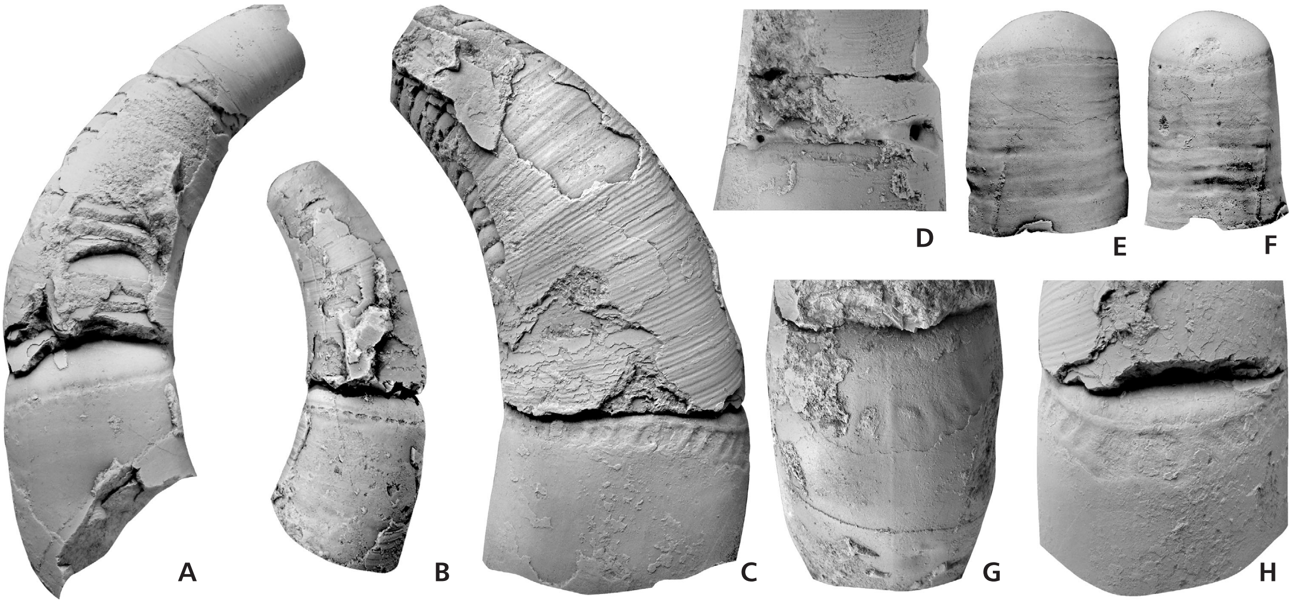

Figure 3. Muscle scars in *Euryrizocerina normata* and selected Oonoceratidae. • A – *Oonoceras acinaces* (Barrande, 1866), lateral view, × 1.2; CGS SM 386; Lochkov, Nad ubikacemi Section (unpublished section); Ludlow, Ludfordian, *Monograptus fragmentalis* Zone, cephalopod limestone biofacies (Kopanina Formation). • B – *Oonoceras acinaces* (Barrande, 1866), lateral view, × 1; CGS SM 388; Lochkov, Nad ubikacemi Section (unpublished section); Ludlow, Ludfordian, *Monograptus fragmentalis* Zone, cephalopod limestone biofacies (Kopanina Formation). • C, H – "*Oonoceras*" *fraternum* (Barrande, 1866), lateral, × 1.1, and ventral views, × 1.2; CGS SM 387; Praha-Podolí, swimming pool area (unpublished section); Ludlow, Ludfordian, *Monograptus fragmentalis* Zone, cephalopod limestone biofacies (Kopanina Formation). • D, G – *Euryrizocerina normata* (Barrande, 1877), dorsal and ventral views, × 1.1; CGS SM 378; Lochkov, U topolů Section; Přídolí, *Pristiograptus parultimus* Zone, cephalopod limestone (Kopanina Formation). • E, F – *Oonoceras* aff. *acinaces* (Barrande, 1866), lateral and ventral views, × 1.5; CGS SM 385; Nová Ves, Bílá skála, bed No. 22 (unpublished section); Přídolí, *Monograptus transgrediens* Zone, cephalopod limestone with *Orthocycloceras fluminese* Assemblage (Požáry Formation).

panied by a reduction in the number of muscle scars and an expansion of the ventral muscle scars. The extension of the annular elevation towards the aperture is a distinct feature. These changes in the muscle attachment pattern probably correspond to an increase in the length of the body-chamber and the increased flexure of the shell, which affected the orientation of the shell during life (*i.e.* the aperture was shifted forward and upwards – Fig. 4).

It is striking that a similar reduction in muscle scars was described in the rutoceratoid (*i.e.* oncocerid superfamily Rutoceratoidea Hyatt, 1884) *Doleroceras resimum* Zhuravleva, 1972a from the Eifelian of the Sverlovsk District (see also fig. 7 in Zhuravleva 1972b). In terms of their flexure and general proportions, the shells of *Doleroceras* bear a strong resemblance to *Euryrizocerina*. Similarly reduced ventral muscle scars, but shifted more towards the aperture, were described by Turek & Marek (1986) in the coiled Pragian rutoceratoid *Ptenoceras alatum* (Barrande, 1865) from Bohemia. The supposed ancestral stock of the rutoceratoids (Silurian-Early Devonian genus *Projovellania* Hyatt, 1900, see Manda 2001) and the Pragian rutoceratoid *Aphyctoceras annulatum* (Barrande, 1865) (see Manda & Turek 2009b, fig. 13b–d) possess annular elevations around the base of the body-chamber, multiple paired muscle scars similar to those seen in *Oonoceras*.

In summary, there is evidence for convergence in the arrangement of muscle scar attachments in *Euryrizocerina,* as well as in some openly coiled rutoceratoids, which also reflects convergence in the shell form and consequently the poise of the organism during life. It also documents a high degree of evolutionary plasticity in the muscle attachment patterns in the Oncocerida. In *Euryrizocerina,* a distinct change in the pattern of muscle attachment took place during the interval (probably less than 0.2 Ma) of the latest Ludlow, Ludfordian, *Monograptus fragmentalis* Zone (Fig. 4). The high variability in the number of muscle scars and their shape as well as the convergence observed in the morphotype, indicates that they represent a derived feature under adaptive control rather than an ancestral metamery (see discussion in Kröger 2007b).

It is interesting that in *Euryrizocerina* and its ancestor "*Oonoceras*" *fraternum* the ventral furrow is commonly preserved, while in *Oonoceras* and allied genera, it has not been observed yet. According to Chirat & Boletzky (2003, p. 167), the ventral furrow represents a taxonomically unimportant developmental by-product originating "from the inner part of the initial, calcified shell apex, in line with the ventral termination of the central linear depression of the cicatrix" (see also Klug *et al.* 2008). This means that the ventral furrow is shared by all nautiloids. The taxonomic selectivity in the preservation of the ventral furrow is striking. Moreover, in the holotype of *Euryrizocerina pulchra,*

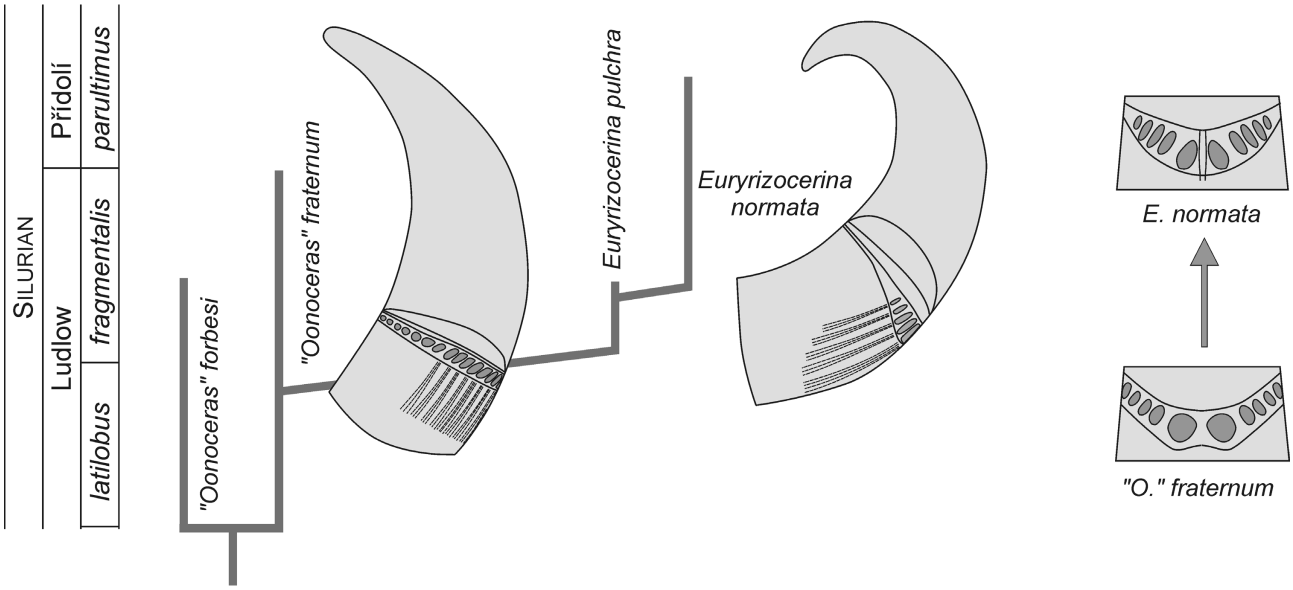

Figure 4. Phylogeny of *Euryrizocerina* line, evolution of shell form and muscle attachment.

except for the true mid-ventral conchal furrow, a similar furrow is developed on the lateral side close to the dorsum (both in the body-chamber and phragmocone, Fig. 7I, J). Dimensions of both structures are similar, and they both terminate at a similar distance close to the aperture. It may be supposed that such similar structures have the same origin. Nevertheless, according to Chirat & Boletzky (2003), the mid-ventral furrow arises at the inner ventral termination of the central linear depression of the cicatrix (*i.e.* embryonic shell). Nautilids exhibit a narrow linear cicatrix. The embryonic shell of oncocerids is poorly known, although there is a circular or elliptical cicatrix with additional radial depressions (Barrande 1877). The lateral furrow may have been originally connected with one of these radial depressions of the cicatrix. Enlargement of the conchal furrow within the annular elevation of *Euryrizocerina* may suggest that it was involved in some way with the musculature (Fig. 3G). It may be significant that the conchal furrow separates the ventral pair of muscle scars.

Systematic palaeontology

Subclass Nautiloidea Agassiz, 1847
Order Oncocerida Flower, 1950
Family Oonoceratidae Flower, 1942

Diagnosis of the family. – Oncocerids with an exogastrically cyrtoconic shell; shell curvature varies only slightly within a species; siphuncle without deposits, marginal, in later ontogenetic stages slightly sub-marginal; phragmocone chambers are low; suture with broad lateral lobes; hyponomic sinus usually well developed; body-chamber relatively short, slightly longer than wide; cross-section laterally compressed. Embryonic shell is cup-like, early shell less curved than adult shell (after Manda & Turek 2009).

Discussion. – Barrande (1865–1877) described many Silurian oncocerids with an exogastrically curved shell and a thin siphonal tube lacking intrasiphonal deposits. These taxa are in need of revision. They are usually placed in *Oonoceras* or allied genera (Hyatt 1884, Gnoli & Serventi 2006). Recent examination of new collections from single beds (*i.e.* focusing on variability in individual palaeopopulations) show that these taxa exhibit relatively low intraspecific variability in shell flexure, cross-section, inner structure and muscle scars. By contrast, the shell sculpture seems to be rather variable in certain species *e.g.* "*Oonoceras*" *haueri* (Barrande, 1886), "*Oonoceras*" *patulum* (Barrande, 1866) and *Oonoceras acinaces* (Barrande, 1866). Differences in the muscle attachment scar pattern between *Oonoceras acinaces* and allied forms and "*Oonoceras*" *fraternum* (noted above) may indicate that there are two distinct groups within the Oonoceratidae, but a detailed study is required.

The vast majority of Silurian Oonoceratidae from Bohemia possess shell with compressed cross-section. Only a few species possess a circular cross-section as is seen in *Euryrizocerina*. *Cyrtoceras obesum* Barrande, 1866 has a slightly curved exogastric shell with a circular cross section. The length of the body-chamber is approximately equal to, or slightly greater than the shell height at the aperture. Shell morphology is similar to that of the type species of *Euryrizoceras* Foerste, 1930 from the middle Silurian of Illinois (Sweet 1964). Barrande (1866, 1877) described

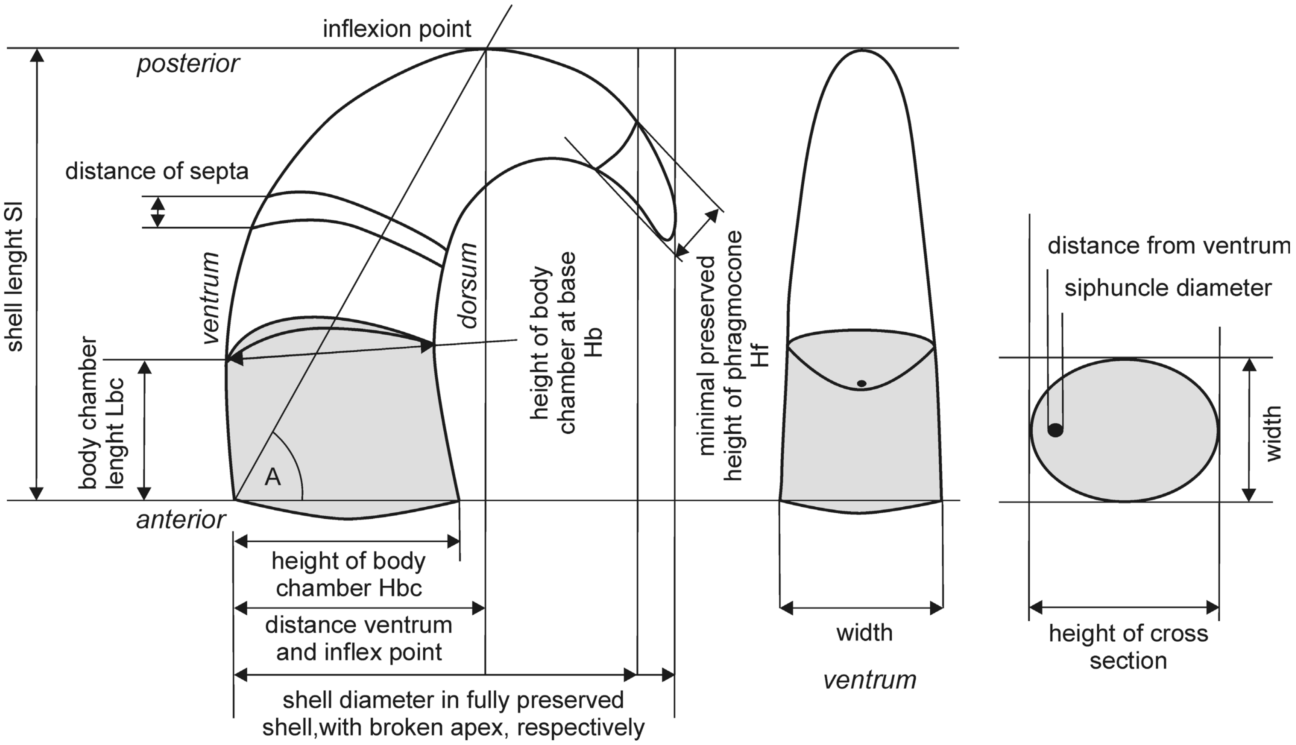

Figure 5. Shell dimensions of a cyrtocone shell: lateral and ventral views, and cross-section.

this long ranging species from the early Wenlock, *Monograptus belophorus* Zone (St. Iwan, pl. 521, refigured here in Fig. 6), early Ludlow, Gorstian, *Colonograptus colonus* Zone (Butowitz e1, pl. 114), late Ludlow, Ludfordian, *Monograptus fragmentalis* Zone (Kozorz, pl. 508) and probably late Přídolí (Novy Mlyn, pl. 114). *Euryrizoceras obesum* strongly resembles *Euryrizocerina*, but differs in the higher angle of expansion, shorter body chamber and less curved shell. In addition, the muscle attachment scars consist of multiple paired muscle scars around the base of the body chamber, which on the dorsal side are missing where the annular elevation narrows (Fig. 6). Consequently, *Euryrizocerina* and *Euryrizoceras* are not considered to be closely related. It seems likely that there are many convergences in shell form in the Oncocerida. Muscle scars may be useful in the recognition of such convergences.

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

Genus *Euryrizocerina* gen. nov.

Type species. – *Cyrtoceras normatum* Barrande, 1877. Latest Ludlow, early Přídolí of Bohemia (Prague Basin).

Etymology. – The diminutive form, derived from the generic name *Euryrizoceras*.

Diagnosis. – Strongly curved exogastric cyrtoconic nautiloid with circular or slightly depressed cross-section, body chamber distinctly longer than wide, length of body chamber about half the shell length, shell diameter greater than shell length in fully grown shell, muscle scars positioned on ventrum, reduced; regular growth lines.

Discussion. – *Oonoceras acinaces* (Barrande, 1866), the type species of *Oonoceras,* differs from the new genus in having a less curved and longer shell, the degree of shell flexure decreases during growth of the shell. The shell cross-section is strongly depressed, and the annular elevation is well developed around the base of the body chamber. The septa are relatively deep, and the suture more oblique, with distinct lateral saddles. The growth lines are rather irregular, and in large shells form irregular flanges. *Oonoceras acinaces* ranges from the latest Ludlow (Ludfordian, *Monograptus latilobus* and *M. fragmentalis* Zone) to the early Přídolí (*Pristiograptus parultimus* Zone) of the Prague Basin, and is thus coeval with *Euryrizocerina.* This further suggests that separate phylogenetic lines are represented.

Euryrizocerina pulchra sp. nov. shares similar shell flexure and relatively long body chamber with *E. normata*, but differs in its more elaborate growth lines and higher angle of expansion. “*Oonoceras*” *fraternum* (Barrande,

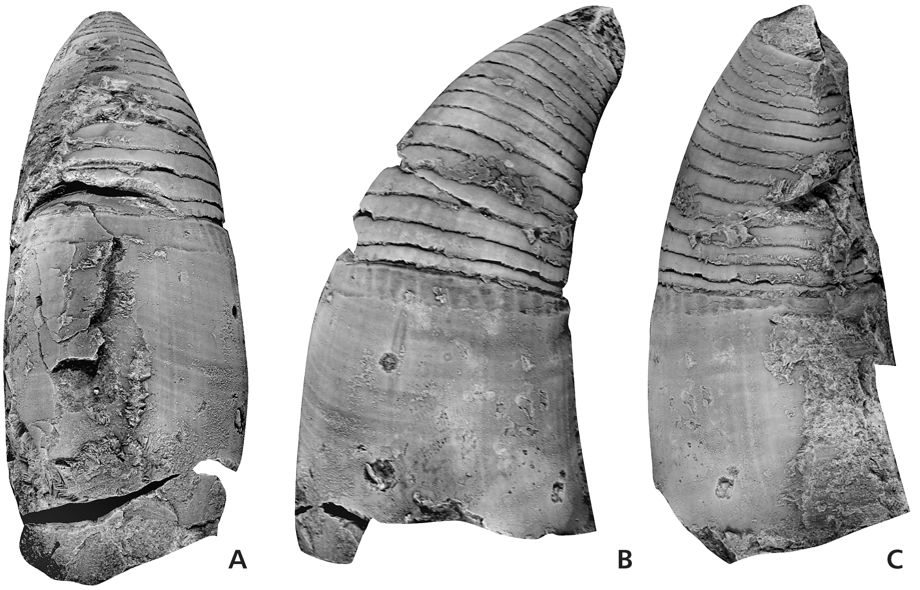

Figure 6. An example of muscle scars in *Euryrizoceras obesum* (Barrande, 1866), an original specimen figured by Barrande (1877, pl. 521, figs 10–13), locality Environs de St. Iwan e2 ("vicinity of Svatý Jan pod Skalou Village"), based on the character of the rock, the specimen comes from U elektrárny Section (old collector pits), *Monograptus. belophorus* Zone, middle Sheinwoodian, Wenlock, brachiopod-trilobite limestone, Motol Formation (see Havlíček & Štorch 1990, Havlíček 1995). Ventral, lateral and dorsal views, all × 0.7; MCZ 173057, Šáry's Collection.

1866) differs from *Euryrizocerina pulchra* sp. nov. in having a higher angle of shell expansion, a short body chamber, a more compressed conch cross-section, and in particular, a much less curved shell; both species have a similar pattern of growth lines. In summary, "*Oonoceras*" *fraternum* is considered to be the ancestor of *Euryrizocerina pulchra,* from which *E. normata* diverged. The sucession of these species in the fossil record corresponds well with their assumed phylogeny.

"*Oonoceras*" *fraternum* and the closely related "*Oonoceras*" *forbesi* (Barrande, 1866) appeared in the late *Monograptus latilobus* Zone (Ludlow, Ludfordian); they belong to the enriched cephalopod assemblages that originated during the recovery that took place after the Kozlowskii extinction event. This event caused a drastic decline in the cephalopod faunas of the Prague Basin and no nautiloids are known from the early *Monograptus latilobus* Zone (Manda, unpublished data). Most of the nautiloids appearing in the late *Monograptus latilobus* Zone are immigrants from lower latitude carbonate platforms. The coiled tarphycerid *Boionautilus* Turek, 2008 is a well-documented example (Turek 2008). Consequently, tracing the phyletic links of these immigrants is a problematic exercise.

"*Cyrtorizoceras*" *fosteri* (Hall, 1860) from the early Ludlow Series, Port Byron Dolomite, Illinois (see also Foerste 1930b) strongly resembles "*Oonoceras*" *forbesi* in its shape and the dimensions of the conch, nevertheless, detailed comparison is impeded by the poor condition of preservation in the dolomite. Still un-described species strongly resembling "*Oonoceras*" *forbesi* also occur in the Wenlock and Ludlow rocks of Gotland (collection of The Swedish Museum of Natural History).

Species included. – Euryrizocerina normata (Barrande, 1877) and *Euryrizocerina pulchra* sp. nov. from the late Silurian of Bohemia.

***Euryrizocerina normata* (Barrande, 1877)**

Figures 2, 3D, G, 7A–H

1877 *Cyrtoceras normatum* Barr.; Barrande, p. 159, pl. 528, figs 22–24.

Holotype. – Holotype by monotypy is specimen NM L 21830 figured by Barrande (1877, pl. 528, figs 22–24). Late Silurian (most probably early Přídolí, on the evidence of the mode of preservation), Kopanina Formation, locality Lochkov e2 (*i.e.* Praha-Lochkov).

Material. – The holotype and six additional specimens collected during recent field studies by the authors and Ladislav Zedník; CGS SM 378, 379 (Praha-Lochkov, U topolů Section, earliest Přídolí, *Pristiograptus parultimus* Zone), CGS SM 380, 381 (Praha-Podolí, swimming pool, latest Ludlow (Ludfordian), *Monograptus fragmentalis* Zone), and CGS SM 382, 383 (Praha-Lochkov, "Pod borovicemi" Section, latest Ludlow (Ludfordian, *Monograptus fragmentalis* Zone).

Diagnosis. – Euryrizocerina with circular cross-section, subventral siphuncle and fine growth lines.

Descriptions. – An exogastric cyrtocone with a circular cross–section and a low angle of expansion. The septa are parabolic with a maximum depth coinciding with the shell axis. The sutures straight and oblique and oblique to the normal of the conch axis. The distance between septa in-

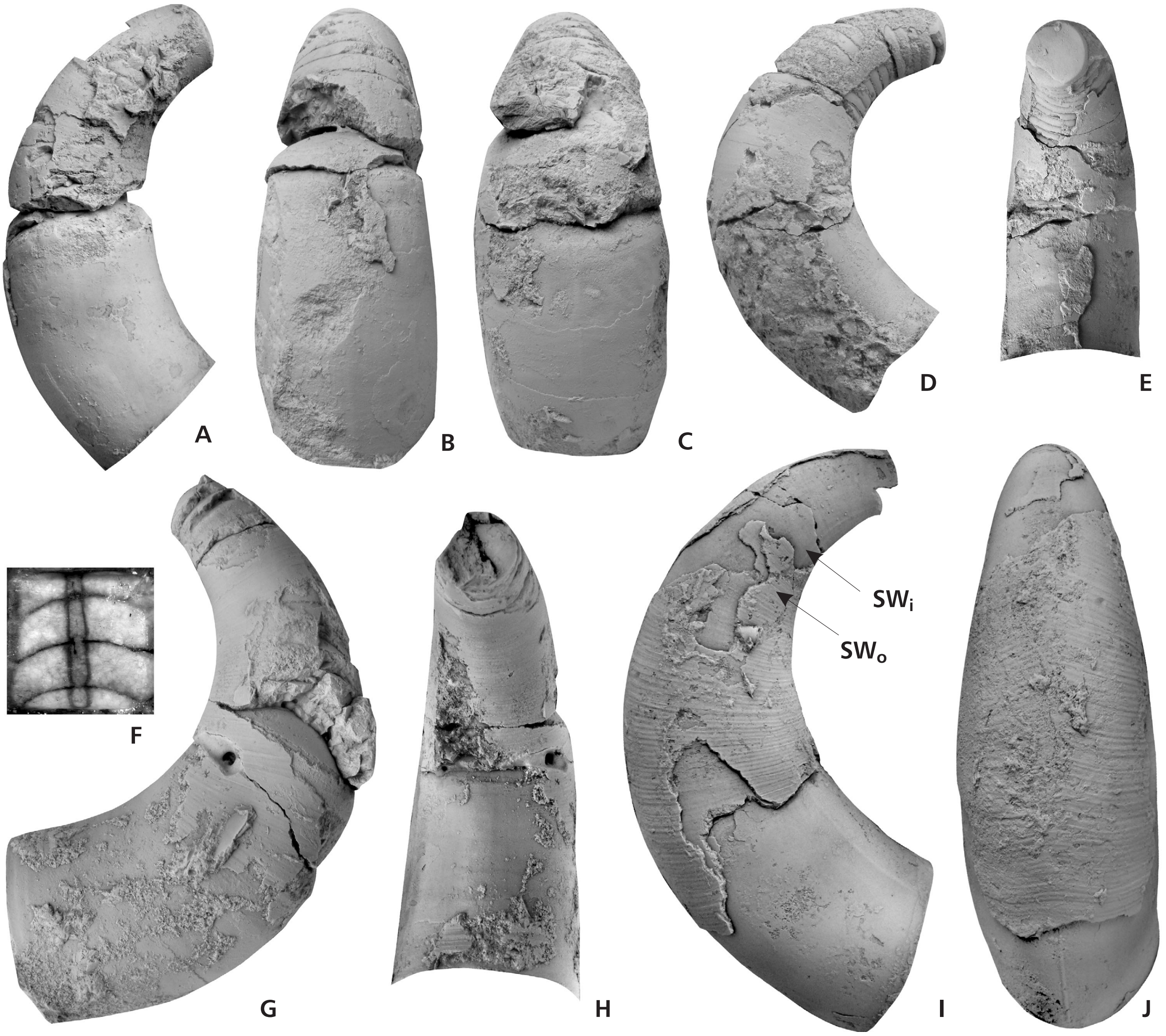

Figure 7. A–H – *Euryrizocerina normata* sp. nov. • A, B, F – NM L 21830, lateral and ventral views, × 1, and detail of siphuncle, × 2.6; holotype figured by Barrande (1877) in pl. 528 as figs 22–24, late Silurian (most probably early Přídolí, on the basis of the mode of preservation), Kopanina Formation, locality Lochkov e2 (*i.e.* Praha-Lochkov). • C, G, H – CGS SM 378, ventral, × 1, lateral and dorsal views, × 0.9; Lochkov, U topolů Section; Přídolí, *Pristiograptus parultimus* Zone, cephalopod limestone (Kopanina Formation). • D, E – CGS SM 379, lateral, × 0.9, and dorsal views, × 0.8; Lochkov, U topolů Section; Přídolí, *Pristiograptus parultimus* Zone, cephalopod limestone (Kopanina Formation). • I, J – *Euryrizocerina pulchra* sp. nov., CGS SM 384, lateral and ventral views, × 0.8; Kosov Quarry near Beroun, latest Ludlow, *Monograptus fragmentalis* Zone. Arrows indicate the two layers of the shell wall: sw$_{\mathrm{i}}$ (inner layer) and sw$_{\mathrm{o}}$ (outer layer).

creases from *ca* 1 mm (at a shell height of 10 mm) to *ca* 3 mm (at a shell height of 27 mm). The siphuncle is thin and subventral in position; its diameter increases from 0.5 mm (at a shell height of 10 mm) to 1.5 mm (at a shell height of 31 mm). The septal necks are very short, and the connecting rings thin and only moderately vaulted. The body-chamber is relatively long. Four pairs of muscle scars are present, the ventral pair being the largest. The muscle scars are elongated in the direction parallel to the shell axis on the lateral side of the shell. A narrow, but distinct ventral furrow may be seen in the holotype. The aperture is open with a straight, well-developed hyponomic sinus. In one specimen, the aperture becomes slightly contracted. Fine, dense growth lines are present. These are almost straight and oblique to the normal of the conch axis. Shallow and broad ventral lobes are formed by the growth lines, and some growth lines are slightly more accentuated than others. The shell is relatively thin, reaching a maximum thickness of 0.4 mm (at a shell height of 33 mm).

Dimensions. – Sl – shell length, Lbc – length of body chamber, Hbc – height of body chamber at aperture, Hb –

height of body chamber at base, Hf – minimal preserved height of phragmocone, Sdia – shell diameter, A – angle between apertural line and point inflexion; see Fig. 5. All measurements except A are in millimetres.

Specimen	Sl	Lbc	Hbc	Hb	Hf	Sdia	A
NM L 21830	43.5	31.5	21	19.5	9	48.5	*ca* 50°
SM 378	56	41	27	25	10.5	61	*ca* 50°
SM 379	49	34	22.5	24	9	55	*ca* 55°
SM 380	–	–	–	21.5	16	–	–
SM 381	63	49	31.5	28.5	17.5	60	–
SM 382	59	35	28	24.5	13	52	*ca* 55°
SM 383	48	42	25	24	16	58.5	*ca* 55°

Occurrence. – Late Silurian of Bohemia, latest Ludlow, Ludfordian (*Monograptus fragmentalis* Zone) and earlier Přídolí (*Pristiograptus parultimus* Zone), Prague Basin, upper part of the Kopanina Formation.

Praha-Lochkov, U topolů Section (see Svoboda & Prantl 1950), earliest Přídolí, *Pristiograptus parultimus* Zone, facies of dark-grey cephalopod limestone, accompanied by a fauna consisting of common cephalopods (*Arionoceras* sp., *Boionautilus tyrannus*, *Cinctoceras* sp., *Kopaninoceras* sp., *Mandaloceras* sp. div., *Michelinoceras michelini*, *Oonoceras* div. sp., *Ophioceras simplex*, *Parakionoceras originale*, *Peismoceras optatum*, *Pseudocycloceras* sp., *Umbeloceras* sp. div.), bivalves (*Cardiola conformis* Community *sensu* Kříž 1999), less common gastropods (*Pleurorima* a.o.), trilobites (*Cromus*), and graptolites.

Praha-Lochkov, "Pod borovicemi" Section, an undescribed section, natural outcrops in the upper part of the Kopanina Formation on a south-inclined slope in Radotín Valley, 1143 m SW from the bus station in Praha-Lochkov, latest Ludlow, Ludfordian, *Monograptus fragmentalis* Zone, grey weathering cephalopod limestone with a poorly preserved fauna (*P. normata* and *Arionoceras* sp., *Kopaninoceras* sp., *Kosovoceras sandbergeri, Michelinoceras michelini,* and unidentified cardiolid bivalves).

Praha-Podolí, swimming pool, an unpublished section, latest Ludlow (Ludfordian), a 20 cm thick bed just below base of Přídolí (identified by *Cardiola bohemica* accumulations and *Pristiograptus parultimus*), *Monograptus fragmentalis* Zone (former *Prionopeltis archiaci* Horizon). Facies of dark-grey cephalopod limestone. *E. normata* occurs together with common cephalopods (*Arionoceras* sp., *Kopaninoceras* sp., *Kosovoceras sandbergeri, Kosovoceras nodosum*, *Lechritrochoceras degener*, *Mandaloceras* sp. div., *Michelinoceras michelini*, *Oonoceras* div. sp., *Ophioceras simplex*, *Ovocerina* sp., *Parakionoceras originale*, *Pseudocycloceras* sp., *Umbeloceras* sp. div.), bivalves (*Cardiola conformis* Community *sensu* Kříž 1999), rare gastropods, bryozoans, graptolites, and trilobites.

***Euryrizocerina pulchra* sp. nov.**
Figure 7I, J

Etymology. – Derived from the Latin adjective *pulchra* (beautiful) referring to the excellent preservation of the holotype and elegant shell design.

Holotype. – CGS SM 384 figured as Fig. 7I, J. From Kosov Quarry near Beroun, latest Ludlow, Ludfordian, *Monograptus fragmentalis* Zone.

Diagnosis. – *Euryrizocerina* with slightly compressed cross-section and regular prominent growth lines.

Descriptions. – The holotype is an almost complete exogastric, slightly expanding, longiconic cyrtoconic shell. Only the apical part of the shell is missing. The length of the preserved portion of shell is 65 mm, and the maximum shell height is 30 mm, with a width of 28.5 mm. The cross-section is slightly compressed and the ratio of shell height to width decreases during growth from 1.2 to 1.05. The septa are concave and the suture oblique with very shallow lateral saddles. The distance between septa varies from 2.5 to 3 mm. A siphuncle has not yet been observed. The body-chamber is relatively long (40 mm) and the base of the body-chamber has a height of 31 mm and a width of 27 mm. A narrow (0.9 mm) ventral furrow is visible on the body-chamber; it disappears just before the aperture. A similar, but less distinct furrow is visible on the right lateral side of the body-chamber, close to the dorsum. The aperture is open and straight, with a well-developed hyponomic sinus. Growth lines are regular and straight. They are oblique to the normal of the conch axis and a prominent shallow but broad hyponomic sinus is present. The distance between growth lines in the adult portion of the shell is *ca* 1 mm. The maximum thickness of the shell is about 1.2 mm. The shell wall consists of two layers, an outer, thicker layer which carries growth sculpture, whilst the inner, thinner layer has a smooth surface (see Fig. 7I).

Occurrence. – The holotype was collected from the uppermost part of the cephalopod limestone bank, *Monograptus fragmentalis* Zone, latest Ludlow, Ludfordian, in new Kosov Quarry, 1st level, south wall, close to section number 783 (actually quarried out) measured by Kříž (1992, p. 60, fig. 44). The section was recently re-measured by Vokáč (1999). These cephalopod limestones consist of rusty, coarse pack-grainstone. The exceptional preservation of the holotype is caused by fossilisation in a fine rusty mudstone inside the body-chamber of a large pseudorthocerid (see Turek 1974). The accompanying fauna consists of a diverse cephalopod assemblage (*Arionoceras* sp., *Dawsonocerina caelebs*, G*eisonoceras rivale, Hexameroceras panderi, Kopanonoceras* sp., *Kosovoceras nodosum, Kosovoceras* *sandbergeri, Lyecoceras neptunicum, Oonoceras acinaces*, "*Oonoceras*" *forbesi*, *Ophioceras simplex, Oxygonioceras* sp., *Plagiostomoceras* sp., "*Sactoceras*" *pellucidum*, *Tetrameroceras* sp.; see Turek 1992), with less common bivalves (*e.g.*, *Cardiola conformis*), rugose and tabulate corals, gastropods, and trilobites (*e.g.*, *Prionopeltis archiaci*) occur rarely. The cephalopod fauna from the limestone bank corresponds with the cephalopod assemblage developed in several sections in the Prague territory in the lower part of the *Monograptus fragmentalis* Zone (former *Prionopeltis archiaci* Horizon). It is probable that the upper bedding plane of the cephalopod limestone bank in Kosov Quarry coincides with the Ludlow-Přídolí boundary and represents a condensed surface and a hiatus.

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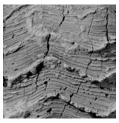
PŘÍLOHA 7

Publikovaná práce

Manda, Š., Turek, V. 2009b. Revision of Pragian Rutoceratoidea Hyatt, 1884 (Nautiloida, Oncocerida) from the Prague Basin. Bulletin of Geosciences 84, 127–148.

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) encompases 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 *Aphyctoceras* 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 xxx, 2009.

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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;

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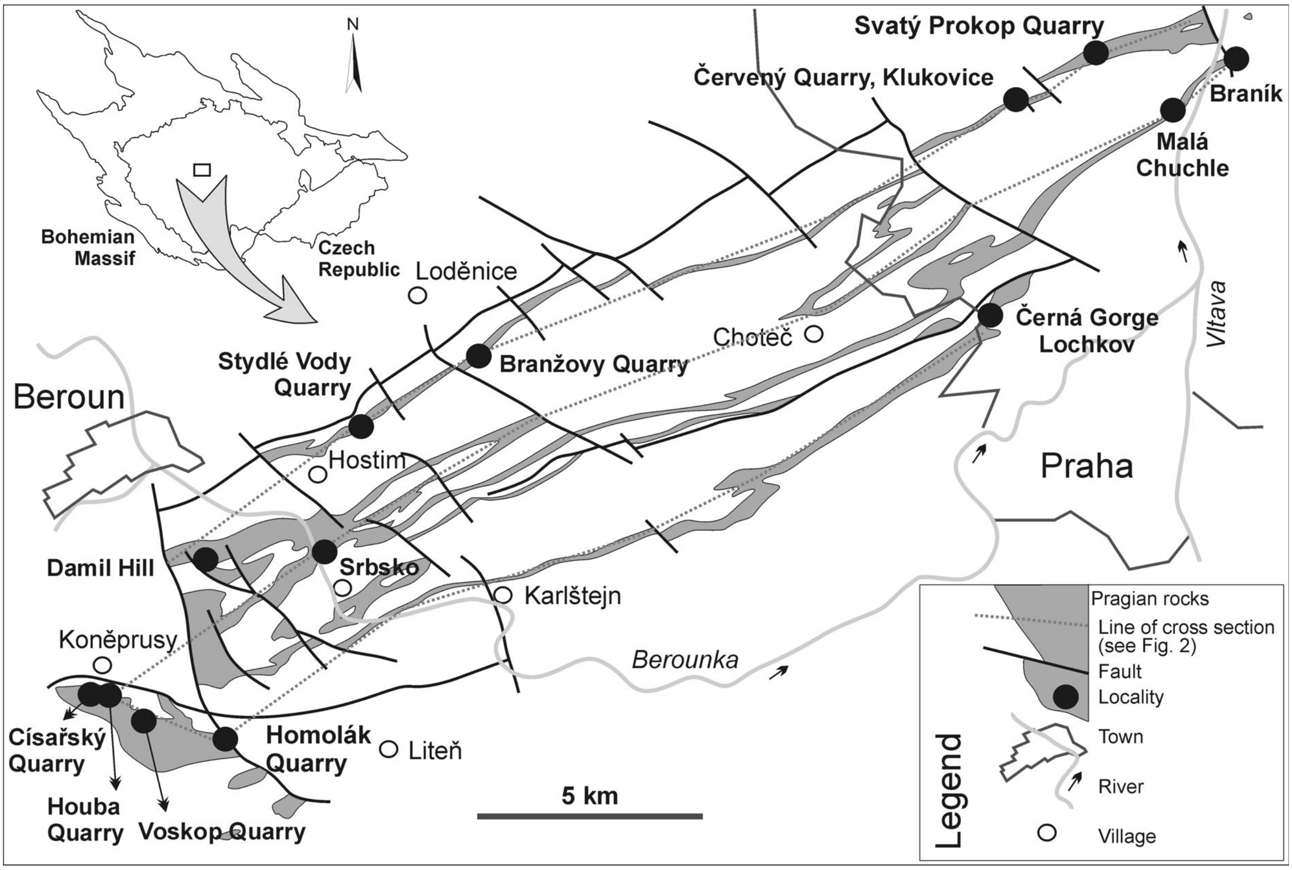


Figure 1. Distribution of the Pragian rocks in the Prague Basin and position of the mentioned sections (after Havlíček & Vaněk 1998, Röhlich 2007). • Notes on localities: Braník, Barrande's locality Branik G-g_1, most probably a small quarry SSE of the Braník Rock, weathered lower part of the Dvorce-Prokop Limestone, earlier Pragian; *Parauloceras pupus, Ptenoceras alatum, Michelinoceras* sp., *Kopaninoceras barbarum, Suloceras pulchrum, Cancellspyroceras 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_1, lower part of Dvorce-Prokop Limestone, early Pragian (Chlupáč 1957, 1983); *Ptenoceras alatum, Aphyctoceras 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_1, exsact 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, Dawsonocerina discretum, "Orthoceras" woodwardi* a.o. • Homolák Quarry, Koněprusy Limestone, Pragian (Havlíček & Vaněk 1998); *Otomaroceras tardum, Ptenoceras alatum, Suloceras pulchrum, Spyroceras patronus, Naedyceras branzovensis* 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 illustrations 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.

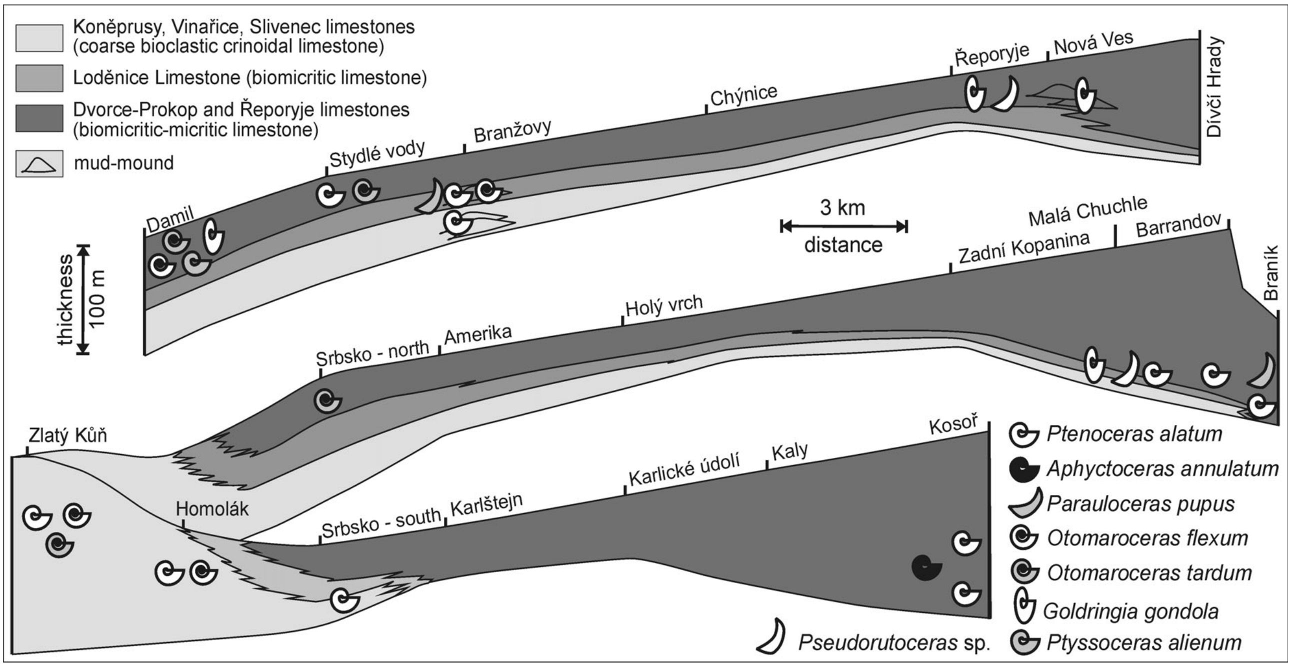


Figure 2. Facies development of the Pragian Praha Formation (modified after Chlupáč 1998) and distribution of rutoceratoids.

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 dehiscens* (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 Rutoceratoidea 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 *Aphyctoceras* 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

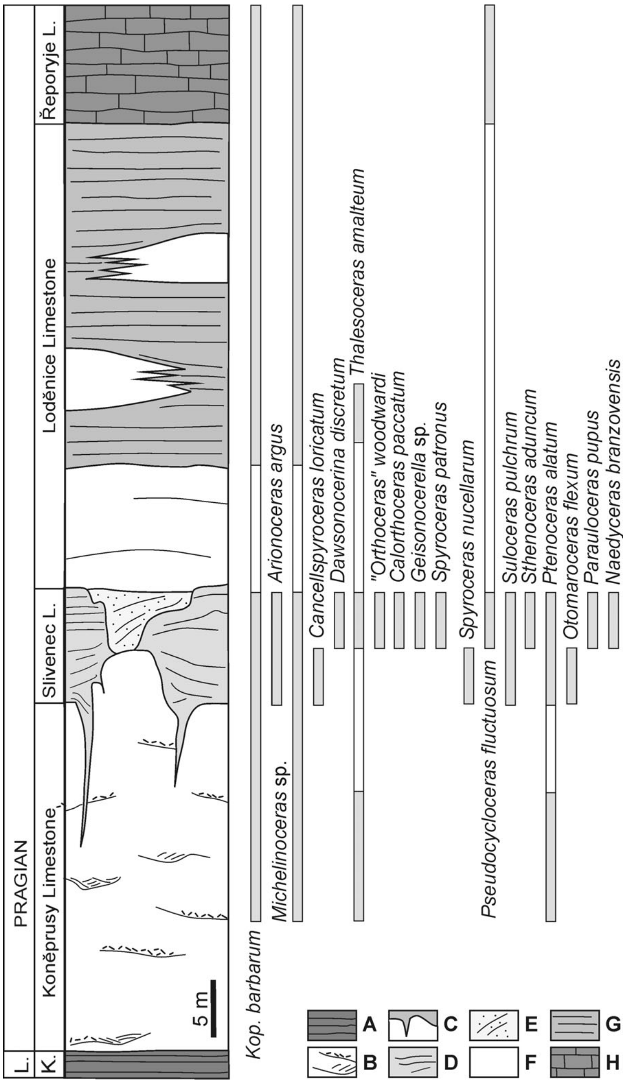


Figure 3. Early Pragian deepening up sequence exposed in Branžovy Quarry, earliest Pragian corresponds with low stand followed by transgressive tract. An instructive example of cephalopod succession in the Pragian strata of the Prague Basin. Note facial dependence of cephalopods and restriction of diverse 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 (*Kopaninoceras, 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.* – *Kopaninoceras*.

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

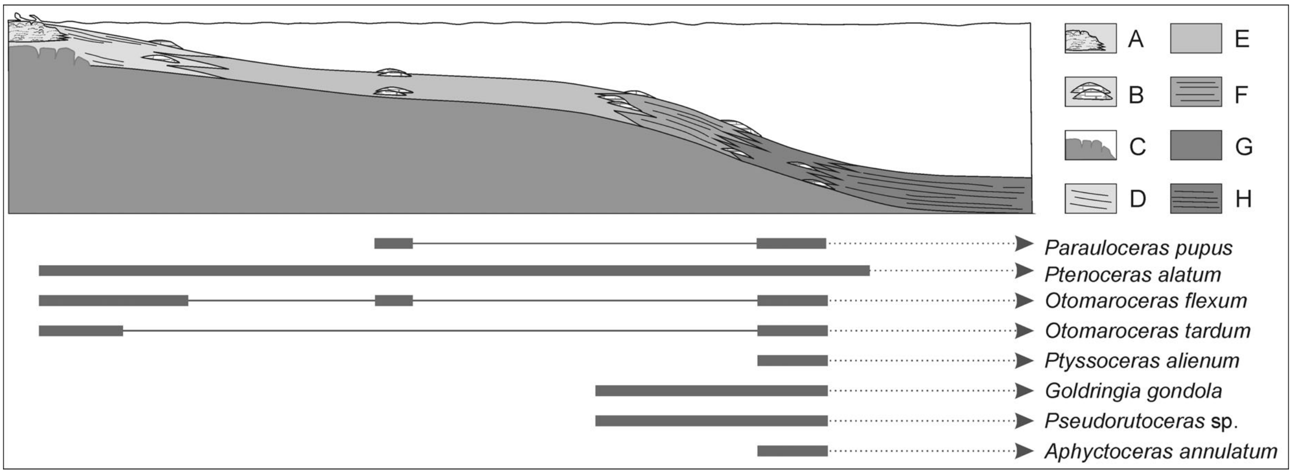


Figure 4. Distribution of the Pragian rutoceratoids of the Prague Basin in relation to the facies (depth) zones. • A – reef core limestone (Koněprusy Limestone *s.s.*). • B – mud-mounds. • C – eroded Lochkovian Kotýs Limestone functioned as submarine cliffs during the earliest Pragian. • D – white-grey coarse cross-bedded crinoid limestone (Koněprusy Limestone *s.s.*). • E – white grey, grey and reddish crinoid limestone (Koněprusy Limestone *s.l.*, Slivenec 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, Nephriticeratidae 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 reconstruction 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

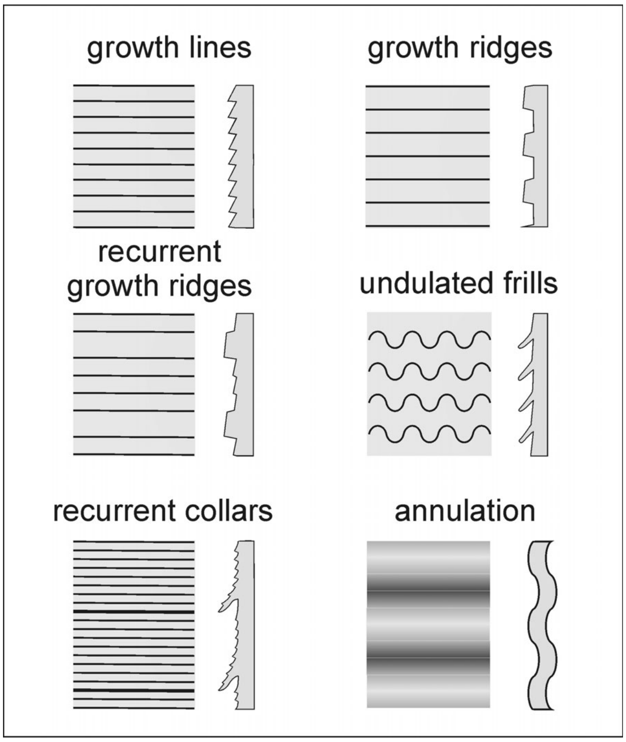


Figure 5. Classification of growth structures among rutoceratoids.

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 Paraulоceratidae. 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.

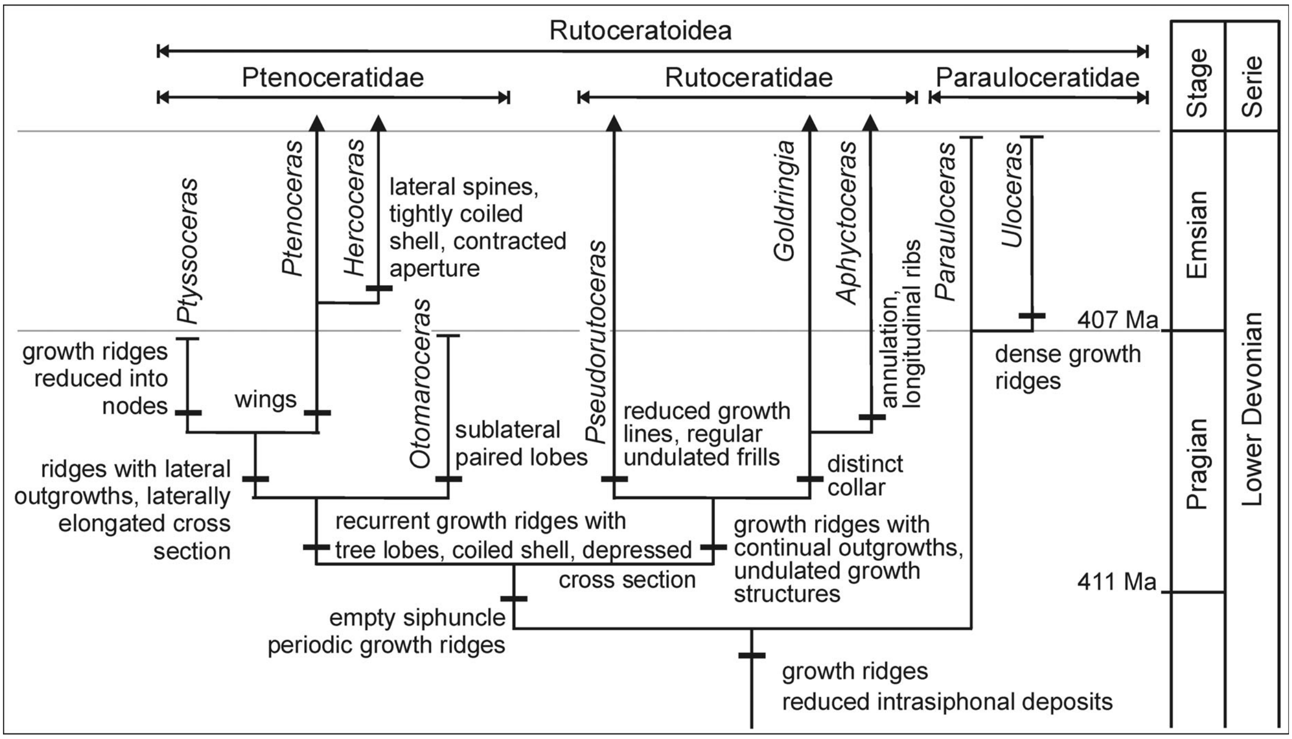


Figure 6. The Pragian-Emsian radiation of the rutoceratoids in the Prague Basin. Note that in the latest Pragian, and especially in the early Emsian, rutoceratoids migrated into other regions of the Old World Realm (Baltica, Laurentia). Some poorly known genera (*e.g.*, late Emsian *Adelphoceras* Barrande, 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 (Pragian-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.

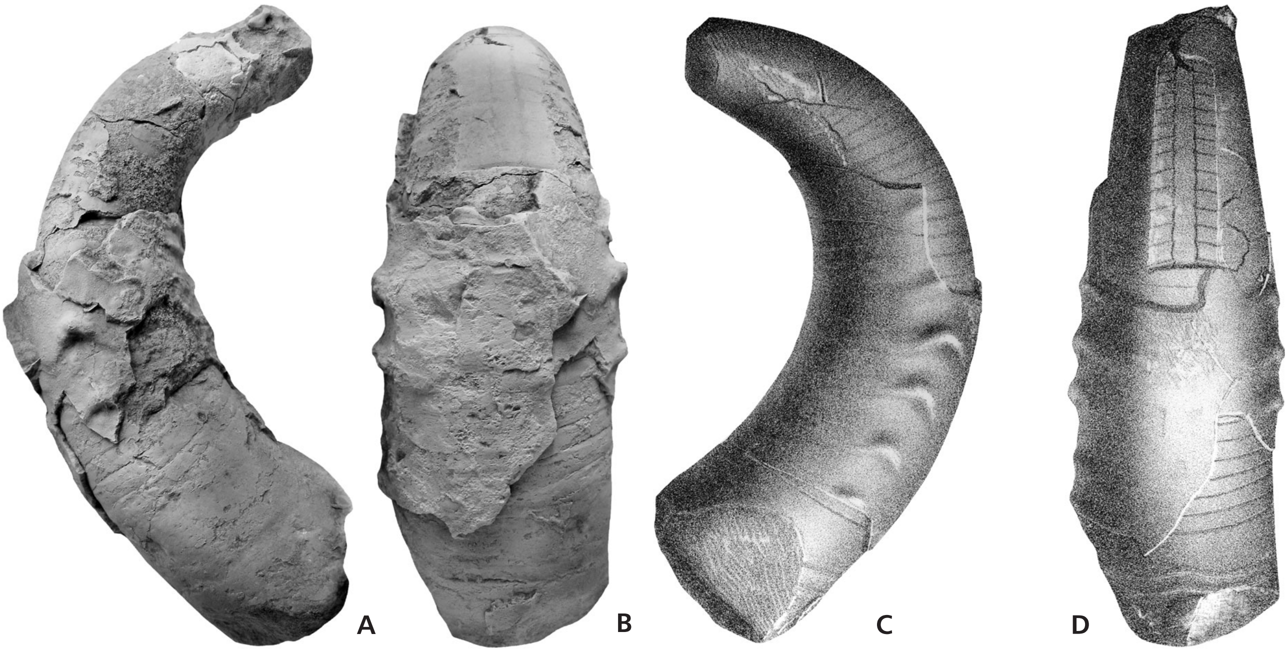


Figure 7. *Ptyssoceras alienum* (Barrande, 1866). • A, B – Holotype, lateral (dextral) and ventral views; × 1.1; NM L 40507, Damil Hill near Tetin; late Pragian; Dvorce-Prokop Limestone. • C, D – the same specimen, lateral (sinistral) and ventral views, adopted from Barrande (1866), pl. 127, figs 1,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

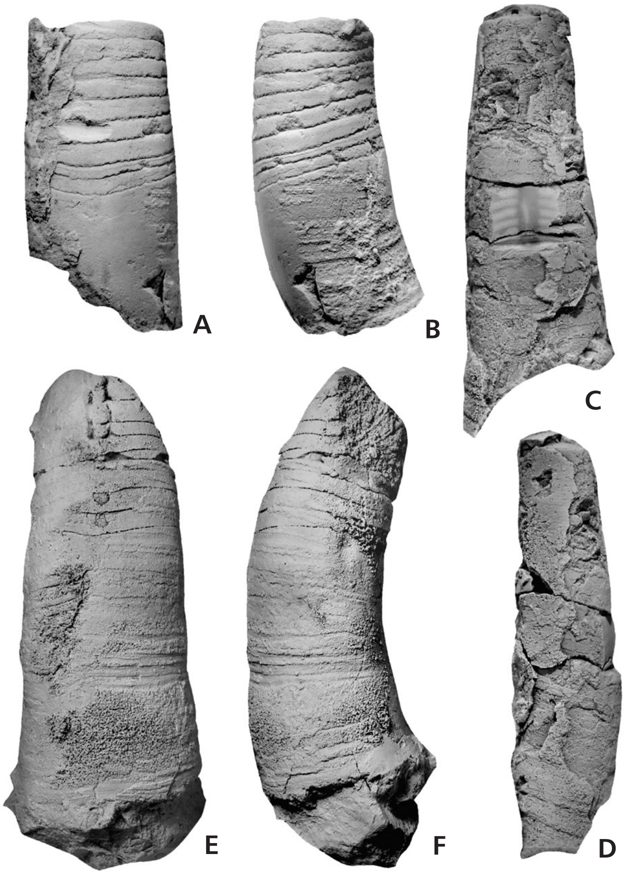


Figure 8. *Parauloceras pupus* (Barrande, 1877). • A, B – ventral and lateral views (a specimen figured by Barrande on pl. 465, figs 13–16 as "*Cyrtoceras nepotulus*" Barrande, 1877); × 1; NM L 13795; Braník locality, Early Pragian; Dvorce-Prokop Limestone. • C, D–- ventral (× 1.3) and lateral (× 1.2) 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) [= *Doleroceras* 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.

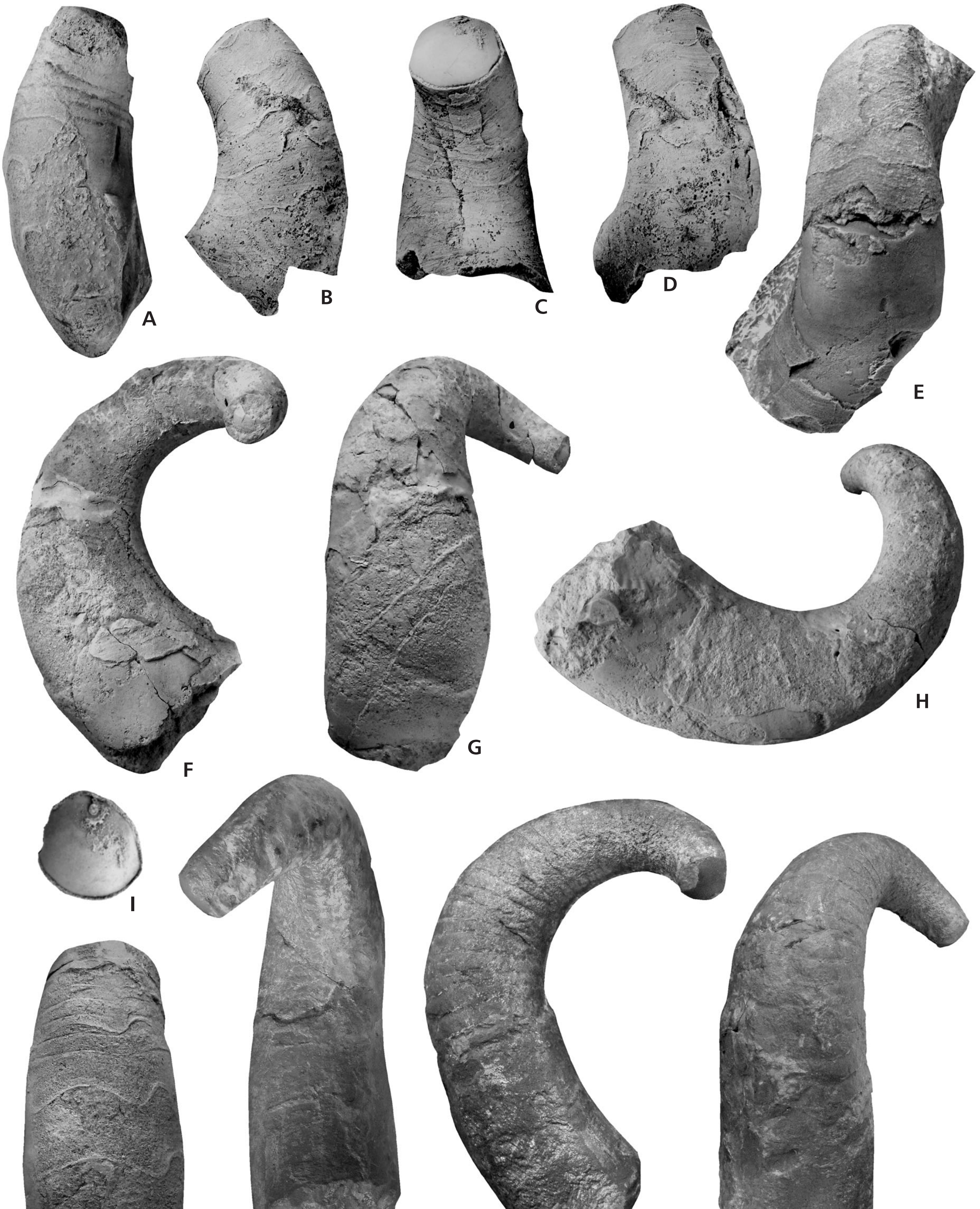
Type locality. – Barrande's locality "Tetin" in the Damil Hill area near Beroun, exact site unknown.

Type horizont. – Devonian, Early Devonian, Pragian (Barrande's etage G, bande G-g$_1$).

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, subtrapezoidal; 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.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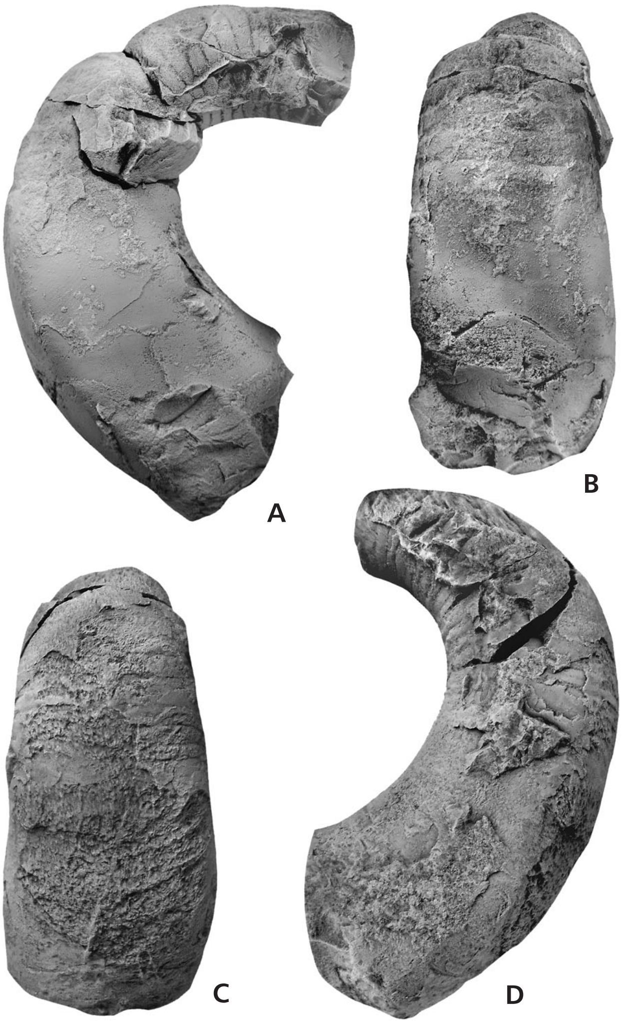

Figure 10. *Otomaroceras tardum* (Barrande, 1865). • A, B – lateral and ventral views; holotype NM L 40501; × 1; Damil Hill near Tetin; late Pragian; Dvorce-Prokop Limestone. • C, D – ventral and lateral views; CGS SM 390; Damil Hill near Tetin; late Pragian; Dvorce-Prokop Limestone.

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 synonymy 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 Kodym *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 horizont. – Devonian, Early Devonian, late Pragian (Barrande's etage G, bande G-g_1).

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

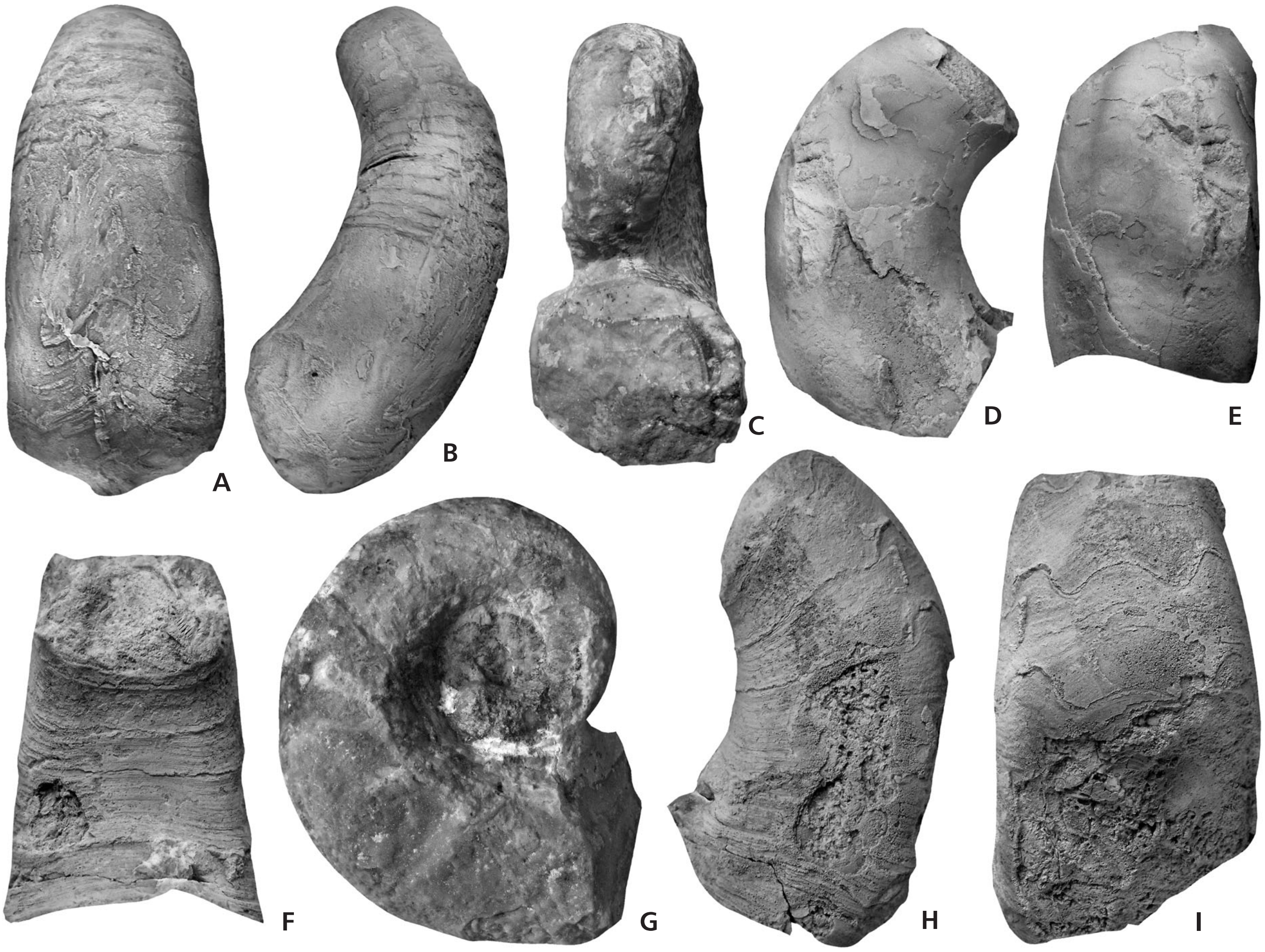

Figure 11. *Otomaroceras tardum* (Barrande, 1865). • A, B - ventral and lateral views, × 0.6; MCZ 133261; Srbsko; late Pragian; Dvorce-Prokop Limestone. • C, G – dorsal and lateral views, × 0.7; NM L 40505; Koněprusy, exact site unknown; Pragian; Koněprusy Limestone. • D, E – lateral and ventral views,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

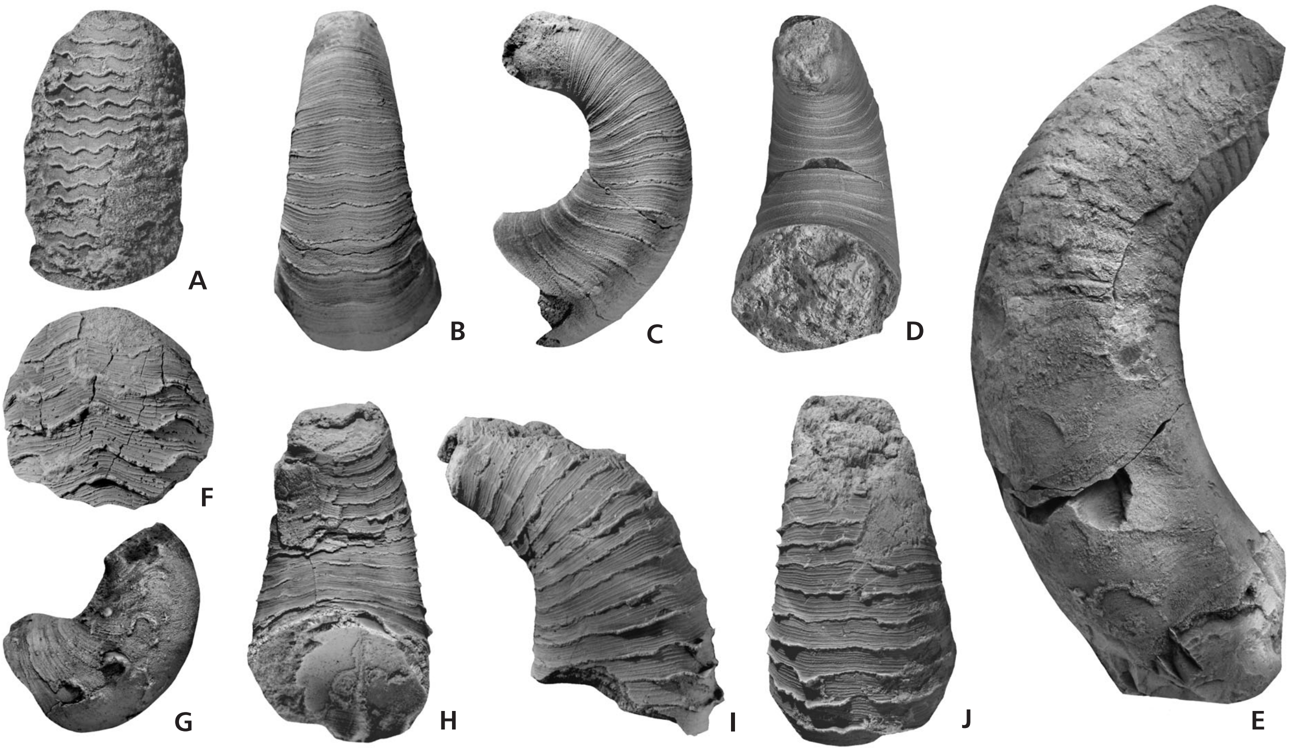

Figure 12. A – *Pseudorutoceras* sp., × 1.8; CGS SM 5; Malá Chuchle; Pragian; Dvorce-Prokop Limestone. • B–D – *Ptenoceras alatum* (Barrande, 1865), ventral, lateral and dorsal views, × 5.4; CGS SM 331; Houbův Quarry; Pragian; Koněprusy Limestone. • E – *Otomaroceras flexum* (Barrande, 1865), lectotype of "*Trochoceras distortum*" Barrande, 1865, lateral view, × 0.9; NM L 197; Damil Hill near Tetin; late Pragian; Dvorce-Prokop Limestone. • F – *Pseudorutoceras* sp., lateral view, × 1.7; NM L 4050; Klukovice, Červený Quarry; late Pragian; Dvorce-Prokop or Loděnice Limestone. • G – *Hercoceras mirum* Barrande, 1865, lateral view, × 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, × 2; CGS SM 323; Hlubočepy, Svatý 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 *Aphyctoceras* 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 *Aphyctoceras*. Thus, *Gyroceras annulatum* represents the oldest known species of *Aphyctoceras*.

Aphyctoceras 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_1. 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 adapertural width of the shell. Aperture slightly constricted. Surface with distinct, transverse, widely spaced annuli

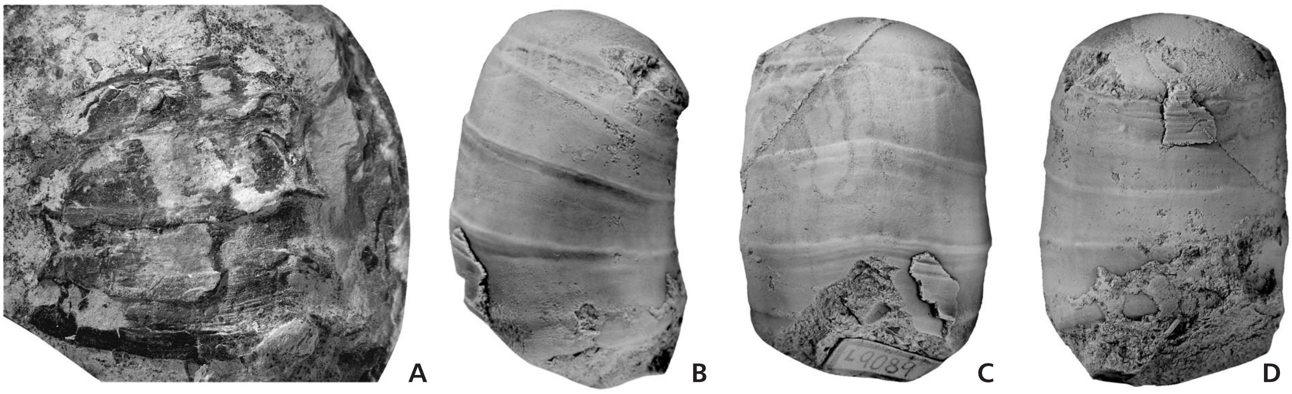

Figure 13. A – *Goldringia gondola* Manda, 2001, ventolateral view, × 1; Damil Hill at Tetín, Modrý Quarry; early Emsian (earlier Zlíchovian); Zlíchov Formation. • B–D – *Aphyctoceras annulatum* (Barrande, 1865), holotype, lateral, ventral and dorsal views, × 1; NM L 9089; Praha Lochov locality; early 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)], *Aphyctoceras* [*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, *Aphyctoceras* 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 & Kukal 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 valnevenzis* 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 & Kukal 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.*, Kukal & 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, palaeobiogeographicaly 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 Lechritrochoceratidae, 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.

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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
    Pleuroncoceras 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
        Pleuroncoceras 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
      Pleuroncoceras 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
Aphyctoceras Zhuravleva, 1974
Bastindoceras Zhuravleva, 1974
Casteroceras Flower, 1936
Capricornites Zhuravleva, 1974
Centolitoceras 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 Tetragonioceratidae 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)
Aphyctoceras 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 Paraulоceratidae 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)
Aphyctoceras 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)

PŘÍLOHA 8

Publikovaná práce

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Minute Silurian oncocerid nautiloids with unusual colour patterns

ŠTĚPÁN MANDA and VOJTĚCH TUREK

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

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

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Introduction

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

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

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

Material and terminology

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

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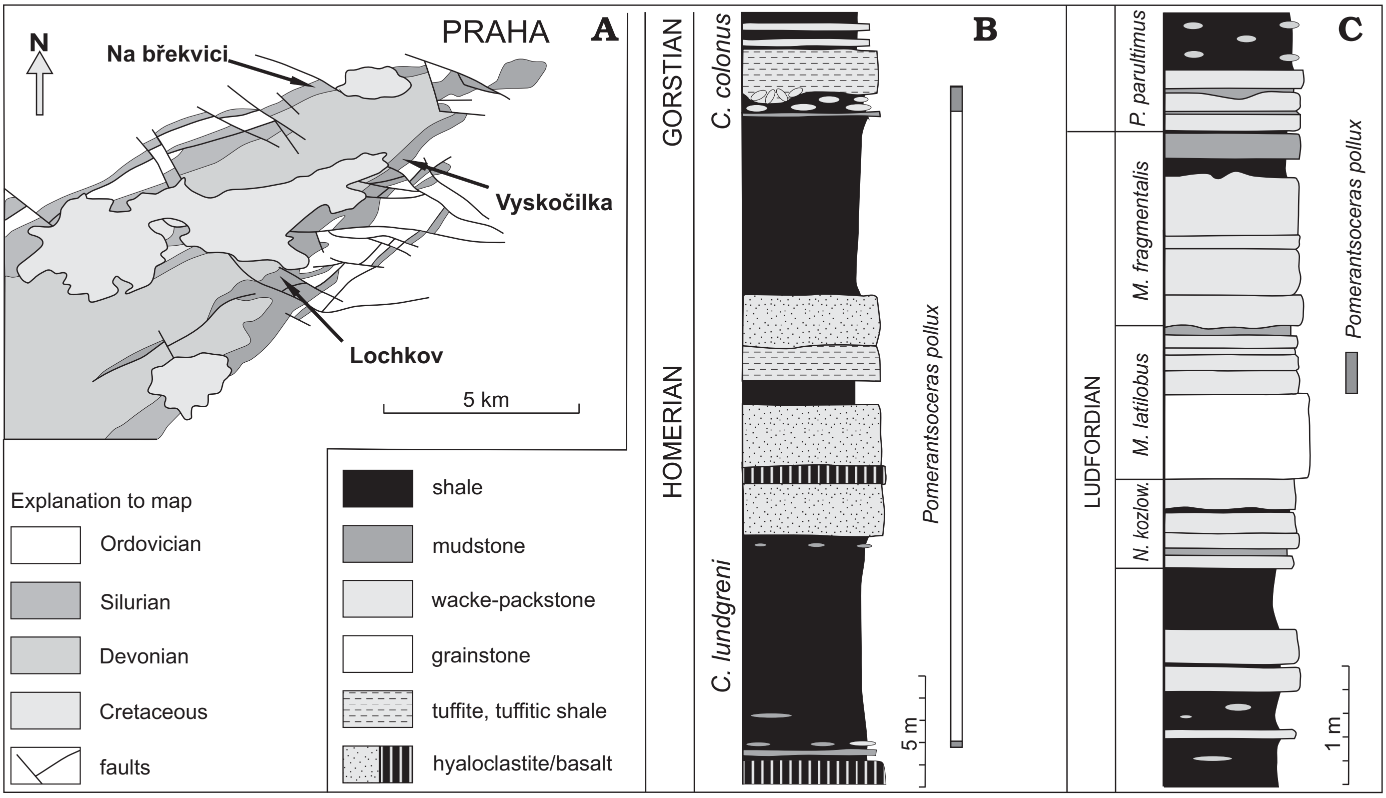

Fig. 1. **A**. Distribution of Silurian rocks in the eastern part of the Prague Synform and position of named localities (see Kříž 1992, Röhlich 2007). **B**. Butovice, Kační Quarry-Na břekvici Section, stratigraphy, graptolite zones, lithology (adopted from Kříž 1992, Kříž et al. 1993) and range of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

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

Remarks on nautiloid shell size

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

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

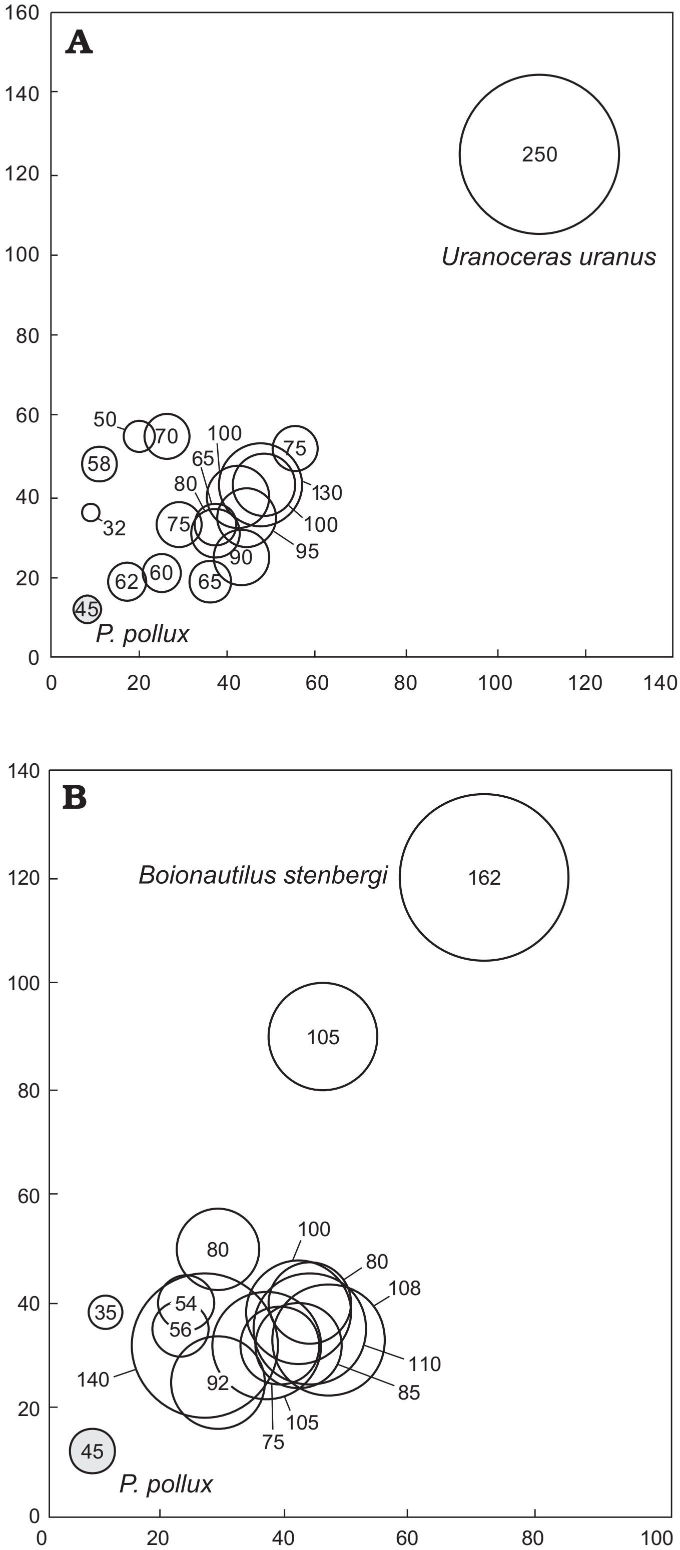

Fig. 2. Shell size of nautiloids: shell height (axis x), length of body chamber (axis x), and shell length (diameter of circle), Butovice Na břekvici Section, Ludlow, Gorstian, *Colonograptus colonus* Zone (**A**) and Lochkov Nad ubikacemi Section, Ludlow, Ludfordian, *Monograptus latilobus* Zone (**B**).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

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

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

Colour pattern of *Pomerantsoceras*

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

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

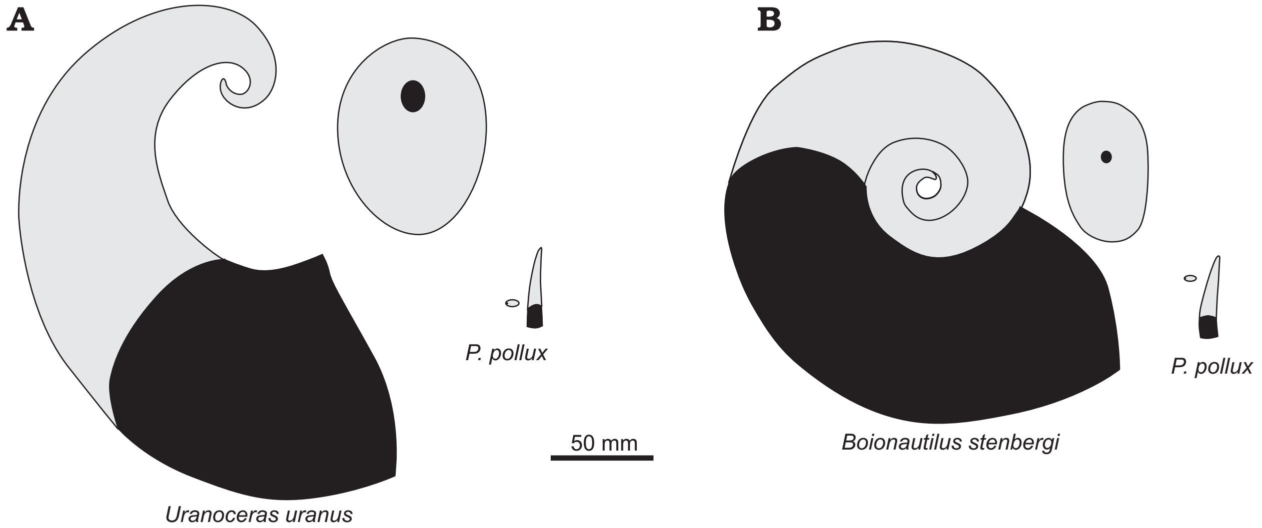

Fig. 3. Comparison of the smallest and largest nautiloids in Butovice Na břekvici Section, Ludlow, Gorstian, *Colonograptus colonus* Zone (**A**) and Lochkov Nad ubikacemi Section, Ludlow, Ludfordian, *Monograptus latilobus* Zone (**B**).

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

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

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

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

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

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

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

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

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

Shell malformations in *Pomerantsoceras*

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

The holotype of "*Pomerantsoceras castor*" (NM-L 571, Fig. 9C$_1$) displays a striking anomaly in the arrangement of septa in the adapertural part of the phragmocone, which was not documented on Barrande's illustrations (1866: pl. 184: 20–23). Abrupt change of course in the suture lines appears in the seventh septum (counted from the body chamber towards the apex). A broad lateral lobe changed into a parabolic lobe. During subsequent growth the septa returned to their normal growth pattern so that the course of last three sutures was not affected by this injury. The anomalous growth of septa in this part of the shell was caused by a sublethal crush to the body chamber in the mid-lateral region of aperture. It is indicated by mid-lateral longitudinal depression shallowing adaperturally. During subsequent shell growth and shifting the body adaperturally, the animal secreted new septa in a narrowed internal space resulting in their change of convexity. Due to exfoliation of the shell in this part of phragmocone, superficial manifestation of this injury could not be observed.

In addition to the anomalous growth of septa, a pair of pits has been observed on internal mould of the last phragmocone chamber in the same specimen. Another larger pit, partially filled with shell material (sparitic calcite), is recognisable on the right side of the shell in the adapical part of the body chamber (see Fig. 9C$_2$). No depression is indicated on the cross section of the shell of this single pit. These pits probably correspond to a marked local thickening of the shell wall. This phenomenon was described in detail by House (1960) and Chlupáč and Turek (1983) in Devonian goniatites (see also Klug 2002; Korn and Klug 2002); rather rarely it occurs in nautiloids (e.g., Stridsberg and Turek 1997). House (1960) explained the pitting as pearl-like growth mounds or deposits due to irritation of the mantle by foreign particles that penetrated between mantle tissue and the shell of the animal.

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

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

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

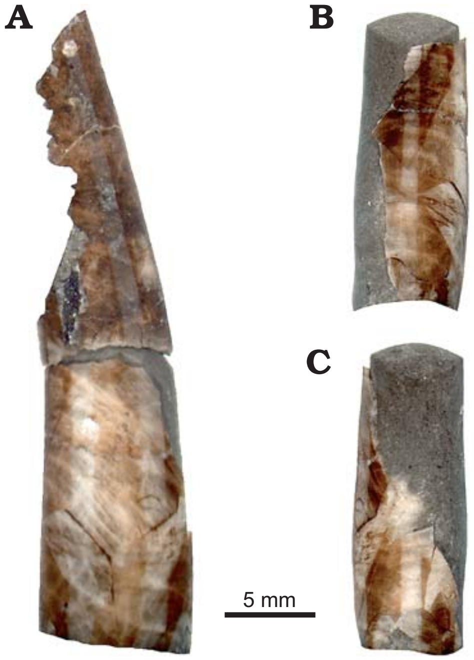

Fig. 4. *Pomerantsoceras pollux* (Barrande, 1866). Specimen CGU SM 319, the body chamber, in lateral (**A**), ventral (**B**), and dorsal (**C**) views. Kační Quarry, *Testograptus testis* Zone, Homerian, Wenlock. Photographed in alcohol.

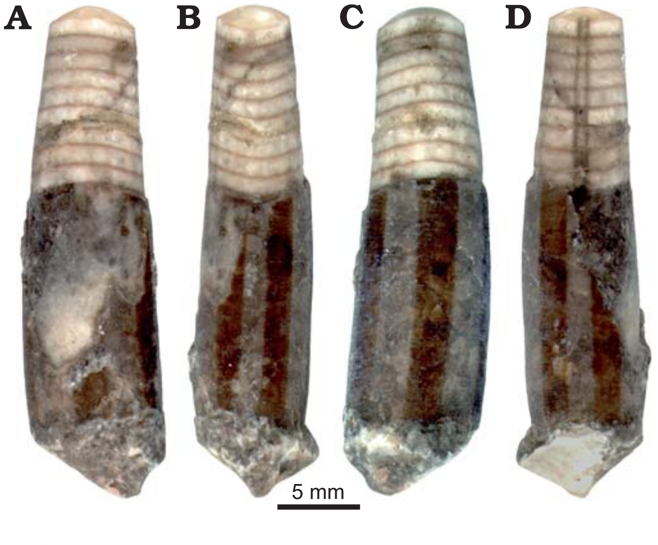

Fig. 5. *Pomerantsoceras pollux* (Barrande, 1866). Specimen CGU SM 322, in lateral (**A**, **C**), dorsal (**B**), and ventral (**D**) views. Lochkov, Nad ubikacemi Section, *Monograptus latilobus* Zone, Ludfordian, Ludlow. Photographed in alcohol.

Systematic palaeontology

Subclass Nautiloidea Agassiz, 1847

Order Oncocerida Flower, 1950

Family Oonoceratidae Flower, 1942

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

Discussion.—Family Oonoceratidae was erected by Flower in 1942, but no diagnosis was given by him. Flower (1942) included three genera in the family, namely *Richardsonoceras* Foerste, 1933 (Ordovician), *Oonoceras* Hyatt, 1884 (Silurian–earlier Devonian), and *Oocerina* Foerste, 1926 (Silurian). However, *Oocerina* in fact belongs to the family Jovellaniidae Foord, 1888 (see Manda 2001). Sweet (1964) synonymised the Oonoceratidae with Oncoceratidae Hyatt, 1884. The diagnosis of the latter family, as refined by Frey (1995), suggests that *Oonoceras* and allied genera cannot by placed here. Late Ordovician species assigned by Flower (1942) to *Oonoceras* probably belong to another genus because they differ from *Oonoceras* in having long body chambers, almost straight sutures and very thin siphonal tubes. The phyletic relationship between *Richardsonoceras* and *Oonoceras* proposed by Flower (1942) and followed by Dzik (1984) is still unclear. In our view, the family Oonoceratidae contains only *Oonoceras* (Silurian and earlier Devonian) and its allied genera. It should be noted that the majority of taxa are known from the Silurian of the Prague Basin, where the family reached its maximal diversity as well as disparity. New material shows that species grouped within *Oonoceras* in fact belong to other, still undescribed, genera that differ in shell curvature, cross section, sculpture and ratio of phragmocone/body chamber length. At last, two morphologically convergent groups of oncocerids with exogastrically curved shells exist. The Silurian jovellaniids including *Oocerina* differs from oonoceratids by the presence of actinosiphonate deposits. Similarly, Ordovician *Richardsonoceras*–"*Oonoceras*" (sensu Flower 1942) and Silurian *Oonoceras* may represent convergent morphotypes of oncocerids. However, without data concerning early shell ontogeny, the systematic position of *Richardsonoceras* and allied forms remain unclear.

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

Genus *Pomerantsoceras* Kröger, 2007

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

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

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

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

Pomerantsoceras pollux (Barrande, 1866)

Figs. 4–10.

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

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

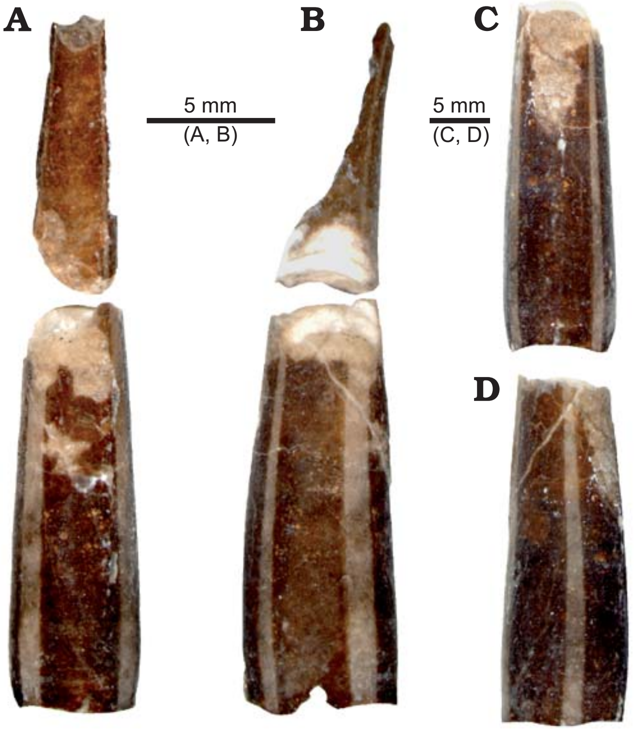

Fig. 6. *Pomerantsoceras pollux* (Barrande, 1866). Specimen CGU SM 323, the body chamber, in dorsal (**A**), lateral (**B**), ventral (**C**), and lateral (**D**) views. Lochkov, Nad ubikacemi Section, *Monograptus latilobus* Zone, Ludfordian, Ludlow. Photographed in alcohol.

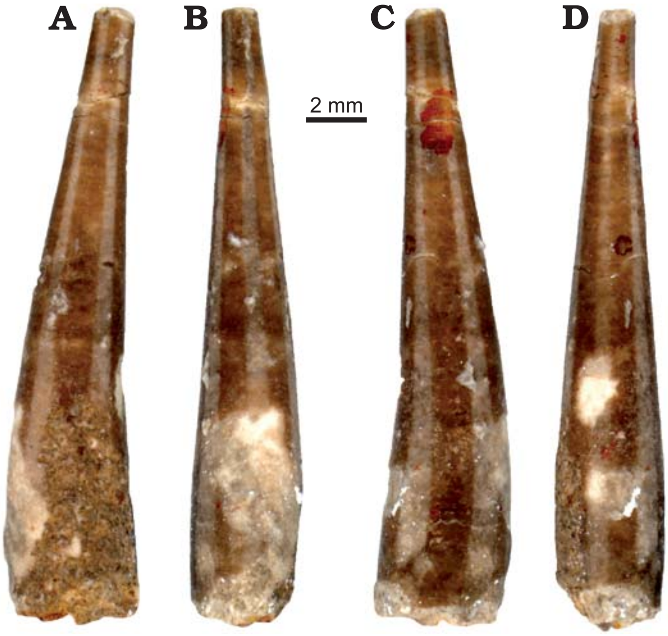

Fig. 7. *Pomerantsoceras pollux* (Barrande, 1866). Specimen CGU SM 321, in lateral (**A**, **C**), ventral (**B**), and dorsal (**D**) views. Lochkov, Nad ubikacemi Section, *Monograptus latilobus* Zone, Ludfordian, Ludlow. Photographed in alcohol.

Type locality: Praha-Malá Chuchle, Vyskočilka e2.

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

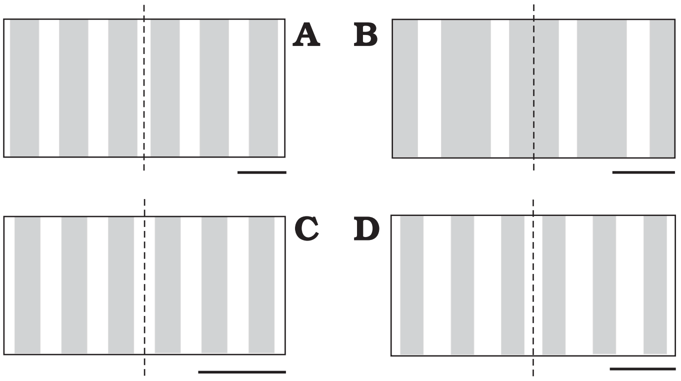

Fig. 8. Sketches of the colour pattern in *Pomerantsoceras pollux* (Barrande, 1866). **A**. Specimen SM 319, Kační Quarry. **B**. Specimen CGU SM 322, Nad ubikacemi Section. **C**. Specimen CGU SM 323, Nad ubikacemi Section. **D**. Specimen CGU SM 321, Nad ubikacemi Section.

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

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

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

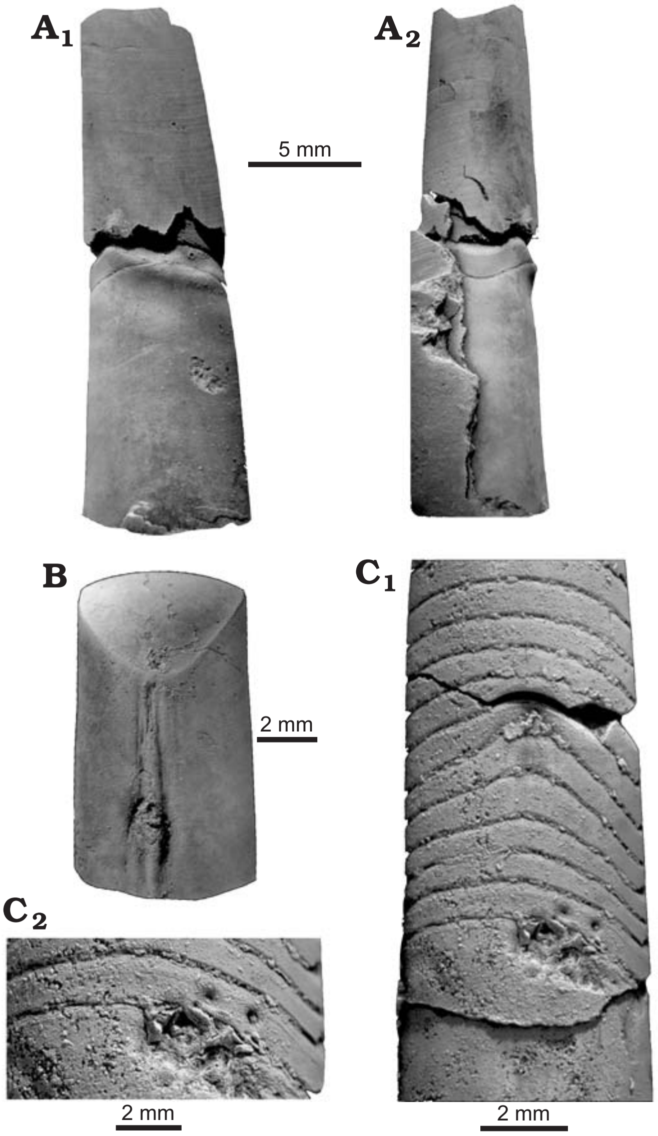

Fig. 9. Shell malformations in *Pomerantsoceras pollux* (Barrande, 1866). **A**. Specimen CGU SM 318 with a false rib at the base of body chamber, in lateral (A_1) and ventral (A_2) views. **B**. Specimen CGU SM 316, body chamber with conchal furrow-like malformation, in ventral view. **C**. Specimen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

Discussion.—Barrande (1866) figured another shell on pl. 148 as figs. 20–23, which he described as "*Cyrtoceras pollux* var. *castor*" (holotype by monotypy; NM-L 571; type locality Butovitz e1, i.e., Praha-Butovice, Na břekvici Section, see Kříž 1992; Ludlow, Gorstian, early *C. colonus* Zone; see Fig. 10A). According to Barrande (1874), "*Cyrtoceras pollux* var. *castor*" differs from *Cyrtoceras pollux* by having a less compressed cross section and slightly deeper ventral and lateral saddles at the suture. The holotype of *Cyrtoceras pollux* is slightly flattened by diagenetic compaction and has slightly deformed original cross section dimensions (Fig. 10B$_1$). Despite the malformation of the sutures in the adoral part of the phragmocone in the holotype of "*Cyrtoceras pollux* var. *castor*" the sutures and spacing between them are similar in dimension to those in *Cyrtoceras pollux* (Fig. 10A$_1$). Consequently, suture and cross section differences are the result of shell malformation and diagenesis and thus, "*Cyrtoceras pollux* var. *castor*" is considered synonymous with *C. pollux*.

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

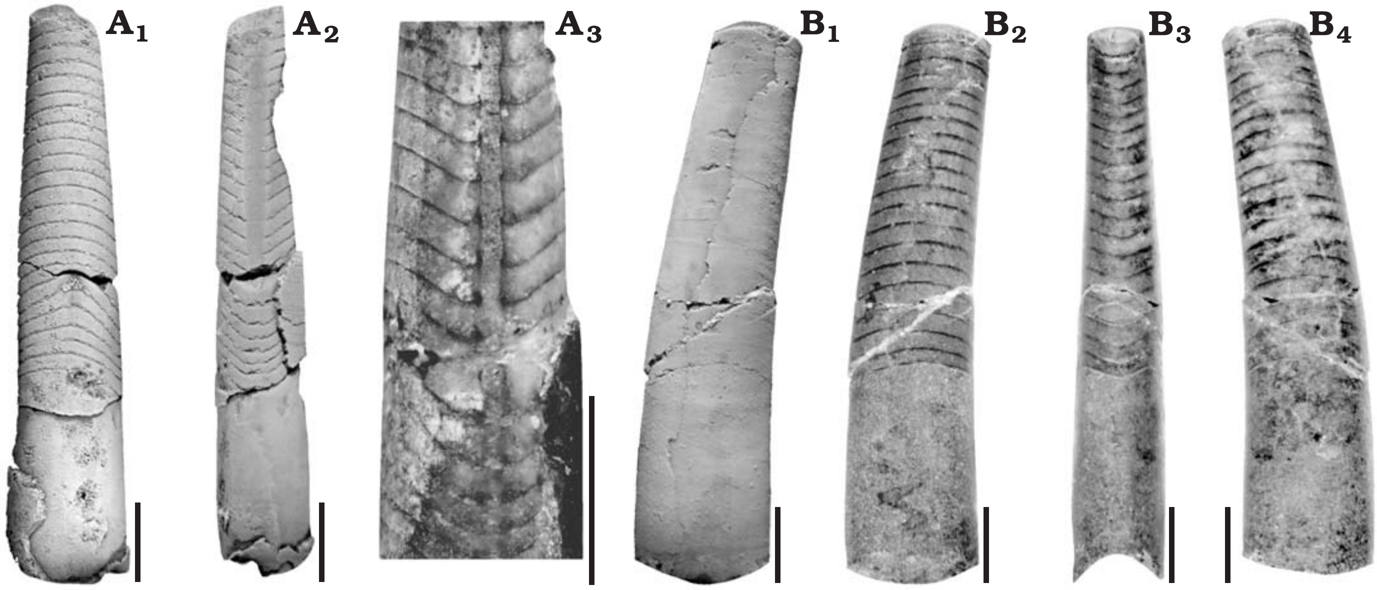

Fig. 10. **A**. Holotype of *Pomerantsoceras pollux* "var. *castor"* (Barrande, 1866). Specimen NM-L 571, in lateral (A_1) and ventral (A_2) views, and detail of the siphuncle (A_3); Butovice Na Břekvici Section, *Colonograptus colonus* Zone, Gorstian, Ludlow. **B**. Holotype of *Pomerantsoceras pollux*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

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

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

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

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

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PŘÍLOHA 9

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

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

Key words. **Nautiloidea, Barrandeocerina, *Peismoceras*, colour pattern, shell abnormalities, Bohemia, Czech Republic.**

INTRODUCTION

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

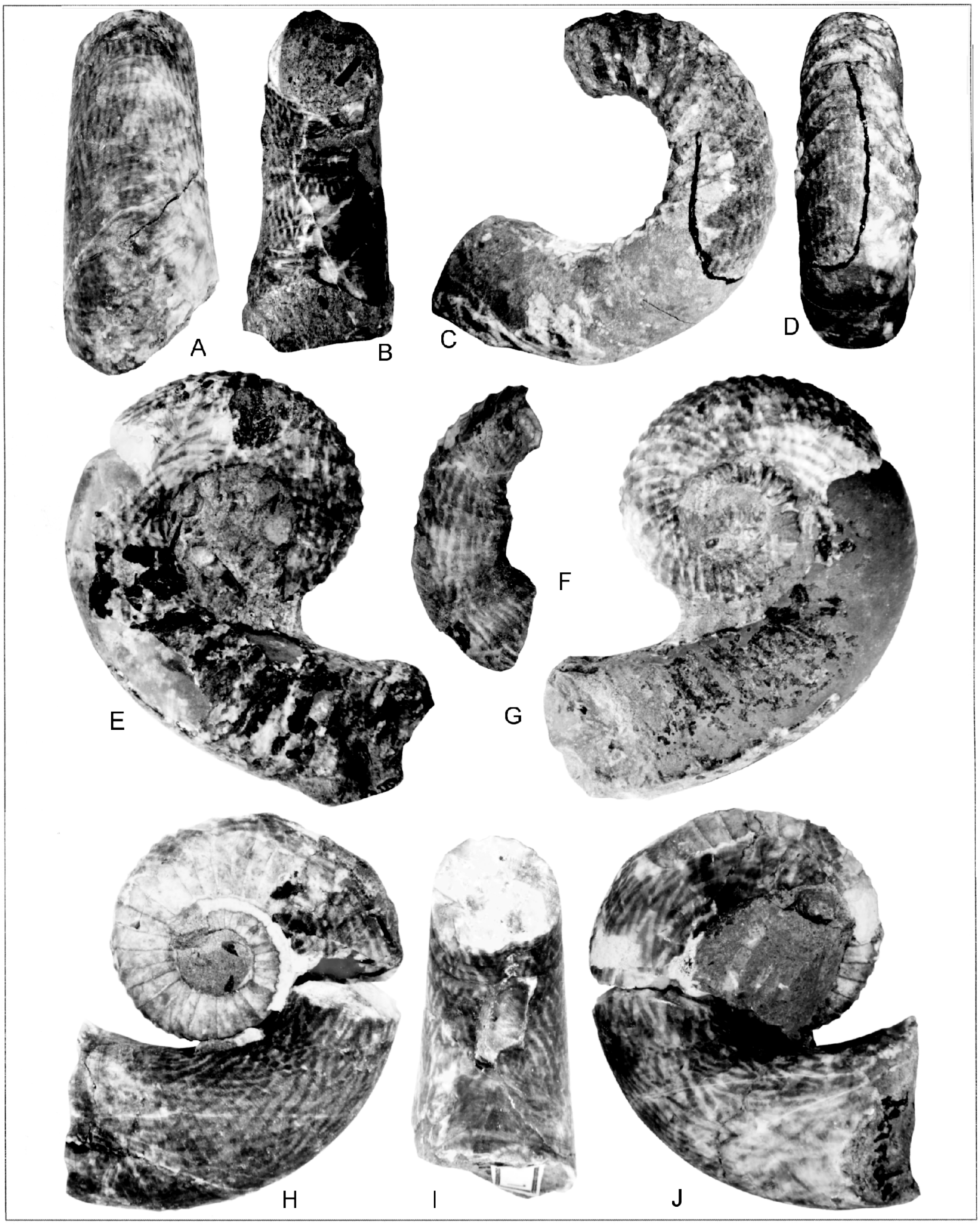

Fig. 1. A, E–J. *Peismoceras pulchrum* (Barrande, 1865). Gorstian, Kopanina Fm., *C. colonus* Zone, Na břekvici, Praha, Bohemia. A, H–J. Almost complete specimen with preserved zigzag colour pattern, A – ventral view; H, J – lateral views; I – body chamber, dorsal view, NMP L 27400, × 0.9; B – incomplete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

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

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

DESCRIPTION OF COLOUR PATTERN AND SHELL ABNORMALITIES IN *PEISMOCERAS*

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

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

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

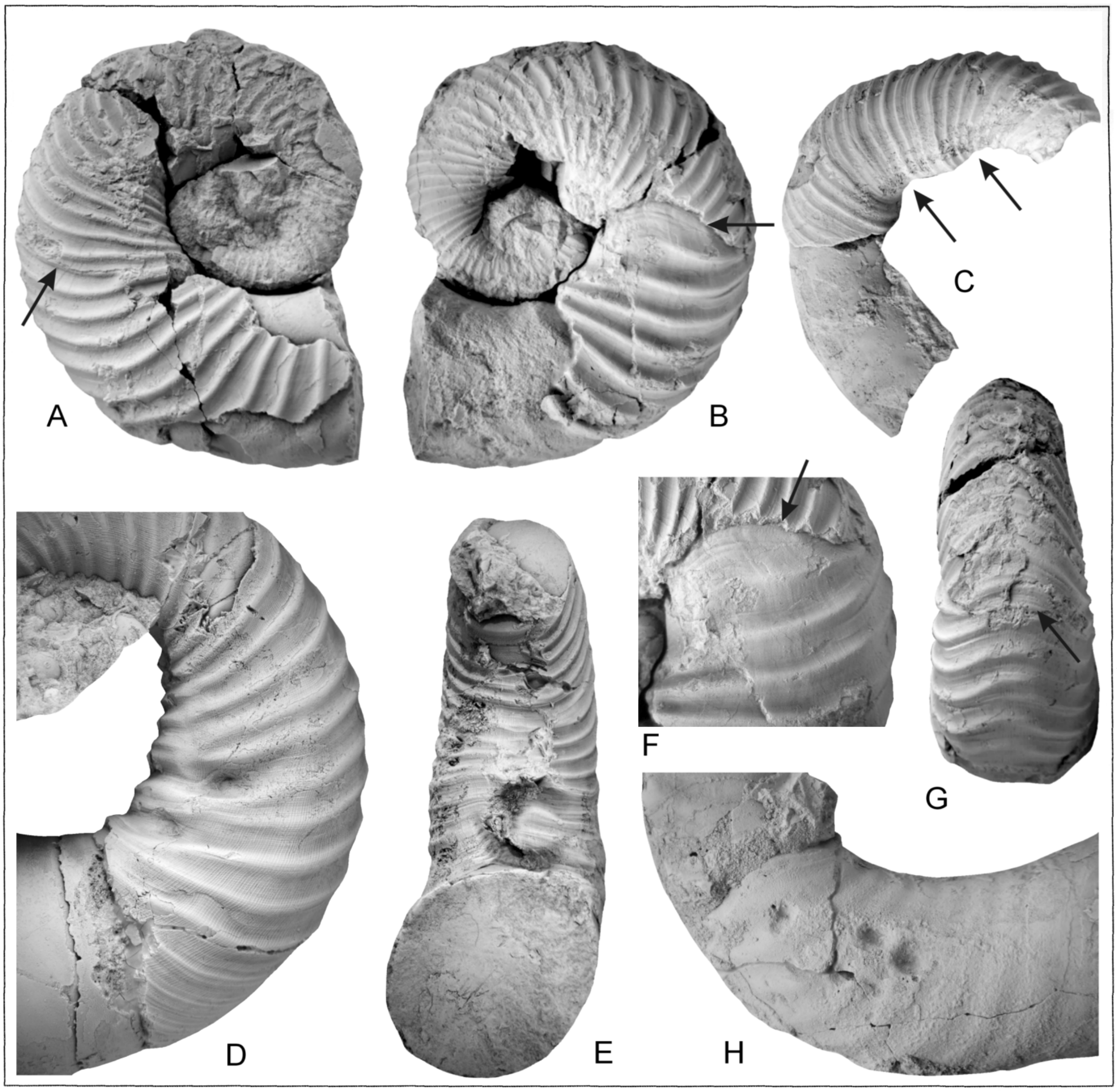

Fig. 2. A, B, F–H. *Peismoceras asperum* (Barrande, 1865). Gorstian, Kopanina Formation, *S. chimaera* Zone. A, B, F, G – Vyskočilka, Praha, Bohemia. Incomplete specimen with preserved shell, heavily damaged in adapertural part of phragmocone (indicated by arrows). A, B – lateral views, G – ventral view,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

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

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

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

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

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

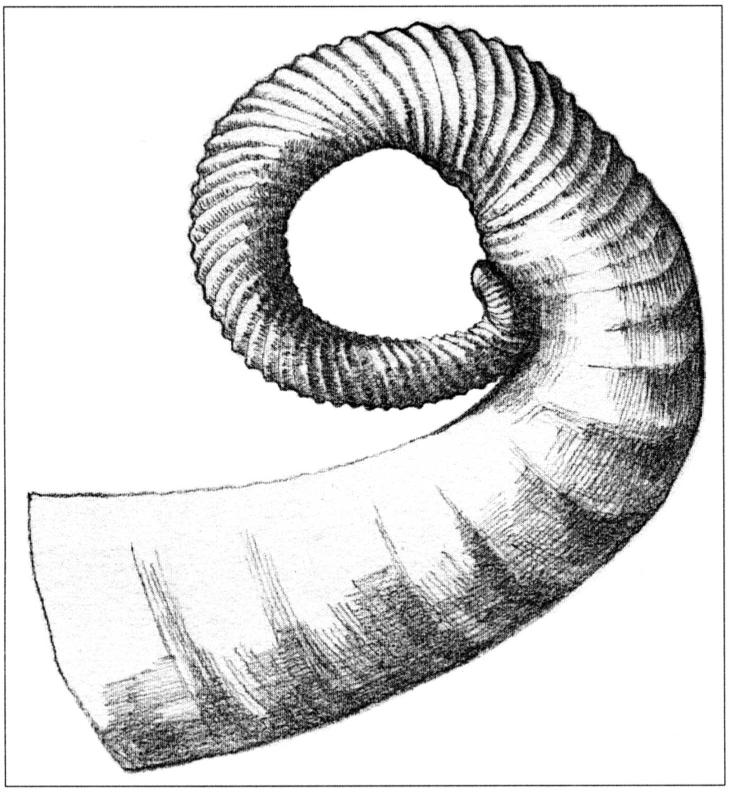

Fig. 3. Reconstruction of anomalous shell of *Peismoceras pulchrum* (Barrande, 1865). Based on specimen NMP L 27406; colour pattern omitted. Drawing by Jan Sklenář.

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

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

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

CONCLUSIONS

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

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

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

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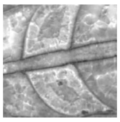
Příloha 10

Publikovaná práce

Manda, Š., Frýda, J. 2010. Silurian–Devonian boundary events and their influence on cephalopod evolution: a comparison of faunal and carbon isotopic records from GSSP area (Barrandian). Bulletin of Geosciences 85, 513–540.

Silurian-Devonian boundary events and their influence on cephalopod evolution: evolutionary significance of cephalopod egg size during mass extinctions

Štěpán Manda & Jiří Frýda



Diversity evolution of 197 of the latest Ludlow–Lochkovian cephalopod species from Bohemia (representing more that 70 percent of all species known worldwide) was analysed and compared with changes in the global carbon cycle in the marine ecosystem. Our results show a distinct relationship between cephalopod species diversity and the global carbon cycle. A progressive increase in $\delta^{13}C$ values in marine carbonates from the *Monograptus lochkoviensis* Zone to the end of the *Monograptus transgrediens* Zone reflects an increase of bioproductivity in the marine ecosystem. This increase was probably caused by a shallowing of the upwelling system, thus importing nutrient-rich water. A progressive cooling during the Přídolí and earliest Lochkovian triggered these changes in the upwelling system. Our data also show an increase in total diversity of cephalopod species, which may be explained by greater availability of new food sources for a period corresponding to the progressive increase in $\delta^{13}C$ values. In the latest Silurian, $\delta^{13}C$ reached its maximal values while the Lochkovian is characterized by steady conditions with a decreasing tendency in $\delta^{13}C$ values. Strong, selective extinction started in the latest Silurian *Monograptus transgrediens* Zone and continued to the earliest Devonian *Monograptus uniformis* Zone. This extinction affected benthic and demersal cephalopod species with relatively large eggs and long incubation times. The change in dynamics of the global carbon cycle thus coincides with the beginning of this extinction. An anoxic or hypoxic event in the period between the LAD *Monograptus transgrediens* Zone (Transgrediens Event) in the latest Přídolí and the base of the Devonian *Monograptus uniformis* Zone (documented also from offshore sequences from Poland) is considered to be a cause for the extinction of non-pelagic cephalopods. Our study also revealed a need to revise and define all earlier established bioevents in the Silurian-Devonian boundary interval more clearly. • Key words: Silurian-Devonian boundary, Klonk Event, Transgrediens Event, cephalopods, carbon isotopes, Prague Basin, peri-Gondwana, extinction, palaeoecology.

Manda, Š. & Frýda, J. 2010. Silurian-Devonian boundary events and their influence on cephalopod evolution: evolutionary significance of cephalopod egg size during mass extinctions. *Bulletin of Geosciences 85(3)*, 513–540 (10 figures, 3 tables). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received January 5, 2010; accepted in revised form September 22, 2010; published online September 30, 2010; issued September 30, 2010.

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The Silurian has been considered as a period with a relatively stable green house climate with the absence of significant extinction events for a long time (see Holland 1991 and Calner 2009 for summaries). Since the nineties of the last century, several prominent extinction events were described from graptolite (Jaeger 1991, Urbanek 1993, Koren' 1993, Štorch 1995, Melchin *et al.* 1998) and conodont successions (Jeppsson 1990, 1998; Jeppsson & Aldridge 2000). Later studies of carbon isotopes show that some of these extinctions roughly correspond with carbon isotope excursions and thus reflect the carbon-ocean cycle (Munnecke *et al.* 2003, Lehnert *et al.* 2007b, Calner 2008). In addition, the oxygen isotopes suggest dramatic changes in water temperature during the Silurian and indicate periods with an ice-house climate (Lehnert *et al.* 2007a, Eriksson & Calner 2008, Calner 2008). Nevertheless, the published considering biodiversity, carbon and oxygen isotope as well as eustatic sea-level data have not yet resulted in generally accepted definitions and explanations of Silurian mass extinction events, particularly due to the lack of precise biodiversity data and the focus on rather small enigmatic groups. A weak point in the existing studies is the unconvincing integration of different approaches, *e.g.* biodiversity data plotted again isotopic curves. Understanding the Silurian mass extinctions and critically evaluating the existing explanations and models requires the careful collection of further data and their evaluation as claimed by Boucot (1990).

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The extinction events close to the Silurian-Devonian boundary are still poorly understood. Walliser (1985) and Schönlaub (1986) considered the "Silurian-Devonian boundary Event" as a prominent turnover in Palaeozoic faunas, however, no definition or precise data was given. On the contrary, Boucot (1990) and Talent *et al.* (1993) did not find any significant change in the generic diversity of brachiopods across the Silurian-Devonian boundary interval. Urbanek (1995) defined the Transgrediens Event as graptolite extinction just below the Silurian-Devonian boundary. Nearly 80% of the 14 graptolite species became extinct. This extinction coincided with the beginning shallowing in the latest Přídolí (Melchin *et al.* 1998). Later, Jeppsson (1998) introduced the name "Klonk Secundo-Unnamed Event" as a conodont extinction event, which is probably identical with the Transgrediens Event. However, this conodont extinction event is known only from a few sections and there are apparent taxonomic discrepancies (Carls *et al.* 2007). These bioevents were based on the diversity dynamics in low diversity graptolite and conodont faunas. Both the ecological requirements and the mode of life of these extinct groups remain controversial.

Hladíková *et al.* (1997) and Buggish & Mann (2004) described the carbon isotope excursion at the Silurian-Devonian boundary, but they did not correlate this excursion with biotic changes. The relation between extinctions and the carbon isotope cycle is a widely discussed topic in connection with many Silurian events (Munnecke *et al.* 2003, Calner 2008). Except for vague statements that positive carbon isotope excursions correspond with extinctions, there is little evidence to support this view. In addition, recent studies of oxygen isotopes suggest that climatic changes reflect the green-ice house status (Joachimski *et al.* 2009 for a review). The relationship between diversity, extinctions and the oxygen isotope curve is still poorly understood; in particular more oxygen isotope data is needed.

In the present study, we compared cephalopod diversity fluctuations and the carbon isotope curve from the latest Silurian and the earliest Devonian based on several sections in the classic area of the Prague Synform, Bohemia (Prague Basin, Barrandian). The highly elaborated biostratigraphy of this area enables detailed correlations in comparison with many other areas. Note that three GSSP stratotypes for the examined intervals occur in the Prague Synform (Ludlow-Přídolí, Přídolí-Lochkovian, Lochkovian-Pragian). We analysed the diversity evolution of 197 of the latest Ludlow–Lochkovian cephalopod species (representing more than 70 percent of all known species of this interval) and compared its dynamics with changes in the global carbon cycle in the marine ecosystem.

Cephalopods were selected as a model group for testing biodiversity changes across the Silurian-Devonian boundary because they represent an animal group with different habitats and ecological strategies; cephalopods inhabited different environmental settings, but usually are not restricted to specific biofacies. The cephalopods also represent a rather diverse group in the Silurian and Devonian. Currently, the best-documented sedimentary succession around the latest Silurian extinction, the Transgrediens Event, is considered to contain a low graptolite diversity fauna consisting of only 14 species (Melchin *et al.* 1998), although only two species are known from Bohemia or Poland (Chlupáč *et al.* 1972). By contrast, the coeval fauna included in our database contains more than 100 cephalopod species worldwide. The main aim of this study is to test whether the Silurian-Devonian boundary events had the same impact on an animal group with different modes of life and whether there is a link between cephalopod diversity and changes in environmental parameters. Carbon isotope composition of marine carbonates (characterizing evolution of the global carbon reservoir in the marine ecosystem) was selected here as a proxy for a description of these changes in the Silurian-Devonian boundary interval.

The Silurian-Devonian boundary and bioevents

The Silurian and Devonian rocks in central Bohemia, SW of Prague, form a large synform with the axis orientated in a NEE-SWW direction. This synform is affected by several faults (Figure 1). Barrande (1846) divided the Silurian-Devonian boundary sequences differently from the present stratgraphic concept. The upper boundary of his "étage Ee2" (late Wenlock–early Lochkovian) included the lowermost Lochkovian beds with a dominance of carbonates. The overlying "étage Ff1" unites sequences of shales and carbonate beds. Barrande's lithostratigraphic units ("étages") were for a long time considered to be also chronostratigraphic units. Krejčí (1877) renamed "étage Ee2" as "budňanské vrstvy" (Budňany beds) and "étage Ff1" as "lochkovské vrstvy" (Lochkov beds). Much later, Prantl & Přibyl (1948) proposed the name "přídolské vrstvy" (Přídolí beds) for the upper part of the Budňany beds. This subdivision is basically still valid (see Chlupáč 1998, Kříž 1998a).

Přibyl (1940, 1943) established the modern biostratigraphic scale of the Přídolí and Lochkovian when he had subdivided this stratigraphic interval into several graptolitic zones. Slightly later, Chlupáč (1953) described the Silurian-Devonian boundary interval in detail. Horný (1955) proposed to split the carbonate sequences into several horizons characterized by common fossils (*e.g.*, horizon with *Dayia bohemica* or uppermost Silurian *Scyphocrinites* Horizon) on the basis of his detailed mapping.

One of the conclusions of the "First international congress on Silurian-Devonian boundary, Prague" in 1958 (Svoboda 1960) was to include the Lochkovian (with the youngest occurrences of graptolites) into the Silurian, and

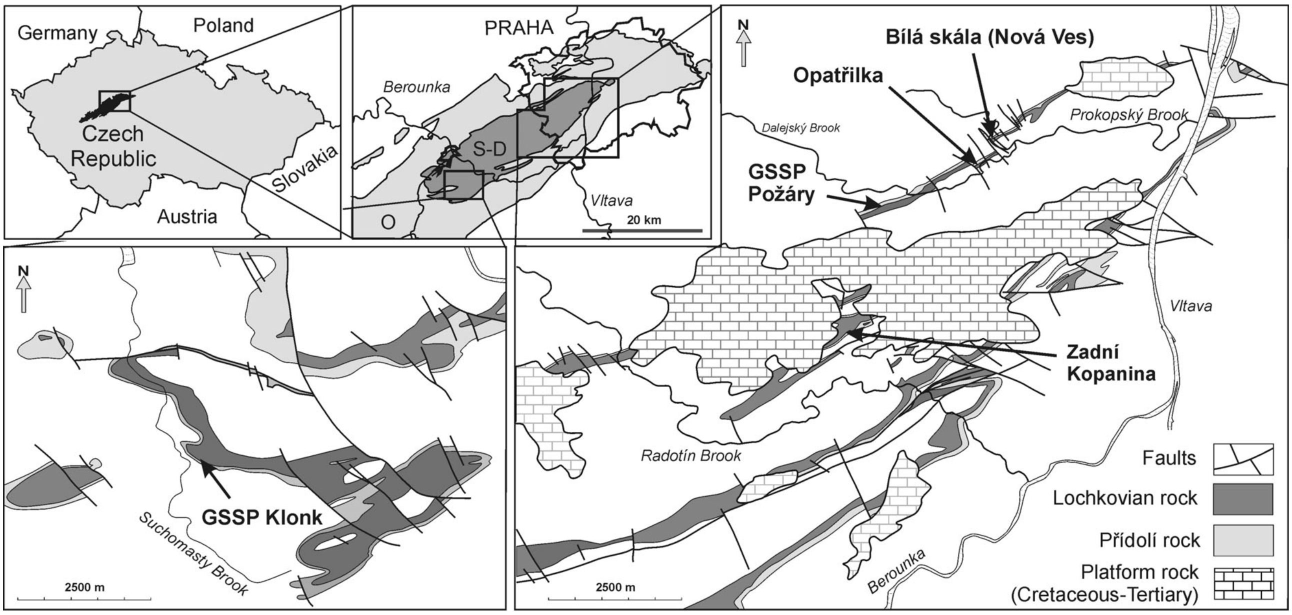


Figure 1. Distribution of the Přídolí and Lochkovian rocks in the southwestern and eastern part of the Prague Synform and position of the sections including the GSSP Klonk and Požáry sections.

the Pragian was established as the oldest Devonian stage. However, Bouček (1966) found the youngest graptolites within Pragian strata and challenged the concept proposed by the Prague congress. These activities resulted in the Silurian-Devonian boundary being defined at the base of the *Monograptus uniformis* Zone (Bouček *et al*. 1966). Subsequently, Chlupáč *et al*. (1972) studied several Silurian-Devonian boundary sections of the Prague Synform in detail and proposed a more detailed biostratigraphical subdivision of this interval. The Klonk Section near Suchomasty (Fig. 1) in the SW part of the Prague Synform was selected in 1972 as the Silurian-Devonian boundary stratotype (GSSP) during the IGC in Montreal.

Detailed biostratigraphic studies revealed that the British series Ludlow is equivalent only to the Kopanina Formation of the Prague Basin and therefore, it was evident that there is an unnamed time period between the Ludlow and the Lochkovian (Jaeger 1960). This time period was named the Přídolí and is roughly equivalent to the Požáry (formerly Přídolí) Formation (Berdan *et al*. 1969). Kříž *et al*. (1983, 1986) thoroughly studied the boundary interval between the Kopanina and Požáry formations and the section Na požárech (Fig. 1) near Řeporyje was proposed as the GSSP for the base of the Přídolí (IGC Moscow 1984).

Later detailed palaeontological studies of the Silurian-Devonian boundary interval of the Prague Basin revealed distinct changes in faunal communities [trilobites (Chlupáč 1971, 1983), brachiopods (Havlíček 1999, Havlíček & Štorch 1999), bivalves (Kříž 1998b, 1999), cephalopods (Manda 2001), gastropods (Frýda & Manda 1997), *etc*.]. However, none of the above mentioned studies evaluated diversity changes quantitatively and thus, it is not known whether the observed faunal changes are considerably different from "normal" levels of faunistic changes at any sequence boundary.

The same is true for several proposed bioevents of the Silurian-Devonian boundary interval such as the Silurian-Devonian boundary Event (Walliser 1985), Transgrediens Event (Urbanek 1995), and Klonk Event (Jeppsson 1998). However, all these bioevents were proposed only on the basis of qualitative evaluation of observed faunal changes.

Studied sections, analytical methods and cephalopod database

Studied sections

Three well-exposed Silurian-Devonian boundary sections in the vicinity of Prague (Na hradišti-Bílá skála, Opatřilka, and Zadní Kopanina) were studied in detail and sampled for $\delta^{13}C$ content. Two of the predominantly carbonate sections were studied previously (see below). In the following chapters, basic information on geographic positions, stratigraphic ranges, lithology, and previous studies of the sections are summarized.

Na hradišti-Bílá skála Section

Large natural outcrops named Bílá skála (White rocks) are located on the western slope of Hradiště hill in the Prokop Valley, about 1100 m southwest of Butovice Village

(Fig. 1). The section was first studied and briefly described by Horný (1961, 1962). Later, Vaněk (1963) described a trilobite fauna from the upper part of the *M. uniformis* Zone (early Lochkovian). The Silurian-Devonian boundary interval (starting from bed No. 31 of our section – see Fig. 2) was studied comprehensively by Chlupáč *et al*. (1972). Because of problems with the identification of some beds in the figured section of Chlupáč *et al*. (1972, fig. 21), we re-measured the complete section (Fig. 2).

The section begins with shales and platy limestone belonging to the *M. lochkovensis* and *M. bouceki* zones (Fig. 3D). The first distinct limestone bank bearing *Dubaria harpyia* and *Dayia minor* communities (*cf*. Havlíček & Štorch 1999) occurs just above the base of the *M. bouceki* Zone. The mudstone-shale sequence is covered by thin-bedded mudstones some of which bearing cephalopod remains (Fig. 3H). Higher up, thick coarse crinoidal limestone beds occur (Fig. 3F, I), which are covered by several layers of cephalopod limestone bearing a *Kopaninoceras fluminese* assemblage of the *M. transgrediens* Zone (Fig. 3E, G). The section continues with a bed containing the common brachiopod species *Septatrypa latisinuata*, and subsequently, characteristic limestone beds with the brachiopod *Dayia bohemica* can be found (Fig. 3A). *Dayia bohemica* is less frequent in the following thin-bedded mudstones, which are intercalated with shales. This sedimentary sequence is replaced by brachiopod limestone beds corresponding to the latest Přídolí (trilobite *Tetinia minuta*) in a younger part of the section (Fig. 3B).

Light grey crinoidal limestone beds overlie these limestones and bear a rich fauna with brachiopods, trilobites (including the index *Warburgella rugulosa*), and other groups, which already belong to the early Lochkovian (Fig. 3C). Large cephalopod shells are relatively common and thus characteristic for the bed just above the base of the Lochkovian (Fig. 3J). Grey wackestones with less frequent large cephalopod shells form the youngest part of the section (Fig. 3K) and already belong to the late Lochkovian (see Vaněk 1963).

Opatřilka Section

The Opatřilka Section (Fig. 2) is located in an abandoned quarry on the north slope of Daleje Valley, about 750 m to the NW from an old chapel in Holyně Village (Fig. 1). The section was already described and measured by Chlupáč *et al*. (1972). The lowermost part of the measured section consists of mudstones intercalated with shales (*M. lochkovensis* and *M. bouceki* zones). A distinct layer of crinoidal limestone with *Dayia minor* occurs at the base of the *M. bouceki* Zone. The section continues with cephalopod limestone beds intercalated with thin mudstone and crinoidal limestone beds (*M. transgrediens* Zone). A diverse fauna of cephalopods, bivalves and gastropods occur in the latter sequence. The cephalopod limestones are overlain by a prominent *Septatrypa*-bearing brachiopod limestone bank and by a *Dayia bohemica*-bearing brachiopod bed above. The brachiopod limestones are covered with platy mudstones intercalated with shales or with thin *Dayia*-bearing limestone beds. Brachiopod limestone beds, with the index trilobite *Tetinia minuta,* characterize the latest Přídolí. The large cephalopods-bearing bituminous limestone beds are covered by mudstones and these beds belong to the basal Lochkovian (identified by FAD *W. rugulosa*). Crinoidal limestone banks form the youngest part of the section.

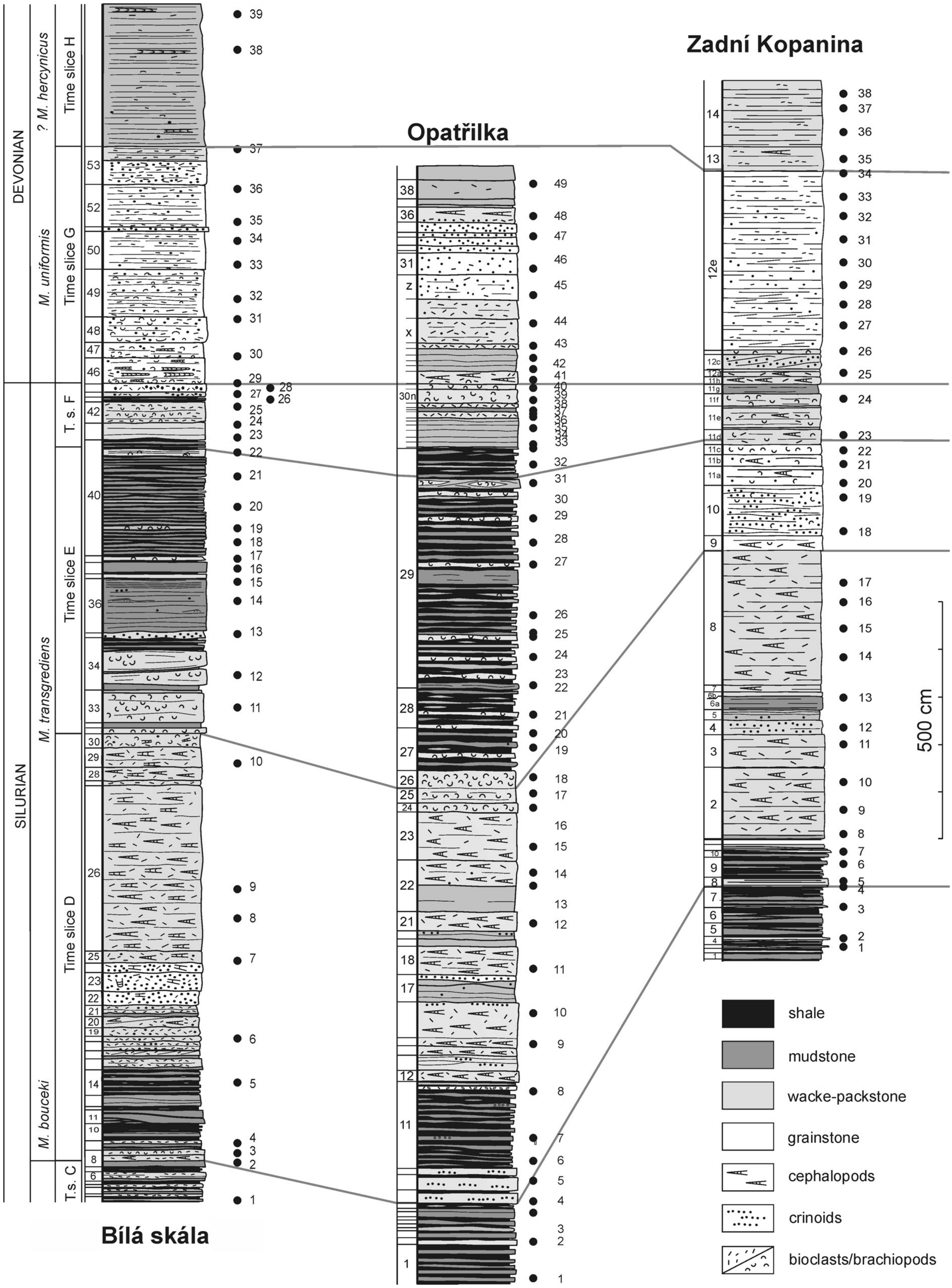
Zadní Kopanina Section

The studied section occurs on a large forested slope in the Mlýnský Brook Valley along the road in Zadní Kopanina Village, about 200 m east of the bus station "Zadní Kopanina" (Fig. 1). The lower part of the measured section is located in the western portion of this outcrop; the middle and upper parts are located about 80 m to the east. The section was briefly mentioned by Kříž (1998b). Stratigraphically, it belongs almost completely to the Přídolí (lowermost part absent) and early Lochkovian (Fig. 2). The section starts with shales and platy limestone beds belonging to *M. lochkovensis* and *M. bouceki* zones. A characteristic crinoidal limestone layer rich in bivalves is developed at the base of the *M. bouceki* Zone. Cephalopod limestone beds occur in the upper part of the *M. bouceki* Zone and lower part of the *M. transgrediens* Zone (Fig. 4), which are covered by crinoidal and brachiopod limestones with the typical brachiopod species *Dayia bohemica*. The latest Přídolí is characterized by thin brachiopod limestone and mudstone beds. A few cephalopod limestone beds appear at the base of the Lochkovian (identified here by FAD *M. uniformis*). Higher up, the section continues with early Lochkovian skeletal limestones. The section ends with grey mudstones probably corresponding to the beginning of the "late" Lochkovian.

Carbon isotope analyses

Carbonates from the late Silurian Požáry Formation and Early Devonian Lochkov Formation were sampled for car-

Figure 2. Nová Ves, Opatřilka, and Zadní Kopanina sections showing biostratigraphy, time slices, bed numbers, lithology, and position of carbon isotope samples (black circles).


Bílá skála
Opatřilka
Zadní Kopanina
DEVONIAN
SILURIAN
? M. hercynicus
M. uniformis
M. transgrediens
M. bouceki
Time slice H
Time slice G
T. s. F
Time slice E
Time slice D
T.s. C
500 cm
shale
mudstone
wacke-packstone
grainstone
cephalopods
crinoids
bioclasts/brachiopods

bon isotope analyses from the three sections in the NE part of the Prague Synform described above. These sections (Bílá skála, Opatřilka, and Zadní Kopanina) are generally characterized by sedimentation in relatively shallow-water environments. The carbon isotope record of these sections has never been studied in contrast to the Klonk Section (GSSP) in the SW part of the Prague Basin (Hladíková *et al*. 1997, Buggisch & Mann 2004) and the Požáry Quarry (GSSP) in the eastern part of the Prague Basin (Buggisch & Mann 2004). The sections discussed above were sampled in detail from the carbonate beds just below the Přídolian *Monograptus bouceki* Zone to the beginning of the Lochkovian *Monograptus hercynicus* Zone.

All $\delta^{13}C$ sampling was related to the number of the beds (Fig. 2). In addition to the carbon isotope analysis, thin sections from the different lithologies were studied for additional facies information. A few milligrams of rock powder (preferably micrite) were recovered using a dental drill from rock samples or polished slabs. Where possible, mudstones and wackestones were sampled, but analyses were also done on grainstones in which micrite was absent. Carbonate samples were decomposed in a vacuum using 100% phosphoric acid at a temperature of 25 degrees Celsius. The carbon and oxygen isotopic composition of the released CO_2 was measured with a Finnigan Mat 251 mass spectrometer. All values are reported in ‰ relative to the V-PDB by assigning a $\delta^{13}C$ value of +1.95‰ and a $\delta^{18}O$ value of 2.20‰ to NSB 19. Accuracy and precision was controlled by replicate measurements of laboratory standards and was greater than ±0.1‰ for both carbon and oxygen isotopes.

Stratigraphic division of Přídolí-Lochkovian used for analysis

Our analysis is focused on the comparison of cephalopod diversity with the course of the $\delta^{13}C$ signal across the Silurian-Devovian boundary beds. Data on the stratigraphic position of each $\delta^{13}C$ sample for the three profiles are very precise (see Fig. 2). This is not true for all cephalopod diversity datasets (see details above). Our priority was to include all known cephalopod species in the analysis and to use the same scale for both datasets. For this reason, eight stratigraphic time slices (A–H) were selected (see their definition below) and these were used for analysis of both biodiversity and $\delta^{13}C$ changes.

Time slice A (latest Ludlow) corresponds to the *Monograptus fragmentalis* Zone (Kříž 1998b) and is roughly identical with the "*Prionopeltis archiaci* Horizon" as described by Horný (1955). This time slice begins with the LAD *Monograptus latilobus* and ends with the FAD *Pristiograptus parultimus* (Manda & Kříž 2006).

Time slice B unites the two-ealiest graptolite zones of the Přídolí, *Pristiograptus parultimus* and *Pristiograptus ultimus* zones, which are relatively easily recognisable in the majority of sections (Kříž *et al*. 1986). This time slice covers the period from FAD *Pristiograptus parultimus* to FAD *Monograptus lochkoviensis*.

Time slice C corresponds to the *Monograptus lochkoviensis* Zone in the sense of Kříž *et al*. (1986). It starts with the FAD *Monograptus lochkoviensis* and ends with the FAD *Monograptus bouceki*.

Time slice D unites more than two graptolite zones, the *Monograptus bouceki* and *Monograptus perneri* zones, and the lower part of the *Monograptus transgrediens* Zone. As mentioned previously by Chlupáč *et al*. (1972) and Kříž *et al*. (1986), determination of the *Monograptus perneri* Zone and of the base of the *Monograptus transgrediens* Zone (interval zone) is difficult in some sections. Nevertheless, the first occurrence of the characteristic brachiopod *Dayia bohemica* is a good stratigraphic marker in the majority of Prague Basin sections (Chlupáč *et al*. 1972). For this reason, this stratigraphic level was used here as the end of Time slice D.

Time slice E starts at the level of FAD *Dayia bohemica* and ends at LAD *Monograptus transgrediens*. Its upper boundary is easily recognisable in most sections of the Prague Basin, except for those with purely carbonate rocks. However, in the latter sections, the level of LAD *Dayia bohemica* may be used as a proxy for the LAD of *Monograptus transgrediens* because the characteristic brachiopod species, *Dayia bohemica*, ends just above it in all studied sections of the Prague Basin where both taxa are present (Chlupáč *et al*. 1972).

Time slice F includes a period between the LAD of *Monograptus transgrediens* and FAD of *Monograptus uniformis* and is easily recognisable in all the studied sections (Chlupáč *et al*. 1972).

The FAD of *Monograptus uniformis* is internationally accepted as a marker for the base of the Devonian (for a summary see Chlupáč 1998) and therefore, it is selected here as the lower boundary of Time slice G. The upper boundary of Time slice G corresponds to the FAD *Monograptus hercynicus*. Time slice G is thus equal to the *Monograptus uniformis* Zone, which was used as an equivalent for the informal unit "lower Lochkovian" by Chlupáč (1977). The lower boundary of Time slice G is also easily recognisable by the appearance of newly occurring bivalves (Kříž 1999, 2008a, b), trilobites (Chlupáč 1971, Chlupáč *et al*. 1972), cephalopods (Manda 2001), and gastropods (Frýda & Manda 1997).

Time slice H starts at the FAD of *Monograptus hercynicus* and ends at the Lochkovian-Pragian boundary. It is thus equivalent to the *Monograptus hercynicus* Zone. As described in detail by Chlupáč (1998), recognition of the lower boundary of the latter zone is sometimes difficult. However, the first appearance of some new faunal elements coinciding with the FAD of *Monograptus* *hercynicus* (*e.g*., the brachiopod *Howellela inchoans*, the bivalve *Hercynella*, first dacryoconarids, *etc*.) and the disappearance of some "early Lochkovian taxa" (the trilobite *Tropidocare index*, scyphocrinids, and graptolite *Monograptus uniformis*) may be used as an indirect indicator of that stratigraphic level (Chlupáč 1977).

Cephalopod biodiversity data

Late Silurian to Early Devonian cephalopod faunas of the Prague Basin were first studied comprehensively by Barrande (1865–1877), who described numerous cephalopod species of the genera *Orthoceras*, *Cyrtoceras*, *Phragmoceras*, *Gomphoceras*, *Ophioceras*, *Trochoceras*, *Ascoceras*, and *Nautilus*. J. Barrande placed the cephalopod faunas of the latest Silurian and lowermost Devonian in his "étage Ee2", but younger Lochkovian faunas to "étage Ff1". Barrande (1877) was a pioneer in cephalopod research in the Barrandian and already described the distinct decrease in cephalopod diversity in his "étage Ff1". Novák (1886), who made a new detailed revision of cephalopod fauna of the latter "étage", confirmed Barrande's observations and described only one new cephalopod species in addition to those previously described by J. Barrande. Hyatt (1883–84, 1894, 1900), and Foerste (1926) were the first authors who undertook a taxonomic revision of Barrande's cephalopod species (a detailed historical review of taxonomic studies on Bohemian cephalopod faunas was published by Gnoli 1997). However, the majority of these revisions were not based on studies of the actual fossils, but only on a re-evaluation of Barrande's descriptions and figures (see Manda & Turek 2009a). Only a limited number of the published studies were based on direct examinations of Barrande's original materials plus newly collected cephalopod specimens from Bohemia (Horný 1956, 1965; Marek 1971; Turek 1975, 1976, 2008, 2010; Kolebaba 1977; Stridsberg & Turek 1997; Manda & Turek 2009c). A general overview of cephalopods from the Přídolí and Lochkovian was published by Turek and Marek in Kříž *et al.* (1986) and by Manda (2001). During the intense mapping after the Second World War, a large amount of new fossil material including cephalopods from many new sections and facies was collected from the latest Silurian and Early Devonian strata of the Prague Basin (Horný 1955, Chlupáč 1953, Chlupáč *et al.* 1972, Kříž *et al.* 1986). Even though J. Barrande had previously evaluated fossil material from only a limited number of localities from this stratigraphic interval, his studies included almost all known species. Only a few new cephalopod species were found later in this newly collected fossil material. The surprisingly high diversity of Přídolí cephalopod faunas of the Prague Basin led Dzik (1982, 1984) to the conclusion that Barrande had not recognized the intraspecific variability of cephalopod species and that the real number of cephalopod species was much lower. However, Turek & Marek (1986) analysed examples mentioned by Dzik (1984) and noted that Barrande's species were correctly established. Barrande and other palaeontologists of the nineteenth century used widely defined morphological genera for newly established cephalopod species, however he united them into smaller groups within each genus, which were characterised by sharing distinct shell features. Barrande's groups were often equal to later introduced genera or families. The vast majority of new revisions of Bohemian cephalopods preserved Barrande's species and the number of species that were synonymised is relatively low (*e.g.* Marek 1971, Stridsberg 1985, Turek 2008, Manda 2008, Manda & Turek 2009b, c).

For an evaluation of changes in cephalopod biodiversity, the data on the stratigraphic distribution of all described late Ludlow to late Lochkovian cephalopod species of the Prague Basin from various published and unpublished sources have been summarised. Many of the described cephalopod species are relatively rare and often, only specimens from old collections are available, thus lacking precise stratigraphic information. In addition, the vast majority of cephalopod species have not been revised since Barrande's classical monographs and some species were not found again later (*e.g.* Gnoli 1997). Our aim was to include all known cephalopod species in this analysis. The uncertainty in stratigraphic position of some cephalopod species allowed us to split the late Ludlow-late Lochkovian period into eight time slices (A–H). At present, this is the most detailed stratigraphic subdivision of the studied period if all cephalopod species of the Prague Basin are included in the analysis. Based on the obtained dataset, we performed simple diversity analyses including counts of boundary-crossing genera of all cephalopod groups. Cephalopods are a rapidly evolving group and for this reason, we also counted the diversity of cephalopod species known from only one stratigraphical time slice (singletons). In addition to simple diversity measures (*i.e*., total diversity, mean standing diversity), we tabulated the number of cephalopod species originating (FAD) or ending (LAD) within each of the eight time slices (A–H). The unequal length of the stratigraphic time slices used biases the resulting pattern of the total biodiversity (i.e., number of species present in each stratigraphic time slice). At present there are, however, no exact datations available on the duration of these time slices and in addition, data on the duration of the Přídolí as well as the Lochkovian is very inaccurate (Gradstein *et al*. 2004, Kaufmann 2006). Thus, there is no possibility to divide the number of cephalopod species present in each time slice by its duration and thereby calculate absolute diversity parameters. Furthermore, the lack of absolute dating of boundaries of the selected time slices A–H cannot be substituted for by estimation of the relative

Table 1. Diversity of Přídolí and Lochkovian cephalopods.

Time slice	A	B	C	D	E	F	G	H
Number of species	62	53	31	97	110	21	28	24
Crossing lower boundary	–	40	25	31	96	19	7	11
Crossing only lower boundary	–	22	0	1	78	13	4	–
Crossing only upper boundary	–	7	6	66	1	1	8	–
Crossing both boundaries	–	18	25	30	18	6	3	–
Singletons	–	6	0	0	13	1	13	–
Mean standing diversity	–	32.5	28.0	63.5	57.5	13.0	9.0	–
Mean standing diversity + singletons / 3	–	34.5	28.0	63.5	61.8	13.3	13.3	–
Origination rate	–	0.25	0.19	0.68	0.13	0.10	0.75	0.54
Extinction rate	0.35	0.53	0.00	0.01	0.83	0.67	0.61	–

duration of the time slices inferred from the sedimentary record (*i.e.* from a comparison of relative thickness of individual stratigraphic time slices or from numbers of regular sedimentary cycles) because such data are also lacking. Moreover, the studied sections are characterized by shallow water carbonate sedimentation with different carbonate facies. Presence of hiatuses in such a shallow water environment (carbonate platform) is rather typical. Therefore, the comparison of relative thickness of individual time slices with different carbonate facies also cannot be used for the estimation of their duration. To eliminate the bias produced by the different duration of the time slices, we calculated variables such as mean standing diversity and relative origination and extinction rates. The latter measures are defined as the number of originating (or ending) species divided by total number of cephalopod species being present within the particular time slice.

Cephalopods were selected as a model group to test biodiversity changes across the Silurian-Devonian boundary time slice for several reasons. Firstly, the cephalopod fauna of the Prague Basin was highly diversified and 197 cephalopod species were described from the latest Ludlow–late Lochkovian period (Table 1). Analysis of all cephalopod occurrences (ŠM, unpublished dataset) showed that Bohemian species represent more than 70 percent of all known cephalopod species from this stratigraphic time slice (Table 2). We have more knowledge on the stratigraphic ranges of individual cephalopod species from the Prague Basin than from other areas of the world. Secondly, all known cephalopod faunas from Gondwana, peri-Gondwanan terrains, Avalonia, and particularly Baltica were highly diversified but almost identical in whole regions. All these facts indicate that the analysis of biodiversity of the Prague Basin cephalopod faunas has global rather than only regional significance.

In addition, the latest Ludlow–late Lochkovian cephalopod fauna of the Prague Basin includes members of seven orders (Actinoceratida, Ascocerida, Discosorida, Oncocerida, Orthocerida, Pseudorthocerida, and Tarphycerida) with different shell morphologies and different juvenile and adult life strategies (Fig. 5, see also the next chapter). These data make it possible to analyse the impact of the changing carbon cycle on cephalopod species with different life strategies (Fig. 5).

The data on stratigraphic ranges of individual cephalopod species as well as on their shell morphologies and ontogenetic strategies were evaluated by standard numerical methods. Jaccard and Dice (Sorensen) association similarity indices were selected for evaluating the presence/absence data and measuring the relative distance between each of the eight time slices. Cluster analysis was utilised for identifying hierarchical groupings within the cephalopod faunas. The unweighed pair-group average (UPGMA) and single linkage (nearest neighbour) algorithms were selected for this analysis from a large number of possible algorithms. In the UPGMA algorithm, the clusters are joined based on the average distance (similarity) between all members in the two groups (faunas). By contrast, clusters in the single linkage algorithm are joined based on the smallest distance between the two groups.

Cephalopod mode of life

Three different characteristics of cephalopod species (size of embryonic shell, juvenile mode of life, and adult mode of life) were included in our analysis (Fig. 5). All published data as well as hitherto unpublished data on late Ludlow to Lochkovian cephalopod species were carefully evaluated and tabulated with respect to the above-mentioned characteristics. A description and brief definition of the selected features are summarised in the following paragraphs.

Cephalopod embryonic strategies

Cephalopods, in contrast to some other molluscan classes, have a simple ontogeny lacking a true larval stage. Hatching cephalopods are morphologically similar to adults. Generally two basic embryonic strategies may be found in cephalopods. Engeser (1996) suggested using the size of the embryonic shell and presence or absence of a cicatrix as a tool for determination of yolk quantity in the eggs. A small spherical embryonic shell indicates a small embryo with a small yolk sac. Relatively large embryonic shells with a cicatrix indicate a rich yolk supply in the eggs such as in the living *Nautilus* (see also Kröger 2006). The juvenile cephalopods with a small apex without a cicatrix may be considered as planktotrophic because early hatching animals did not have enough food and probably lived in the water column as macro-planktonic predators. Cephalopods having a large apex with a cicatrix (*i.e.* large, yolk rich eggs) had a much longer incubation time and hatching animals were benthic. Engeser (1996) proposed distinguishing these two types of early cephalopod ontogeny by morphological characters of their early shell. However, the distribution of early post-hatching shells in different sedimentary facies may also indicate the type of early cephalopod strategy. Small embryonic shells of cephalopods considered to be planktotrophic also commonly occur in deeper water sediments (shales) together with juvenile bivalve and gastropod shells (Kolebaba 1973, 1977; Kříž 1998b, unpublished data). Their occurrence in deeper water sediments provides evidence for their living early post-hatching in the water column as macro-plankton. In contrast the early post-hatching cephalopod shells considered to have adopted a lecitrophic strategy (*i.e.*, shells with a large embryonic chamber) occur only in shallow water facies and in comparison to the adults have a reduced geographic distribution. Thus hatching places occur only in part of areas inhabited by adults and these embryonic shells do not occur in shales or in dysoxic facies (Manda 2008). Facies distribution of these two basic types of embryonic shell testifies well to the interpretation of early shell morphology proposed by Engeser (1996).

Pseudorthoceratids have a cup-like and slightly curved shell apex with cicatrix, but a straight shell with cameral-intrasiphonal deposits. Their adult distribution pattern resembles nautiloids, but juvenile post-hatching shells also occur in deeper water sediments suggesting life in the water column.

Cephalopod adult strategies

Examination of the early and adult shell morphology as well as of the distribution of cephalopod shells in different facies allowed the recognition of changes in the mode of life in late Ludlow to Lochkovian cephalopods. Cephalopod species having the same mode of life during early post-hatching stages may have quite different life strategies as adult animals and *vice versa*. Evaluation of all available data on the late Ludlow–Lochkovian cephalopods revealed seven basic types of life strategy, which can be used for biodiversity analysis and are described briefly below (Fig. 5).

Pelagic cephalopods

This group comprises cephalopods, which are pelagic during their entire life. It encompasses orthocerids with a small spherical apex, which is sometimes constricted as in bactritoids. The diameter of the embryonic shell usually varies between 0.3–1 mm (Ristedt 1968, Kolebaba 1973, Serpagli & Gnoli 1977). The shell of pelagic orthocerids is straight with a shallow apical angle and a thin, central or slightly subcentral siphuncle. Cameral deposits are absent or restricted only to the apical part of the phragmocone (*e.g.*, Sweet 1964, Dzik 1984). This type of shell morphology was interpreted as reflecting a vertical orientation in life and that the shell passively drifted with the water current (for a summary see Dzik 1984, Westermann 1998, Mutvei 2002). Maximal shell diameter does not usually exceed 20 mm. At least two convergent groups of pelagic orthocerids occured in the Silurian times: the Michelinoceratidae (*Kopaninoceras*, *Michelinoceras*) with a spherical apex and the Arionoceratidae (*Arionoceras*) with a contracted apex (for details see Kolebaba 1975, Dzik 1984).

A special shell adaptation was found in the genus *Parakionoceras* (?Arionoceratidae; see Dzik 1984) which has empty, longitudinal cavites between the inner and outer shell wall (Barrande 1865–1877, Kolebaba 1977) probably improving buoyancy control. Pelagic orthocerids are a dominant part of the cephalopod faunas in cephalopod limestone biofacies (Figs 3, 4; Ferretti & Kříž 1995, Kříž 1998b) and shales (Turek 1983), but they are known from all facies. Pelagic orthocerids usually represent cosmopolitan taxa (see Gnoli 2003). The rate of morphological change in individual evolutionary lineages of the pelagic orthocerids is very low. These species usually had long stratigraphic ranges. For example, the species *Parakionoceras originale* is known from the Wenlock up to the Lochkovian and the genera *Kopaninoceras, Michelinoceras, Arionoceras* and *Parakionoceras* range from the late Llandovery to the Emsian or even to younger strata (Barrande 1865–1877, Zhuravleva 1978). The diversity of pelagic cephalopods is usually low.

Nektonic forms with a pelagic early stage

This group unites orthocerids belonging to two closely related families, the Plagiostomoceratidae and the Sphooceratidae, with uncertain systematic positions within the order Orthocerida (Dzik 1984, Marek 1998, Zhuravleva & Doguzhayeva 2004). Plagiostomoceratids have a small spherical embryonic chamber with a diameter less than

1 mm, typically about 0.5 mm. Their juvenile shell is constricted in the area of the first few phragmocone chambers (Ristedt 1968). The morphology of embryonic and early shell (no hyponomic sinus and the usually smooth shell) suggests that the early mode of life was pelagic as in other orthocerids. Cephalopods placed in this group have a straight adult shell and well developed cameral deposits. According to Flower (1957), the cameral deposits functioned as a counterweight, helping to orient their shell horizontally during life. In some species, the siphuncle was even open in the distal part of the phragmocone, connecting phragmocone chambers with the siphuncle (see Kolebaba 1999, 2002). The shell aperture is typically oblique, expanding on the ventral side, and the hyponomic sinus is well developed. Septa are commonly modified (truncation; see Barrande 1865–1877) and in some species (*Sphooceras*) the apical part of the phragmocone was periodically discarded (Turek, unpublished data). In cross section, the shell is subcircular and usually laterally compressed. Maximal shell diameter was about 20 mm. The above-described shell morphlogy was interpreted as an adaptation for active swimming, resembling that of some coleoids (see Flower 1957).

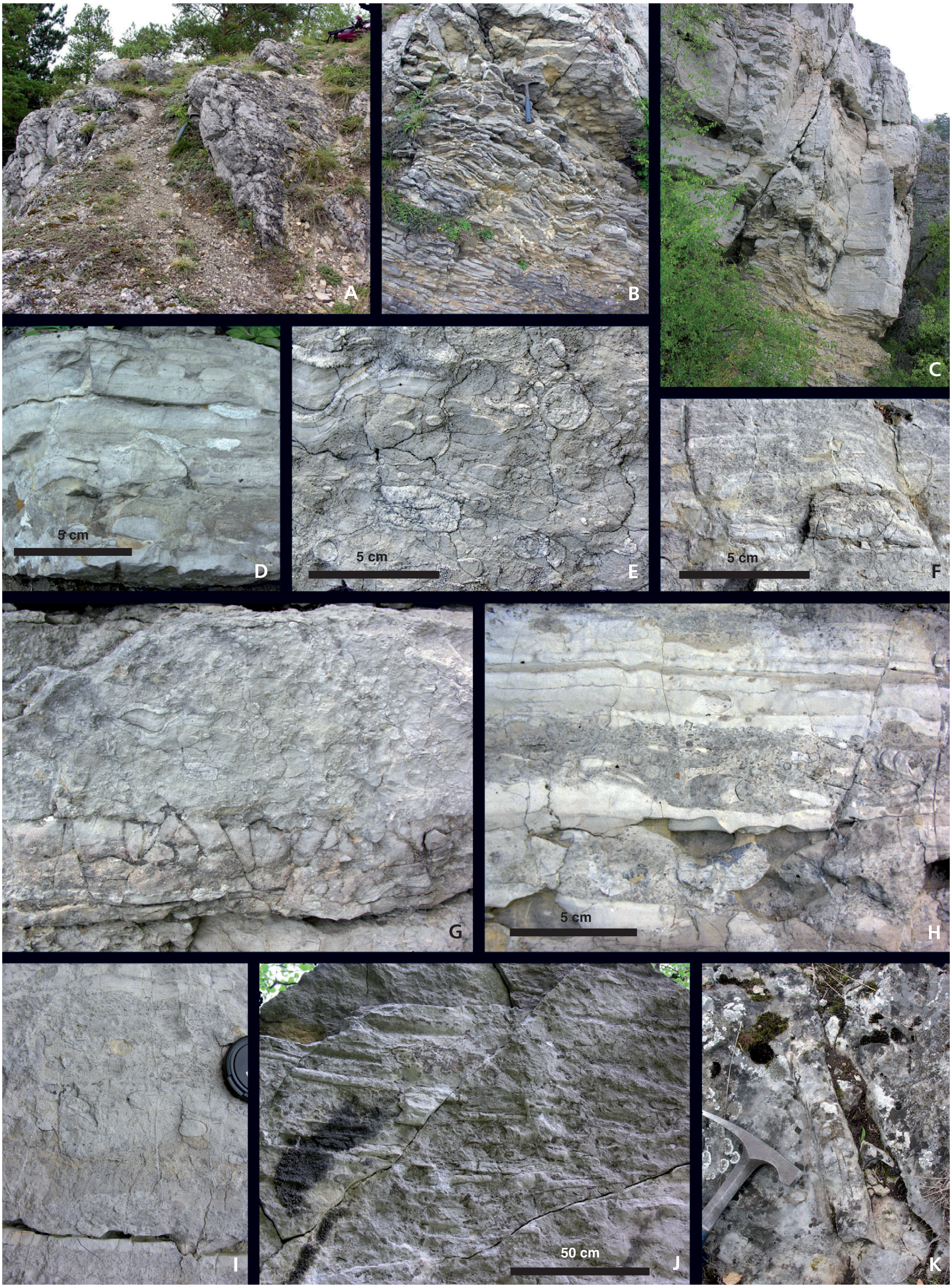
The genus *Murchisoniceras* (Ludlow–Přídolí; Babin 1966) is closely related to the plagiostomoceratids and may represent an exception to the typical live mode of Plagiostomoceratidae. Species of this genus have a large shell with extensive cameral deposits (Barrande 1865–1877), suggesting a demersal rather than a nektonic mode of life in the adult stage. The Plagiostomoceratidae as well as the Sphooceratidae appeared in the early Silurian and their relationship to the Ordovician orthocerids is uncertain (see Dzik 1984). Diversity among nektonic orthocerids is always low with usually one common and a few rare species per assemblage. Plagiostomoceratids are generally long ranging species with a large geographic distribution (*e.g.* *Plagiostomoceras placidum* in Lochkovian strata). The rate of change in shell morphology in individual lineages is relatively slow, but much higher than in pelagic orthocerids. Nektonic orthocerids occur in slope facies, but are most abundant close to the margin of carbonate platforms. Faunal assemblages dominated by plagiostomoceratids are relatively common.

Nektobenthic adults with a pelagic early stage

Some orthoceratids and members of the family Lechritrochoceratidae (Tarphycerida, Barrandeocerina) are united in this group. These orthocerids have a spherical early shell without constriction, the diameter varies between 1–2 mm and they are straight or slightly curved (*Cyrtocycloceras, Dawsonocerina*: Barrande 1865–1877, Dzik 1984; *Dawsonoceras*: Kröger & Isakar 2006). During later ontogeny, various shell modifications may be developed (at shell size about 1–2 cm) including annulations, various types of sculpture, and a hyponomic sinus. The shell may be slightly curved and the angle of its expansion usually increases. These modifications are probably caused by the change from a pelagic to a nektobenthic mode of life. Such shell adaptations connected with a nektobenthic mode of life were developed independently in members of the families Arionoceratidae and especialy Michelinoceratidae. Adult nektobenthic orthocerids occur typically in assemblages with a low diversity of demersal nautiloids (*e.g.* in early Lochkovian). For example the species *Kopaninoceras fluminese* (for description see Serpagli & Gnoli 1977) has an early shell similar to other pelagic orthocerids, but during later ontogeny distinct straight annulation is developed on the shell (Fig. 4F). These annulae become oblique during subsequent shell growth. In addition the straight shell aperture becomes oblique and a distinct hyponomic sinus appears. Closely related families to the Orthoceridae, the Paraphragmitidae and the Dawsonoceratidae both probably had a nektobenthic mode of life as adults. A well-known example is the Silurian *Cyrtocycloceras* (see Marek 1971).

In addition to some orthocerids described above, members of the tarphyceratid family Lechritrochoceratidae belong to this group. These cephalopods have a secondarily reduced embryonic shell lacking a cicatrix. Their early shells are straight or slightly curved, but the more adult shells become curved or coiled, bearing characteristic annulations on their surface (Turek 1975, 2010). Such shell morphology resembles that of some orthocerids (Paraphragmitidae). This morphological convergence previously caused some taxomonical problems. For example, the lechritrochoceratoid *Calocyrtoceras* (Ludlow–Přídolí)

Figure 3. Nová Ves, Bílá skála Section. • A – upper part of the Požáry Formation, Přídolí, late *M. transgrediens* Zone, boundary between cephalopod and brachiopod (*Dayia bohemica*) limestones. • B – uppermost part of the Požáry Formation, Přídolí, latest *M. transgrediens* Zone, thin-bedded mudstones intercalated with shale and overlaying skeletal limestone with *Tetinia minuta* just bellow base of the Devonian. • C – Silurian-Devonian boundary interval and early Lochkovian limestones, the Silurian-Devonian boundary occurs just above base of limestone sequence. • D – bed No. 6, middle part of Požáry Formation, mudstone with thin beds of skeletal limestones above hardgrounds and erosive surfaces. • E, G – bed No. 28, Požáry Formation, Přídolí, late *M. transgrediens* Zone, cephalopod limestone overlaying erosive surface in mudstone. • F, I – bed No. 23, Požáry Formation, Přídolí, late *M. transgrediens* Zone, coarse crinoidal limestone interbedded with thin mudstone beds. • H – bed No. 17, Požáry Formation, Přídolí, *M. transgrediens* Zone, cephalopod accumulation with small intraclasts (cross bedded packstone) filling bottom depression above erosive surface. • J – bed No. 46, lowermost part of Lochkov Formation, earlier *M. uniformis* Zone, lower bedding plane of skeletal limestone with numerous well oriented shells of *Pseudocycloceras* sp. • K – bed No. 54, middle part of Lochkov Formation, late *M. uniformis* Zone, upper bedding plane of mudstone with *Pseudocycloceras* sp.


A
B
C
5 cm
D
5 cm
E
5 cm
F
G
5 cm
H
I
50 cm
J
K

was for a long time considered to be an orthocerid (Sweet 1964, Marek 1971, see discussion in Manda 2001).

The rate of change in shell morphology throughout ontogeny is relatively high and the majority of these nektobenthic species have relatively short stratigraphic range. Most genera of nektobenthic orthocerids are cosmopolitan (in the temperate to tropical zones), but individual species are usually endemic.

Nektobenthic early stage with nektic-nektobenthic adults (Pseudorthocerida)

A unique combination of shell characters such as a cup-shaped apex with a cicatrix (as in the Nautiloidea) and a longiconic shell with cameral and intrasiphonal deposits (Barskov 1963) characterise members of this group, the pseudorthoceratids. The representatives of this group are large Silurian cephalopods with the maximal shell diameter so far recorded being 18 cm, and with the shell length reaching 150 cm. Members of the pseudorthoceratid family Geisonoceratidae had a large straight or slightly curved longiconic shell with a straight and oblique aperture. The cameral-intrasiphonal deposits are well developed. Shell diameter is typically about 5 cm, but shells with 15 cm diameter are known from some species. Gnoli (1987) interpreted the geisonoceratids as living close to the bottom (Gnoli 1987). They occur especially in limestone facies and less commonly in shales. The geisonoceratids are known since the Ordovician but are rather rare cephalopods in Přídolí and Early Devonian strata.

A very unusual shell ontogeny was documented in the common pseudorthocerid genus *Pseudocycloceras*, which developed three disctinct ontogenetic stages. The first stage is characterised by a straight shell having regular oblique growth lines, low phragmocone chambers, a relatively thin siphuncle, and a shallow hyponomic sinus. The maximal diameter of this growth stage varies between 3 to 5 mm. The second stage of shell ontogeny is characterised by a slightly endogastrically curved shell with well-developed annulations, longer phragmocone chambers, and cameral deposits. Maximal shell diameter in this stage varies from 8 to 15 mm. A straight shell, irregular or missing growth lines and very long phragmocone chambers characterize the third stage again. Maximal shell diameter in this stage is about 180 mm. According to Flower (1957) and Gnoli (1987), all of the above-mentioned stages were probably nektobenthic with the shell orientated horizontally (cameral deposits); the distinct hyponomic sinus indicates active swimming and jet propulsion. Shells of the first and early-late second stages occur in shallow water facies. Third stage shells occur in shallow (limestone) as well as deeper water sediments (mudstone and shale). Adult animals thus migrated apparently from shallow water areas to the deeper water areas.

Lyecoceras and allied genera represent another form of pseudorthocerids included in this group. Their shell is longiconic, slightly curved and endogastric, the body chamber is short, and the aperture is frequently modified (weak constriction, protruding hyponomic sinus). The shell surface is smooth or, more frequently, with highly elaborated sculpture (radial-transversal ribs). Cameral deposits are reduced and the phragmocone chambers bear characteristic oblique sutures with lateral lobes. Unlike other pseudorthoceratids, their shells were orientated vertically during their adult life (reduced cameral deposits, inclination in suture). A well-developed hyponomic sinus and relatively short body chamber suggest active swimming and good buoyancy control (Mutvei 1957). Their occurrences in shallow water facies suggests that this genus preferred shallow water environments.

Nektobenthic early stage and nektobenthic-benthic adult (Actinoceratoidea)

Actinoceratids comprise cephalopods with a relatively long, usually large, straight shell. The large embryonic shell bears a large caecum (initiation of siphuncle). The siphonal tube is thick with intrasiphonal deposits forming complicated system of tubes. Cameral deposits may also be present in some species. Teichert (1933, 1964) suggested that actinoceratids were probably poor swimmers living very close to the bottom, similarly to endoceratids. In some Silurian and Devonian taxa, the siphonal deposits and thickness of the siphuncle may be reduced during shell growth (*e.g.*, Niko 1998). Actinoceratids especially inhabited warm-water carbonate platforms. Actinocerid cephalopods have been interpreted as indicators of tropical and temperate water masses (Flower 1957), but some actinocerids are also known from higher latitudes (Serpagli & Gnoli 1977, Kröger 2008). The actinoceratids are rare in the Wenlock and Ludlow strata of Bohemia, but in the Přídolí, their diversity distinctly increased, but only one species is known from the Lochkovian. The abundance of actinoceratoids in Bohemia is very low, they were found in relatively deep water limestone and shale intercalated with mudstone.

Benthic early stage with nektobenthic adult (Nautiloidea)

The demersal nautiloids (Oncocerida and Discosorida) consist of cephalopods with longiconic cyrtoconic shells and typically with breviconic shells (straight or slightly curved). Variability in shell form is high. Demersal nautiloids have a large shell apex with a cicatrix and the aperture is usually modified (constriction) during life, aperture was oriented downward or foreward. A typical feature of this group is the very high rate of morphological change in the shell throughout ontogeny. The vast majority of its species have very short stratigraphic ranges. Adaptive radiations of demersal nautiloids are documented after some Silurian extinction events (unpublished data). Species of this group are usually restricted to a small geographic area (one basin), but there are many shared taxa between Bohemia and Gotland (Stridsberg 1985, Manda 2008).

Members of the family Oonoceratidae are characterised by having a slender, curved exogastric shell, a thin and marginal siphuncle, and a short body chamber (Manda & Turek 2009b). In life position, their aperture was slightly oblique to the bottom, they were probably slow swimming cephalopods, living close to the bottom (*i.e.* demersal; compare Westermann 1998).

Members of the family Oocerinidae are morphologicaly convergent with the Oonoceratidae, but their siphuncle is thicker with lamellar, intrasiphonal deposits (Zhuravleva 1974, Manda 2001). Furthermore, the Mandaloceratidae have a straight or slightly curved breviconic shell and their aperture is constricted just before the end of shell growth (Flower & Teichert 1957). The balloon-shaped shells of the mandaloceratids with contracted apertures suggest that they lived close to the bottom with a downward orientated aperture (Holland 1984).

The family Hemiphragmoceratidae includes, as in the Mandaloceratidae, nautiloids with a breviconic shell and constricted aperture, but their shell is curved and endogastric. The aperture is very complex, having 2–8 lobes. Their siphuncle is relatively thick with lamellar deposits. These morphological features suggest that hemiphragmoceratids were better swimmers than mandaloceratids, but lived close to the bottom as previously suggested by Stridsberg (1985).

The Rizosceratidae form a group of oncocerids with a short, straight or slightly curved breviconic shell with an unconstricted (endogastric as well as exogastric). Their body chamber is short and their siphuncle very thin and marginal. Intrasiphonal deposits are unknown in rizosceratids. The shell apex is straight and spherical with a cicatrix (its diameter varies in individual species between 2 to 6 mm). Shell length at hatching stage does not exceed 8 to 10 mm (unpublished data). Rizosceratids lived close to the bottom with the aperture orientated downward (species with straight shells) or obliquely to the bottom (species with curved shells).

Benthic early stage with nektonic adult (Nautioidea)

Tarphyceratids and oncocerids with coiled shells were placed in this group. The apex of their shells is relatively large, cup-like and bearing a cicatrix. The embryonic shell diameter is greater than 3 mm (Turek 2010). Early post-hatching specimens lived close to the bottom, however, a distinct hyponomic sinus was developed at the completion of one or two whorls. This morphologic feature suggests a transition from a benthic to a more active nektonic mode of life. In adult animals, the aperture was orientated anteriorly. The best-known example represents the genus *Boionautilus,* having a shell strongly resembling the present-day *Nautilus* (Turek 2008). Coiled shells also appeared in some lineages of oncocerids. The Oxygonioceratidae have a narrowly coiled and laterally compressed shell with a ventral keel and a ventral marginal siphuncle (Chen *et al.* 1981). In contrast, the Naedyceratidae include oncocerids with a widely (depressed) coiled shell. Their siphuncle is also ventrally situated, but its diameter is greater. Lamellar intrasiphonal deposits were also documented in this group (Manda 2001). Coiled exogastric shells with few whorls (1–4) and a thin marginal siphuncle were also described in some Oonoceratidae (*e.g. Eurizoscerina*; Manda & Turek 2009c).

Results

Carbon isotope record

The Zadní Kopanina Section

Carbon isotope sampling began in the Požáry Formation about 12 m below the Silurian-Devonian boundary and about 1.3 m below the FAD of *Monograptus bouceki*. The last sample was collected about 6 m above the Silurian-Devonian boundary. In total, 39 samples were analysed for δ^{13}C content, 23 samples were taken from the Silurian part of the section and 16 samples from the Early Devonian Lochkov Formation. The δ^{13}C values increase from –0.3‰ in the oldest sample (Time slice C – 1.3 m below the FAD of *Monograptus bouceki*) to values of about +2 ‰ in the middle of Time slice E (FAD *Dayia bohemica* to LAD *Monograptus transgrediens*). δ^{13}C values began to increase rapidly from the middle of Time slice E to its end, at which point the maximum δ^{13}C value (+3.42 ‰) for the Silurian part of the Zadní Kopanina Section was recorded. The following interval, slice F (LAD *Monograptus transgrediens* to FAD *Monograptus uniformis*) is relatively thin. Two samples analysed from this time slice show a reduction in δ^{13}C values, down to about +2.2‰. This trend changed in the first Devonian samples (Time slice G, FAD *Monograptus uniformis* to FAD *M. hercynicus*), which revealed a continuous increase in δ^{13}C values, to +3.6‰ at about 95 cm above the Silurian-Devonian boundary. Further upward, in Time slice G, the δ^{13}C values gradually decreased to about +1.1‰ at the end of the time slice. The last four samples from Time slice H (above FAD *M. hercynicus*) again showed some increase, rising to +2.7‰ and then a decrease to +1.1‰.

The Opařilka Section

The first carbon isotope sample was taken from the upper beds of Time slice C in the Požáry Formation, about 19.8 m below the Silurian-Devonian boundary and about 1.6 m below the FAD of *Monograptus bouceki*. The last sample was collected about 5.2 m above the Silurian-Devonian boundary, at a level where the Opařilka Section ends. From the Silurian part of the section, 40 samples were analysed for δ^{13}C content and 11 samples were analysed from the Early Devonian Lochkov Formation. Similarly to the Zadní Kopanina Section, δ^{13}C values gradually increased from –0.24‰ in the oldest sample (Time slice C – 1.6 m below the FAD of *Monograptus bouceki*) to values of about +2.3‰ at the end of Time slice D (FAD of *Monograptus bouceki* to FAD *Dayia bohemica*). δ^{13}C values in Time slice E (FAD *Dayia bohemica* to LAD *Monograptus transgrediens*) were scattered, reaching the highest δ^{13}C value (+3.2‰) close to the end of Time slice E. The following Time slice F (LAD *Monograptus transgrediens* to FAD *Monograptus uniformis*) is characterised by high fluctuations in δ^{13}C values. Eight samples measured from Time slice F range from +2.1‰ to +4.3‰. Except for one sample, the remaining ten δ^{13}C values from the Devonian (Time slice G, FAD *Monograptus uniformis* to FAD *M. hercynicus*) show less fluctuation (from +2.3‰ to +3.2‰) than samples from the last Silurian time slice.

The Bílá skála Section

From the Bílá skála Section, 39 samples were analysed for δ^{13}C content (27 samples from the Silurian part of the section and 12 samples from the Early Devonian Lochkov Formation). Sampling began in the Požáry Formation, 11 m below the Silurian-Devonian boundary and about 0.5 m below FAD of *Monograptus bouceki* and ended 7.75 m above the Silurian-Devonian boundary. Only one δ^{13}C value was measured in Time slice C (0.5 m below FAD of *Monograptus bouceki*). Generally, δ^{13}C values gradually increased from about +0.34‰ at the beginning of Time slice D to +2.5 ‰ at the end of Time slice E (from FAD of *Monograptus bouceki* to LAD *Monograptus transgrediens*) with two fluctuations (in the middle of Time slices D and E). Six samples measured from the narrow Time slice F (LAD *Monograptus transgrediens* to FAD *Monograptus uniformis*) range from +2.4 ‰ to +2.8 ‰. The first ten Devonian samples of Time slice G (to a level about 3.5 m above the Silurian-Devonian boundary) show greater fluctuations (from +2.3‰ to +3.4‰) than samples from the last Silurian time slice. The last two values from Time slice G indicate a decrease in δ^{13}C content and only two samples measured from Time slice H again suggest a rise in δ^{13}C, similarly as in the Zadní Kopanina Section.

The δ^{13}C composite record

The δ^{13}C data from the three studied sections of the carbonate platform of the Prague Basin were combined in one composite record to characterize general trends across the Silurian-Devovian boundary of the Prague region. Isotope data were grouped into the time slices used for biodiversity analysis of cephalopods. Such grouping resulted in a loss in stratigraphic resolution of the δ^{13}C signal, but one has to keep in mind that the course of isotopic changes in any study of the fossil record is reconstructed only from discrete values (isotope samples). Thus, no record is completely sampled (*i.e.*, not all carbonate layers were sampled). In addition, in the relatively shallow environment of the carbonate platform, one has to also expect an incomplete rock record (because of possible sedimentary gaps). Grouping of δ^{13}C data into one composite record thus characterises the general regional trend in δ^{13}C (Fig. 6) and allows for analysis of the relationship between the δ^{13}C record and cephalopod biodiversity changes on the same scale.

Comparison of median δ^{13}C values from two neighbouring time slices (Fig. 6) revealed a distinct and statistically significant increase in δ^{13}C values from Time slice C to Time slice F (the last Silurian time slice). On the other hand, there is no statistically significant difference between Time slices F and G, or between G and H. Therefore, our data from the Prague Basin clearly shows that the latest Silurian (Time slice F: LAD *Monograptus transgrediens* to FAD *Monograptus uniformis*) was a time when the increase in δ^{13}C values reached its maximum and subsequently, in the Early Devonian, is characterized by relatively constant δ^{13}C values. The latest Silurian is therefore a time of change in dynamics of the global carbon cycle in the marine ecosystem and the early Lochkovian is characterized by more steady conditions following these changes.

Cephalopod biodiversity

Total cephalopod species diversity and turnover rates

Analysis of the cephalopod diversity dataset revealed extremely high species diversity in the Time slices D and E (FAD *M. bouceki* to LAD *M. transgrediens*). The total number of cephalopod species reached 97 and 110 in these mid-Přídolí time slices, which is globally the highest recorded cephalopod diversity in the latest Silurian. These values are three times higher than the most diversified Přídolian cephalopod faunas outside the Prague Basin (Tables 2, 3). Except for this peak, the "background" diversity shows a decreasing trend from the late Ludlow to the end of the Lochkovian. The pattern in mean standing diversity (Figs 6, 7) is the same as that in total diversity and thus,

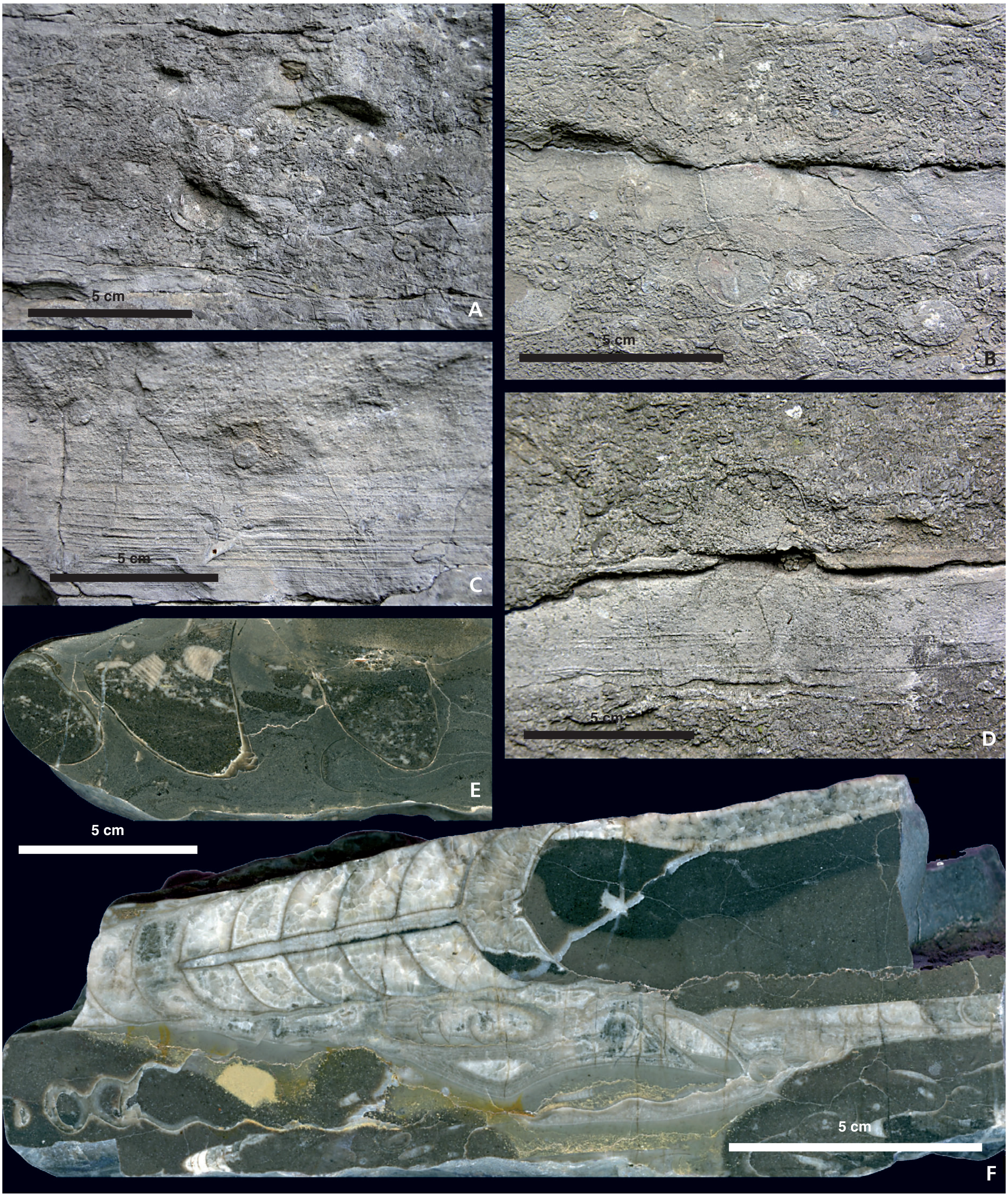


Figure 4. Zadní Kopanina Section, Požáry Formation, Přídolí, *Monograptus bouceki* Zone. • A, B, D – bed No. 13, base of thick cephalopod limestone sequence which consists of up to 15 cm thick beds of cephalopod cephalopod packstones separated with erosive surfaces and thin beds of mudstones with upper erosive surfaces. • C – bed No. 13, laminated mudstone with rare crinoid debris passes into cephalopod wackestone. • E – bed No. 10, polished slab of a thin mudstone bed with common large shells of gastropod *Orthonychia* cf. *anguis*, gastropod shells are filled with coarse crinoidal debris. • F – bed No. 13, polished slab of cephalopod limestone with annulated shells of *Kopaninoceras fluminese*.

Table 2. Data summarising the diversity of cephalopods in the Přídolí and Lochkovian. P – number of species from Přídolí, L – number of species from Lochkovian, SD – number of species from Silurian-Devonian boundary in area where the Přídolí and the Lochkovian are not distinguished. Column B – mean number of species shared with Bohemia. An asterisk designates fauna at which age is determined as Lochkovian–Pragian.

Area	P	B	L	B	SD	B	References
Liévin, N France	–	–	–	–	21	13	Gosselet *et al.* (1912), Barrois *et al.* (1912)
Wales	5	2	–	–	–	–	Holland (2000)
Ebbe Inner, Germany	–	–	–	–	7	5	Dahmer (1951)
Harz, Germany	16	15	–	–	–	–	Heritsch (1930)
Massiv Armorican, France	3	3	–	–	–	–	Babin (1966), Babin *et al.* (1979), Kříž & Paris (1982)
Sardinia	17	16	16	15	–	–	Gnoli (1982), Gnoli & Serpagli (1991)
Carnic Alps, Austria	16	15	–	–	–	–	Bogolepova (1998), Histon (2002)
Spain	3	3	–	–	–	–	Bogolepova *et al.* (1998)
Graz, Austria	7	7	–	–	–	–	Histon et al. (2010)
Morocco	6	4	14	5	–	–	Kröger (2008)
S of Gotland (Beyrichien Kalk)	7	4	–	–	–	–	Krause (1877), Dzik (1984), Dzik & Kiselev (1985)
Poland	2	2	–	–	–	–	Dzik (1984)
Estonia	16	5	–	–	–	–	Saldzius (1966), Kiselev *et al.* (1990)
Podolia	8	3	16*	1	–	–	Kiselev *et al.* (1987), Zhuravleva (1972, 1974, 1978)
Caucaus Mts	–	–	–	–	7	7	Janisechevskij (1917)
North Urals	25	23	15	10	–	–	Kiselev (1984)
Tian-Shan	35	15	31	19	–	–	Kiselev *et al.* (1993)
Japan	–	–	9	0	–	–	Niko (1996, 1998, 2003)

Table 3. Similarity in cephalopod faunas between Time slices A–H (latest Ludlow–late Lochkovian).

DICE/Jaccard	Time slice A	Time slice B	Time slice C	Time slice D	Time slice E	Time slice F	Time slice G	Time slice H
Time slice A	–	0.53	0.24	0.13	0.11	0.09	0.05	0.02
Time slice B	0.70	–	0.42	0.20	0.17	0.10	0.05	0.03
Time slice C	0.39	0.60	–	0.32	0.27	0.27	0.07	0.04
Time slice D	0.23	0.33	0.48	–	0.86	0.18	0.05	0.02
Time slice E	0.20	0.29	0.43	0.93	–	0.17	0.05	0.02
Time slice F	0.17	0.19	0.42	0.31	0.29	–	0.17	0.07
Time slice G	0.09	0.10	0.14	0.10	0.09	0.29	–	0.27
Time slice H	0.05	0.05	0.07	0.03	0.03	0.13	0.42	–

the rapid increase in cephalopod diversity pattern in the Time slices D and E appears to be a real feature and not an artefact caused by the different durations of time slices used for the diversity analysis or by the high number of singletons.

The relative origination rate value varies considerably across the analysed period (Fig. 6). During the Přídolí, the relative origination rate is below 0.25, with the exception of Time slice D. Almost 70% of the recorded cephalopod species originated during this time slice (Figs 6, 7). The early Lochkovian had the highest relative origination rate value, which reached 0.75 %. Similarly, the relative origination rate is also high during the late Lochkovian. Taken together, the analysed data revealed two periods of rapid origination of new cephalopod species, the first during the period between the FAD of *M. bouceki* and that of *Dayia bohemica* and the second during the Lochkovian.

Relative extinction rate values also vary considerably during the analysed period (Figs 6, 7). They are relatively high at the beginning of the Přídolí from Time slice E to the end of the Lochkovian; in Time slice B, the extinction rate amounted to 0.53, *i.e.*, about half of the recorded cephalopod species. The highest value for relative extinction rate occurs in Time slice E, which is the time slice with the highest cephalopod species diversity with 110 recorded species. Before the end of Time slice E (*i.e.*, before LAD *Monograptus transgrediens*), more than 80 percent of all recorded cephalopod species became extinct. A comparison of origination and extinction rates within each analysed time slice revealed some additional information. For that

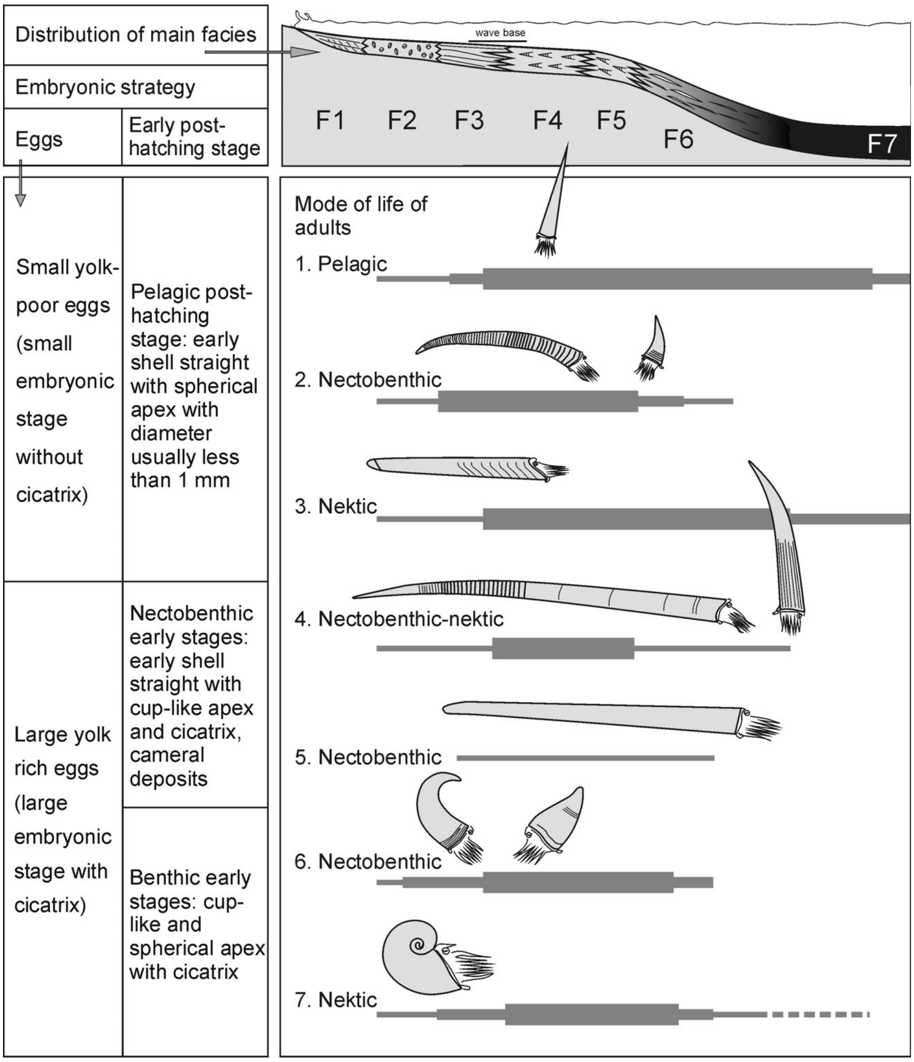


Figure 5. Diagram showing main cephalopod strategies and distribution of adults in relation to facies. Abbreviations of facies: F1 – cross-bedded fine-grained grainstone, F2 – brachiopod packstone and grainstone, F3 – thin bedded crinoidal pack-grainstone, F4 – cephalopod grain-packstone, F5 – cephalopod wacke-mudstone, F6 – wacke-mudstone intercalated with shale, F7 – laminated shale.

comparison, the ratio of extinct to originating species was calculated (Fig. 6). If the latter rises above 1, extinction dominates over origination of new cephalopod species and *vice versa*. This ratio clearly shows that time slices E and F are characterised by very high turnover rates. During these time slices, the number of extinct cephalopod species is about six to seven times higher than that of species originating. By contrast, the previous time slices C and D are characterised by the absence of significant extinction rates (Fig. 6).

Changes in order-level composition of cephalopod faunas

Comparison of diversity of individual cephalopod orders across the analysed period revealed their unequal contributions to the species diversity (Fig. 8). The diversity of Orthoceratida and Pseudorthoceratida is relatively uniform from the late Ludlow to the end of the Lochkovian. Nevertheless, the number of species belonging to the latter order slightly increased during the Time slices D and E (Fig. 8). The number of Tarphycerida and Ascocerida species shows distinctly decreasing trends. However, the latter order has a generally low diversity. By contrast, the diversity of species belonging to the orders Discosorida, Oncocerida, and Actinocerida considerably increased during the Time slices D and E (Fig. 8).

Analysis of the changes in relative abundance in cephalopod orders in individual time slices revealed another pattern. Members of the Discosorida and Oncocerida form a dominant part of cephalopod faunas from the late Ludlow. From the FAD of *Monograptus lochkoviensis* to LAD of *Monograptus transgrediens* (Time slices C–E), about 60% of all cephalopod species belong to one of these two orders. This diversity pattern changes dramatically from the beginning of time slice F (*i.e.* since LAD *Monograptus transgrediens*), when the relative abundance of discosorid and oncoceratid cephalopod species dramatically decreased to 0 and 14%, respectively. In the subsequent time slices G and H (Lochkovian), members of the

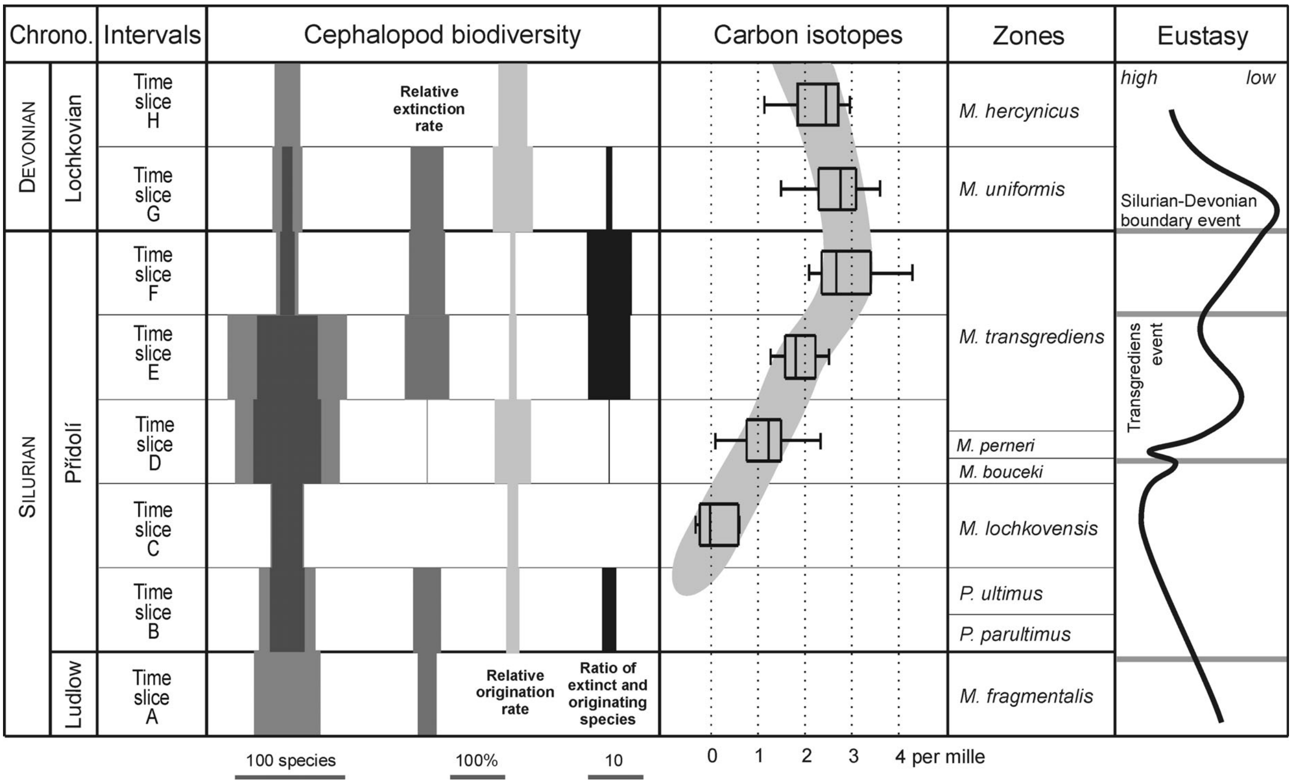


Figure 6. Cephalopod biodiversity, carbon isotopes, biostratigraphy and assumed eustatic curve in the latest Ludlow, Přídolí and Lochkovian of the Prague Basin.

Discosorida and Oncocerida together contain less than 30% of the total cephalopod fauna (Fig. 8). By contrast, the relative abundance of orthoceratids and pseudorthoceratids, which contained less 40% of all cephalopod species from the late Ludlow to LAD *Monograptus transgrediens* (end of Time slice E), greatly increased in the lastest Silurian and in the Lochkovian. Just before the LAD of *Monograptus transgrediens* (during time slice E), the relative abundance of orthoceratids and pseudorthoceratids was 24%. However, during the latest Silurian (Time slice F), orthoceratids and pseudorthoceratids contained 76% of all cephalopods. This large statistically significant increase in their relative abundance is not related to an increase in their total diversity but to a distinct decrease in total species diversity in other cephalopod orders (Figs 7, 8). Taken together, the boundary between intervals E and F represents a time when the most intense change in cephalopod order composition for the period from the late Ludlow to the end of the Lochkovian occurred. Therefore, it appears like the orthoceratids ended the incumbency of the previously dominating groups such as the discosorids and oncocerids.

Faunal similarity

The Jaccard and Dice association similarity indices were calculated in order to characterise faunal similarity in cephalopod faunas for individual time slices. The highest similarity coefficients occur always in stratigraphically neighbouring time slices (Table 3). This means that similarity of cephalopod faunas depends on time and was controlled by relatively rapid cephalopod evolution from the late Ludlow to the end of the Lochkovian. Thus, observed changes in species-level composition of the cephalopod faunas across this time period of about 10 Ma are related mainly to cephalopod evolution and not to changes in other environmental parameters (*e.g.* facies changes). Our analysis revealed that the closest faunal affinity is between cephalopod faunas of Time slices D and E (Dice similarity coefficient equal to 0.93).

A cluster analysis produced dendrograms displaying the same branching topology for both the Jaccard and Dice indices and both clustering modes. The only differences exist in the similarity values and therefore, only a dendrogram based on clustering of the measured Dice distance is figured (Fig. 9). The Dice measure puts more weight on joint occurrences than does the Jaccard coefficient. The constrained dendrogram also shows two relatively well-separated clusters (Fig. 9). The first cluster unites the Silurian cephalopod faunas (Time slice A–F) and the second cluster unites cephalopod faunas from the two Devonian Time slices (G and H).

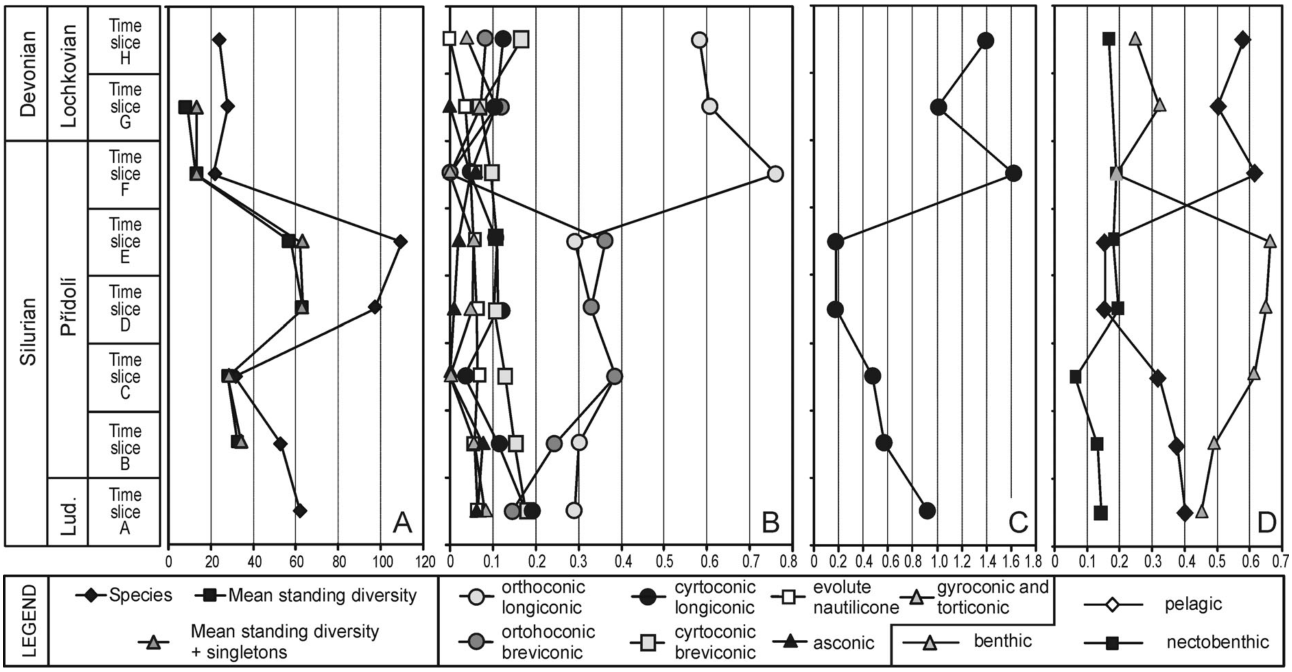


Figure 7. Comparison of cephalopod diversity *versus* morphotypes and strategies in the latest Ludlow–late Lochkovian. • A – simple diversity, mean standing diversity and mean standing diversity plus singletons. • B – relative diversity of morphotypes. • C – ratio between cephalopods with small and large embryonic shell. • D – relative diversity of cephalopods with benthic, nektobenthic and pelagic early stages.

Analysis of relative abundance of shell morphotype

Late Ludlow–Lochkovian cephalopod faunas consist of species belonging to seven cephalopod orders (Fig. 5), generally differing in the morphology of their shells. However, in some orders, there are more than one morphologic type and additionally some morphologic types may occur in more than one order. Therefore, distribution of morphologic types among late Ludlow–Lochkovian cephalopods is not exactly identical with their order-level taxonomy. Morphological disparity within these cephalopods is very high and for the selected analysis, we grouped them into seven morphological categories (Fig. 7).

Analysis of changes in the prefered morphologic shell types for the period from the late Ludlow to the end of the Lochkovian revealed relatively the low frequency of five shell morphologies (CL, EN, CB, GT, and AS; see Fig. 7). The frequency of cephalopod species with the latter shell type is generally about or below 10 percent. By contrast, cephalopods with longiconic and breviconic orthoconic shells were a dominant part of the cephalopod faunas since the beginning of the Přídolí (FAD of *Pristiograptus parultimus*). Since the FAD of *Monograptus lochkoviensis* (beginning of Time slice C) to that of *Monograptus transgrediens* (end of Time slice E), the number of cephalopod species with orthoconic shells was greater than 65 percent of all recorded cephalopod species. The transition from Time slice E to F is connected with the most prominent changes in relative abundance of shell morphologic types for the entire period analysed (late Ludlow-Lochkovian). None of the cephalopod species with an orthoconic breviconic shell occurred in the latest Silurian (Time slice F), even though these species formed more than one third of the cephalopod fauna in several preceeding time slices (Fig. 7). During the Lochkovian, the frequency of cephalopod species with an orthoconic breviconic shell was lower than 10%.

In contrast, the frequency of cephalopod species with an orthoconic longiconic shell dramatically increased from about 30 (Time slice E) to 76% in the latest Silurian (Time slice F). The vast majority of latest Silurian cephalopod species thus had orthoconic longiconic shells (Fig. 7). During the subsequent Lochkovian (Time slices G and H), this shell morphology dominated among the cephalopods.

Analysis of changes in cephalopod life strategies

Three different characteristics of cephalopod species were included in our analysis: size of embryonic shell, juvenile mode of life, and adult mode of life. Relative frequency of embryonic shell size was simply calculated as the ratio of small embryonic to large embryonic shells (Fig. 7). Our analysis revealed a systematic decrease in this ratio from the late Ludlow to Time slice E. In the late Ludlow, the

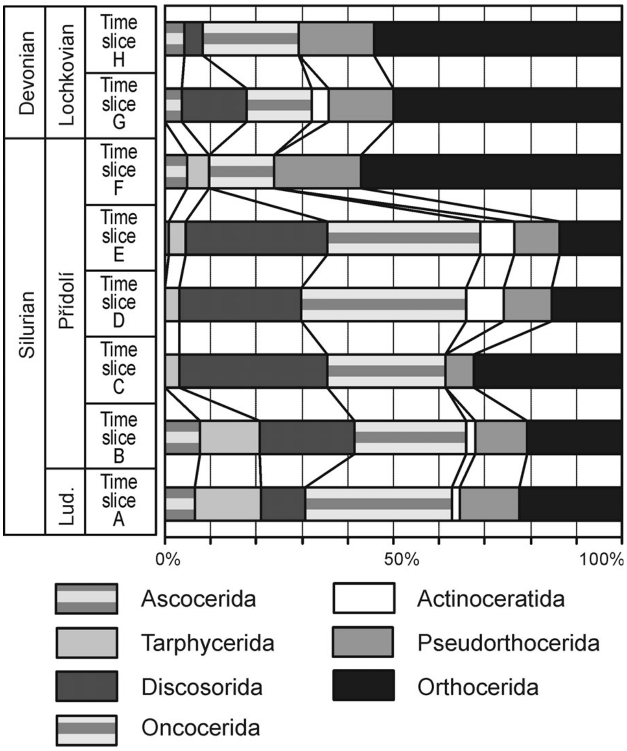


Figure 8. Diversity of cephalopod orders from the latest Ludlow to late Lochkovian.

number of cephalopod species having a small embryonic shell roughly equals the number of cephalopod species having a large embryonic shell. However, cephalopod species with a small embryonic shell formed less than 20% of all recorded cephalopod species during the period from the beginning of Time slice D to the end of Time slice E (*i.e*., since FAD *Monograptus bouceki* to LAD *Monograptus transgrediens*). This pattern changed dramatically during the following time slices (F–H), when species with a small embryonic shell became dominant (more than 60% of cephalopod species during the latest Silurian belong to this group; see Fig. 7C). The transition from Time slice E to F corresponds with the most prominent change in the relative abundance of small embryonic shells during the entire analysed period (late Ludlow–Lochkovian).

The late Ludlow–Lochkovian cephalopods can be placed in one of the three groups (*i.e*. demersal, nektobenthic, and pelagic) according to their early life strategy (see above). A nektobenthic mode of life was the least frequent strategy for the late Ludlow–Lochkovian juvenile cephalopods. Relative frequency of this mode of life varies between 13 and 20% of all species present with only one exception, the period between the FAD of *Monograptus lochkoviensis* and that of *Monograptus bouceki* (Time slice C), when cephalopod species with juveniles exhibiting a nektobenthic mode of life formed only about 6% of the cephalopod fauna. By contrast, relative frequency of species with a demersal juvenile life strategy systematically increased from 45% in the late Ludlow, to 65% in of the cephalopod fauna Time slice E. However, their relative abundance rapidly decreased to less than 20% at the beginning of Time slice F (latest Silurian) and during the whole Lochkovian, it never again rose to the mid-Přídolí level (Figs 8, 10). The relative abundance of cephalopod species with a pelagic juvenile mode of life shows the opposite trend to that of cephalopod species with a demersal juvenile life strategy. Relative abundace of juvenile cephalopod species with a pelagic strategy systematically decreased from 40% in the late Ludlow to 15% in Time slices D and E. Their relative abundance greatly increased to more than 60% at the beginning of Time slice F (latest Silurian) and during the subsequent Lochkovian, this juvenile strategy dominated (Figure 10). The transition from Time slice E to F is thus connected with the most prominent change in relative abundance of pelagic juvenile live strategy for the entire analysed period (late Ludlow–Lochkovian).

Analysis of adult strategies in cephalopod species revealed a similar pattern. All of the 197 late Ludlow–Lochkovian species can be classified into one of three groups (*i.e.* nektobenthic, nektonic, and pelagic). Our analysis clearly showed that the nektobethic adult strategy dominated in the late Ludlow–Lochkovian cephalopod species (Fig. 10) with the nektonic and pelagic adult strategy being less frequent. As in the case of juvenile strategies, the most prominent change in adult strategy occurred at the transition from Time slice E to F. Adult cephalopods with a pelagic strategy formed less than 10% of all cephalopod species during Time slice E. However during the subsequent Time slice F (latest Silurian), the relative abundance of this adult strategy greatly increased to more than 40% (Fig. 10).

Discussion

Cephalopod biodiversity

Analysis of the cephalopod dataset revealed several features of diversity evolution in the Silurain and Early Devonian. The total number of the cephalopod species from the Barrandian included in our analysis represents the majority of all known cephalopod species of this time frame globally and therefore, the results of the analysis also have a global relevance. Our results showed that the faunal similarity of time slices A–H was mainly controlled by the relatively rapid cephalopod evolution in the studied period. Thus, these changes in species-level composition of the cephalopod faunas are rather related to evolutionary changes than to changes in other parameters (*i.e*., environmental changes).

The most distinct changes in the period from the late Ludlow to the end of the Lochkovian occurred between Time slices E and F (*i.e.* around the LAD of *Monograptus transgrediens*). At the transition from Time slice E to F, cephalopod species diversity decreased to a fifth of the original number. At the same time, the most distinct changes occurred in cephalopod order composition and in relative abundance of the basic types of embryonic, juvenile, as well as adult life strategies (Fig. 10). Results of our analyses revealed a strong decline in cephalopod species with large embryonic shells and in cephalopods with demersal juvenile or adult stages. By contrast, cephalopod species with a planktotrophic juvenile strategy and pelagic mode of life were not affected during this crisis in total cephalopod diversity (Time slice F, Figs 6, 7). The latter life strategies also dominated in the Lochkovian cephalopod faunas.

The above mentioned facts clearly show that the tremendous global decrease in cephalopod species diversity in the latest Silurian was caused by processes affecting cephalopod taxa having a long incubation period and living during later ontogeny close to the bottom. This phenomenon can be interpreted as precursor of intense radiation of cephalopods in the Emsian (Klug *et al.* 2010), especially of the Bactritoidea and Ammonoidea. Speculatively, the orthoceratid ancestors of these two groups might shared a trait with these two more derived taxa, which guaranteed the evolutionary and ecological success of all three. Perhaps, it was the reproductive rates, as reflected in small embryonic shells of these three groups.

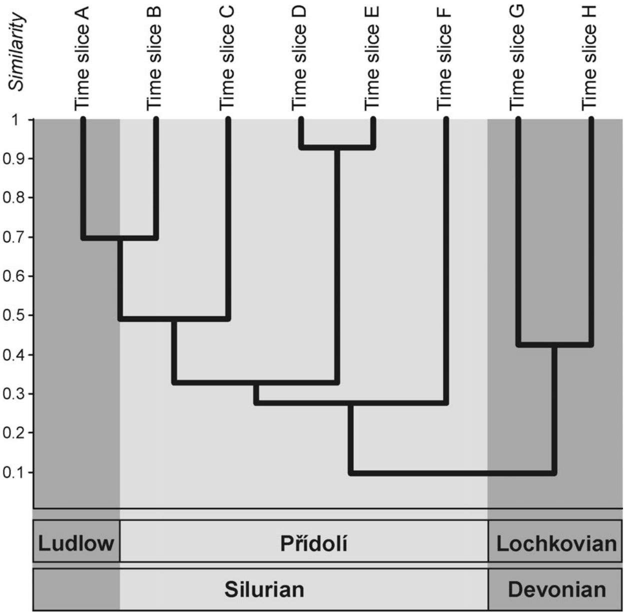


Figure 9. Dendrogram based on clustering of DICE similarities using unweighed pair-group average algorithm.

Relationship between biodiversity changes and the transgressive/regressive curve

Analysis of the relationship between cephalopod biodiversity changes and the transgressive/regressive curve is not trivial because a global transgressive/regressive curve with high stratigraphic resolution has never been published for the time frame under consideration. There is a general consensus on the mid-Přídolí high stand and the general regressive conditions, which continued until the earliest Devonian (Johnson *et al*. 1998). A sea-level curve based on the interpretation of sedimentological data from the Prague Basin may be affected by local tectonics, as has been documented by Kříž (1998a) for Silurian rocks. The most recent synthesis of Palaeozoic sea-level changes (Haq & Schutter 2008) indicates two high-stands during the Přídolí in the Prague Basin curve (also documented in the Appalachian Basin and in Novaya Zemla, see Bell & Smosna 1998). If the curve correctly reflects global sea-level changes during the Přídolí, the results of our preliminary analysis of the relationship between cephalopod biodiversity changes and the transgressive-regressive curve can be considered as being global. Present data suggests that there is no strong link between sea-level changes and cephalopod biodiversity. Nevertheless, our Time slices do not exactly correlate with the transgressive/regressive curve. By contrast, the change in diversity (and composition of the assemblages) between Time slices B and D corresponds well with the Přídolí high-stand (Johnson *et al*. 1998).

Relationship between cephalopod biodiversity changes and global carbon cycle

Analysis of δ^{13}C evolution in the global marine reservoir, based on samples from the Prague Basin, clearly revealed a distinct and statistically significant increase in δ^{13}C values during the Přídolí from Time slices C to F. The earliest Lochkovian is characterized by the same δ^{13}C values with a decreasing trend in the younger Lochkovian. Therefore, the latest Silurian (Time slice F – LAD of *Monograptus transgrediens* to FAD of *Monograptus uniformis*) was a time of change in dynamics of the global carbon cycle in the marine ecosystem and the early Lochkovian is characterised by steady conditions following this change. Our data agree well with results of earlier publications (Andrew *et al*. 1994, Hladíková *et al*. 1997, Porebska & Sawlowicz 1997, Saltzman 2002, Buggish & Mann 2004, Malkowski *et al*. 2009). However, in some cases, a detailed comparison of the δ^{13}C curve with data from the Prague Basin (GSSP area) is difficult because of the lack of high-resolution biostratigraphic data.

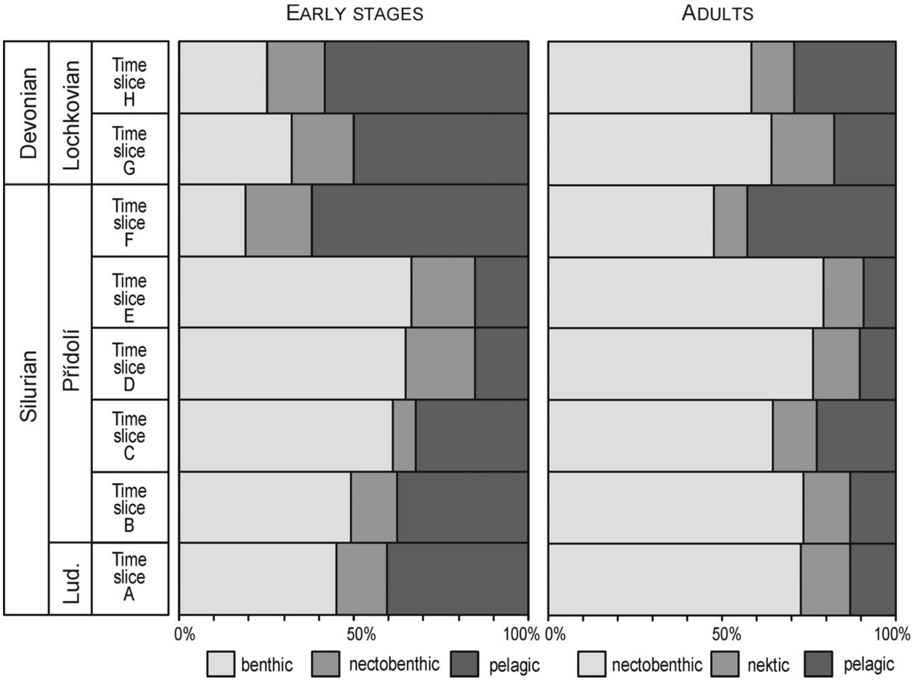


Figure 10. Relative diversity of cephalopods with different embryonic and adult strategies.

Our results show, in contrast to sea-level changes, a distinct relationship between cephalopod biodiversity changes and the global carbon cycle. Time slice F (latest Silurian) was not only a time of change in dynamics in the global carbon cycle, but also a time of tremendous decrease in the global diversity of cephalopod species, mainly affecting cephalopod taxa having a long incubation period and living close to the bottom during later ontogeny.

Relationship between cephalopod biodiversity changes and the Silurian-Devonian boundary crises

Three differrent bioevents – the Silurian-Devonian boundary Event (Walliser 1985), Transgrediens Event (Urbanek 1995), and Klonk Event (Jeppsson 1998) – were defined within the Silurian-Devonian boundary interval. These terms are unfortunately used differently in recent publications. The Silurian-Devonian boundary Event was proposed by Walliser (1985) who defined it by the first occurrence of *Monograptus uniformis*. This bioevent is thus identical with the Silurian-Devonian boundary (*e.g.*, Chlupáč *et al.* 1972). Schönlaub (1986) characterized this bioevent as the period "...when new environments were established". Later, Walliser (1996) reviewed the available data and described also this stratigraphic level as a time of distinct environmental changes. Boucot (1990) did not consider this event as an extinction event. Similarly, Talent *et al.* (1993) did not find any significant change in generic diversity of brachiopods across the Silurian-Devonian boundary. House (2002) confused the Silurian-Devonian boundary Event with the Klonk Event. According to the published data, the Silurian-Devonian boundary is thus not connected with distinct extinction events.

In contrast to the Silurian-Devonian boundary Event, the Transgrediens Event was introduced as an extinction event. Urbanek (1995) defined it as a graptolite extinction event close to the LAD of *M. transgrediens*. Similarly, Jeppsson (1998) introduced the name "Klonk Secundo-Unnamed Event" as a conodont extinction event, which is probably identical with the Transgrediens Event and which "started at or possibly before the extinction of '*P.*' *transgrediens*, at or near the replacement of *Oulodus elegans elegans* by *O. elegans detorta*". Jeppsson thus only established a new name for the same crisis and therefore, we give the priority to the older name Transgrediens Event.

All bioevents mentioned above were based on the evaluation of diversity dynamics of a few graptolite or conodont species. It is thus questionable if these graptolite or conodont crises really represent crises in the global marine ecosystem.

Our analysis of the large cephalopod species dataset revealed the highest relative extinction rate in Time slice E, which also has the highest cephalopod species diversity at 110 species. Before the end of Time slice E, *i.e.*, before the LAD of *M. transgrediens*, more than 80% of all cephalopod species became extinct. However, high extinction rates also characterise the latest Silurian and early Lochkovian (Time slices F and G, see Figs 6, 7). The beginning of the Lochkovian is a time of high origination rate. Cephalopod diversity data show that the crisis happened during time slices E and F (end of Silurian), when the number of extinct cephalopod species was about six to seven times higher than the number of originating cephalopod species. Contrariwise, the earliest Devonian (early Lochkovian) was a time of recovery after the end-Silurian crises (Figs 6, 7), when one order (Ascocerida), one suborder (Tarphycerina), nine families (*e.g.* Hemiphragmoceratidae and Mandaloceratidae), and several genera became extinct.

Interpretation and conclusions

Our results revealed a correlation between cephalopod biodiversity and the global carbon cycle. The latest Silurian (Time slice F) was not only a time of change in dynamics of the global carbon cycle, but also a time of tremendous decrease in the global diversity of cephalopod species. This decline affected mainly cephalopod taxa having a long incubation period and living close to the bottom during their later ontogeny, reflecting possibly a selection for a certain habitat. Selective extinction of these species may be a key to understanding the causes of this crisis.

Based on their analyses of rock geochemistry and graptolite distribution from pelagic sequences in the Polish Bardzkie Mountains, Porebska & Sawlowicz (1997) noted that the latest Silurian *M. transgrediens* Zone and the earliest Devonian *M. uniformis* Zone were separated by a thin interval termed a linograptid "interregnum". They interpreted a distinct change in geochemical composition of the sediments of the linograptid "interregnum" as evidence for a short-term shallowing of the upwelling system, which brought nutrient-rich water. This change in graptolite fauna above the LAD of *Monograptus transgradiens* was, according to Porebska & Sawlowicz (1997), caused by a high productivity of cyanobacteria, which consequently increased the level of the anoxic layer. An upwelling of anoxic water was fatal for uniserial, straight monograptid colonies living deeper (close to the base of the mixed layer or near the top of the denitrification zone) than *Linograptus* populations. A high content of rhenium in sediments of the linograptid "interregnum" is also supporting a decrease in oxygen content of seawater. Porebska & Sawlowicz's model (1997) also explains the demersal cephalopod species diversity decline as well as its low impact on the diversity of pelagic cephalopods.

Recent data on global seawater temperature (Joachimski *et al.* 2009) indicates a progressive cooling during the Přídolí, reaching a minimum global ocean temperature in the earliest Lochkovian. This cooling corresponds well with the regressive trend and the higher erosion rate causing an increase in ^{87}Sr/^{86}Sr isotope values for marine carbonates (Veizer *et al.* 1999, Frýda *et al.* 2002). The relationship between seawater temperature and global oceanic circulation was discussed in detail by several authors (*e.g.*, Wilde & Berry 1984, 1986; Schopf 1980; Bralower & Thierstein 1980; Jeppsson 1990 *etc.*). These studies clearly showed that progressive cooling could trigger a deepening of cooler and denser seawater (at a temperature of about 5 °C) at high latitudes and thus change global oceanic circulation. The subsequent upwelling of nutrient-rich water could have represented a new food supply for marine animals. The observed progressive increase in TOC and δ^{13}C values during the Přídolí could well reflect an increase in bioproductivity. New food sources may also explain the observed increase in cephalopod diversity. An anoxic or disoxic event in the period between LAD *M. transgrediens* and the first Devonian *M. uniformis* Zone (Porebska & Sawlowicz 1997) probably selectively affected benthic communities (thus also demersal cephalopods). This process was perhaps responsible for the strong decrease in total biodiversity and subsequently caused a lowering of bioproductivity and thus the steady conditions in δ^{13}C composition of seawater during the early Lochkovian. Such a destruction of faunal communities could have altered the global carbon cycle of the marine ecosystem in the highest Silurian. Regardless of the end-Silurian crises in benthic communities, the early Lochkovian seawater was still nutrient-rich, which could explain the fast recovery rate of the marine ecosystem (Fig. 6) and subsequent Palaeozoic Plankton (Nützel & Frýda 2003) and Nekton Revolutions (Klug *et al.* 2010). Our data also show that the extinction interval was much longer (from the end of Time slice E to the beginning of the Lochkovian) than had been suggested by graptolite and conodont biodiversity studies. Usage of terms such as the Silurian-Devonian boundary Event (Walliser 1985), Transgrediens Event (Urbanek 1995), and Klonk Event (Jeppsson 1998) thus requires a detailed revision.

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Publikovaná práce

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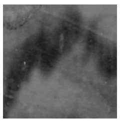
Colour pattern polymorphism in Silurian nautiloid *Phragmoceras* Broderip, 1839

Vojtěch Turek & Štěpán Manda



Flamboyant colour pattern polymorphism documented in Silurian nautiloid *Phragmoceras* has not been observed in any other nautiloid genus. Two specimens of *P. imbricatum* Barrande, one from the early Ludlow of Bohemia and the second from the late Wenlock of England display quite different shell coloration: narrow, densely spaced longitudinal bands subparallel to the shell axis, combined with narrower transversal bands *versus* transverse bands running laterally obliquely to growth lamellae. Two additional types of colouration have been observed in several specimens of *Phragmoceras* from the early Wenlock and late Ludlow of Gotland. The colour pattern in *P. eurystoma flexibile* Hedström consists of zigzags bands around the whole circumference of the shell. In contrast, distinct colour bands following growth lines along the whole circumference of the shell, like that in the Cretaceous nautilid *Eutrephoceras*, are characteristic in *P. dubium* Hedström. If pigmentation pattern served as a form of crypsis, then the quite different types of coloration in *Phragmoceras* indicate different solutions of this problem. Colour pattern has been regarded as a useful tool also for taxonomic purposes in nautiloid cephalopods. Nevertheless, the colour polymorphism in *Phragmoceras* suggests the limited significance of this feature for the taxonomy of nautiloids. Some other remarkable cases of colour variations in Silurian nautiloids are discussed. Changes in colour pattern most probably correspond with depth inhabited; nautiloids that occupied shallow water environments display rather light coloured shells in comparison with forms inhabiting a deeper water setting. • Key words: Cephalopoda, Nautiloidea, colour pattern, polymorphism, Silurian.

Turek, V. & Manda, Š. 2011. Colour pattern polymorphism in Silurian nautiloid *Phragmoceras* Broderip, 1839. *Bulletin of Geosciences 86(1)*, 91–105 (9 figures, 1 table). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received November 5, 2010; accepted in revised form December 14, 2010; published online March 10, 2011; issued March 14, 2011.

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Knowledge concerning colour patterns in fossil cephalopods has been significantly extended since publication of Treatise of Invertebrate Paleontology, Part K, in 1964 (Hoare 1978, Mapes & Hoare 1987, Blodgett *et al.* 1988, Kobluk & Mapes 1989, Mapes & Davis 1996, Sun *et al.* 1999, Turek 2009 and further references therein). Nevertheless, knowledge of some aspects of colour pattern evolution and variability in ancient cephalopod molluscs are still scarce. Turek (2009, p. 492) summarised that colour patterns have been observed in 57 species of Early Palaeozoic nautiloids, which belong to 26 genera but their number is still increasing (Manda & Turek 2009a, b). Large varieties of colour pattern types including zigzag, chevron, radial and transversal colour bands and their combinations have been described in fossil nautiloids. The majority of nautiloids displaying colour patterns come from the Silurian strata of Bohemia and Gotland, and belong to order Oncocerida. In the vast majority of species in which shell colouration is known, the colour pattern is preserved in very few specimens, sometimes even only one. In addition, colouration is usually not preserved in the entire shell. Therefore, opportunities to study intraspecific and intrageneric variation of colour pattern and its evolution and palaeecological significance are quite limited.

Shell colouration in the order Discosorida (Middle Ordovician–Late Devonian) is preserved in the fossil record only rarely. Turek (1990) reported, but did not illustrate longitudinal bands in late Silurian *Phragmoceras imbricatum* Barrande, 1865 from Bohemia. Re-examination of the specimen (NM L 40804), however, shows presence of longitudinal and transversal colour bands on the shell surface, *i.e.* the same pattern as was documented by Barrande (1870, pl. 429, pp. 14–20) in oncocerid *Hexameroceras panderi*. During current comparative study of some cephalopod species described by Barrande (1865–1877) from the Silurian of Bohemia and subsequently reported from England and the Wales Borderland (Blake 1882), the colour pattern has been found in another specimen of *P. imbricatum* (Blake 1882, pl. 25, fig. 2, 2a). Surprisingly, the colour pattern in Blake's specimen differs markedly

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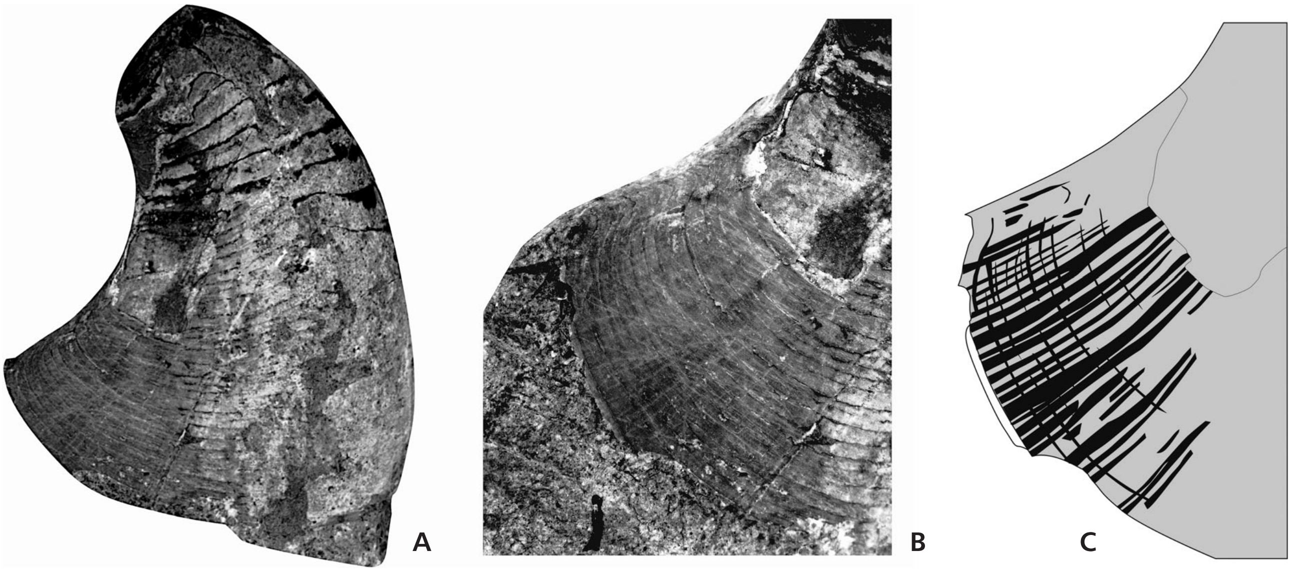

Figure 1. *Phragmoceras imbricatum* Barrande, 1865; NM L 40804; Ludlow, Gorstian, *C. colonus* Zone; Bohemia, Butovice, Na břekvici locality, Kopanina Formation; lateral view, × 1.7 (A), detail of the shell with colour pattern preserved (B) and its sketch drawing (C), both × 3.

from that in the Bohemian specimen in having transverse bands running laterally, obliquely to growth lines. Examining the Silurian cephalopods from Gotland, Sweden we found several specimens of *Phragmoceras* with two other types of preserved colour pattern: narrow zigzags bands in *P. eurystoma flexibile* Hedström from the early Wenlock and transversal bands concordant with growth lines in *P. dubium* Hedström from the middle-late Ludlow. In contrast, irregular spots in *P. dubium* described by Foerste (1930) as original shell pigmentation (see Kobluk & Mapes 1989) we consider to be a false colour pattern. Such a variety of colour patterns within a single species or even genus is remarkable and has not been described in any known nautiloid including present day nautilid genera *Nautilus* and *Allonautilus*.

All known specimens of *Phragmoceras* retaining shell colouration are described in this paper. The variation in colour pattern in this genus is considered to be the first reliable evidence of colour pattern polymorphism in nautiloids. Some others cases of striking variations of colour pattern in tarphycerids and oncocerids are discussed. The term "polymorphism in colour pattern" is used here to describe quite different types of colouration, *i.e.* different geometric patterns. Lesser differences in colour pattern such as width of colour bands and some irregularities occurring, for instance, in separate species of *Nautilus* (see Ward *et al.* 1977) we regard as variations.

Specimens discussed are deposited in National Museum, Praha (prefix NM L), Oxford University Museum, (prefix OUM) and Rickmuseet, Stockholm (prefix RM). All specimens were immersed in alcohol or water before photographing.

Description of colour pattern in *Phragmoceras*

Four types of coloration have been found in *Phragmoceras*. They include 1) longitudinal bands combined with transversal bands, 2) transversal bands oblique to growth lines, 3) zigzag pattern, and 4) transversal bands concordant with growth lines. Each is described in detail below.

Type A. Longitudinal bands combined with transversal bands

This type of colouration was found in only a single specimen of *Phragmoceras imbricatum* Barrande, 1865 (NM L 40804, Fig. 1) from the early Ludlow, Gorstian, *C. colonus* Zone, Kopanina Formation from Bohemia; locality Praha-Butovice, Na Břekvici (*i.e.* Barrande's locality Butowitz e1, for locality description see Kříž 1992). The specimen originates from the collection of J. Barrande. It is an incomplete, not yet fully-grown specimen with widely opened aperture preserved in dark grey biomicritic limestone; maximum dorsoventral length preserved is 56 mm and width about 32 mm. The shell wall is present ventrally and laterally, on the left and right sides is deeply weathered. The ad-apical part of the body chamber is extensively damaged on the ventral side (Fig. 1).

The colour pattern is preserved in the ventrolateral portions of the body chamber. Brownish dark and hardly discernible bands sub-parallel to the axis of the shell are about 1–2 mm wide. Distance between two neighbouring strips varies markedly. Ventrolaterally dark bands cover about 40–50 percent of the shell surface. Density of bands

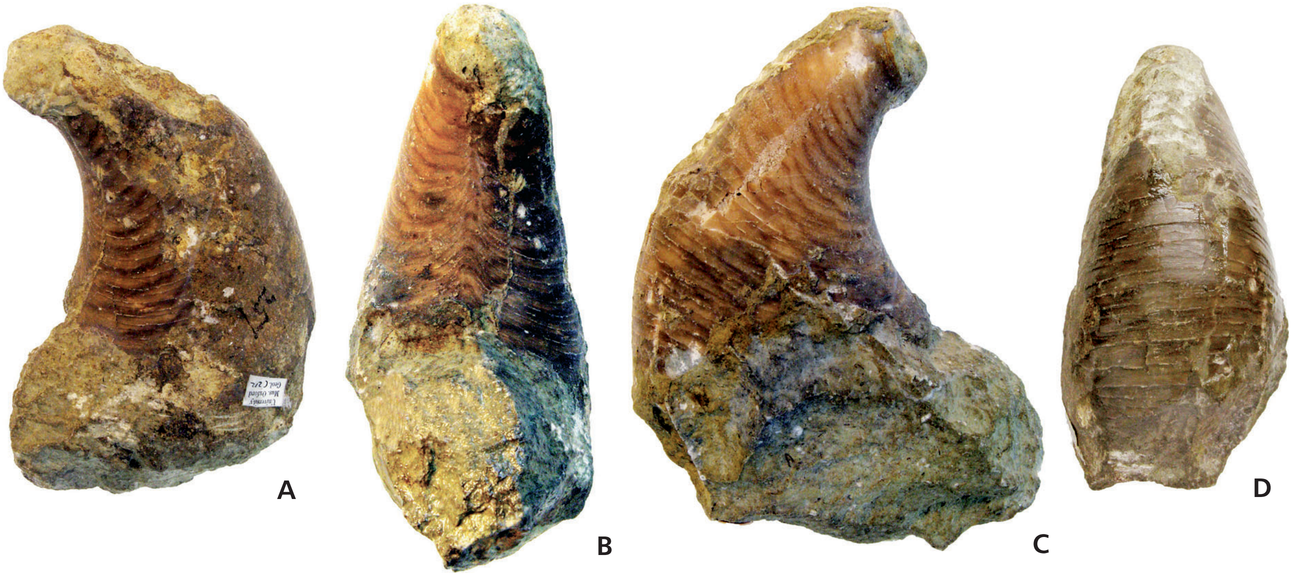

Figure 2. *Phragmoceras imbricatum* Barrande, 1865; OUM C 212, Ludlow, latest Wenlock; Much Wenlock Limestone; England, Ledbury; right lateral (A), ventral (B), left lateral (C) and dorsal (D) views, all × 0.9.

increases laterally. It seems probable that convex side of the endogastric shell was intensively coloured but due to preservation this assumption cannot be confirmed. The longitudinal bands were combined with fine transversal and rather irregular bands to form a reticulate pattern.

Type B. Transversal bands oblique to growth lines

A specimen of *Phragmoceras imbricatum,* OUM C 212, from the late Wenlock, Ledbury, England, was illustrated by Blake (1882, pl. 25, figs 2, 2a) and later refigured by Holland & Stridsberg (2004, fig. 3b, c). The specimen originates from the collection of A. Grindrod. Holland & Stridsberg (2004) revising phragmoceratids from England reinterpreted the age of this specimen as early Ludlow. M.G. Bassett, however (written communication 2009), confirmed late Wenlockian age of this specimen as originally suggested by Blake (1882). The incomplete specimen is strongly dextrally damaged near the aperture and the apical part is missing (for detailed description see Holland & Stridsberg 2004, pp. 306–309). Although the colour pattern is well visible, neither Blake (1882) nor Holland & Stridsberg (2004) mentioned this feature.

The shell colour pattern can be reconstructed along the entire circumference of the shell. It is roughly bilaterally symmetrical (Fig. 2). The colour pattern has an appearance of brownish bands, contrasted by lighter interspaces. On the convex dorsal side they are sub-parallel to imbricate growth lamellae; ventrolaterally, colour bands diverge from the course of growth lamellae adaperturally at an angle of about 30°. Ventrolaterally, their course becomes similar to the course of growth lamellae dorsally forming an adapically-pointing tongue in the middle of ventral side. The interspaces between darker bands are markedly wider on the lateral and dorsal sides.

Type C. Zigzag pattern

Four specimens of *Phragmoceras eurystoma flexibile* Hedström with preserved colour pattern, which come from Silurian of Gotland, were studied. The first three specimens, RM Mo 157731, 152778–79 from the Wenlock rocks are labelled as coming from locality Visby, Norderstrand (*i.e.* north part of Visby Town). Slightly compressed specimens are preserved in grey marlstone; the shell was replaced by light grey calcite.

The first specimen, RM Mo 152778, is a fragment of a phragmocone damaged on the inner (ventral) side (Fig. 3A–C). Dorsoventral length is 29 mm; width of the shell is 21.9 mm. The colour pattern is preserved on the lateral and dorsal sides and is bilaterally symmetrical. It shows that the generally light shell was brightly coloured. Brownish zigzags resemble seismic recordings by their course. Much narrower bands with feathered edges are separated by wide, light grey interspaces. On the convex and slightly flattened dorsal side they form a very deep and narrow saddle (average angle is 30°) passing into a wide, mid-laterally situated lobe. The course of these dorsolateral as well as ventrolateral arms is complicated due to presence of smaller zigzags. Shallow and wide ventrolateral saddles traceable dextrally pass into indicated

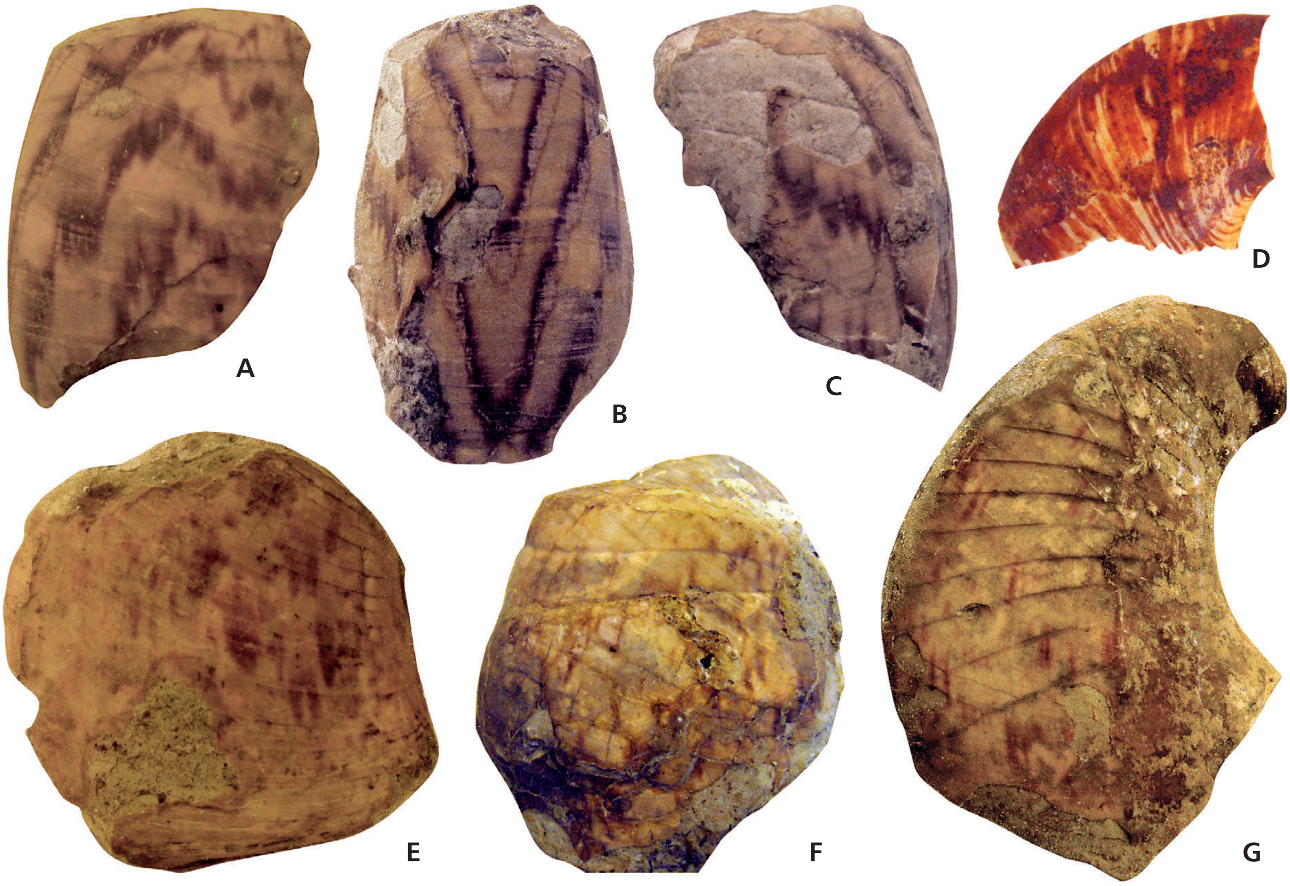

Figure 3. A–C, E–G – *Phragmoceras eurystoma flexibile* Hedström, 1917. Wenlock, locality Visby, Norderstrand. • A–C – specimen RM Mo 152778, left lateral (A), dorsal (B) and right lateral (C) views, × 1.6. • E – specimen RM Mo 152779, lateral view, × 1.1. • F – specimen RM Mo 58340, lateral view, × 1.1. • G – specimen Mo 57731, lateral view, × 1.2. • D – *Phragmoceras dubium* Hedström, 1917. Late Ludlow, locality Mannagärda, Gotland, specimen Mo 52087, lateral view, × 1.4.

ventral lobe. The further course of bands cannot be followed due to preservation of the specimen.

The second specimen, RM Mo 152779 (Fig. 3E) is an incomplete body chamber of a fully-grown specimen showing constricted aperture. Growth lines are widely spaced. Maximum dorsoventral length is 39 mm, width is not measurable, due to preservation. Shell with preserved colour pattern is preserved only sinistrally. Colour pattern is not so well visible in comparison with the former specimen. General character – narrow bands in form of multiple zigzags separated by wider light bands – is identical. Pigment is concentrated on some of them in the form of patches. Brownish bands disappear on the shell adaperturally so that the body chamber near the aperture seems to be primarily less pigmented than its adapical part.

The third specimen, RM Mo 57731 (Fig. 3G, a specimen figured in pl. 24 as figs 7, 8 by Hedström 1917) represents two phragmocone chambers and adapical part of the body chamber; maximal length 50 mm, dorsoventral length 37 mm, maximal width 22.4 mm. Sinistrally preserved shell shows slightly indicated colour pattern of the same type as in previous specimens. Narrow bands resemble seismic recordings. The same general course of bands is also indicated.

The last specimen, RM Mo 58340 (Fig. 3F) represents a part of phragmocone and adapical part of the body chamber, cut in the medium plane. Specimen is preserved in grey limestone of Hamra beds, locality Visby, which is early Ludlow in age. Maximal dorsoventral length of shell is 67 mm, width 43 mm. Shell is preserved only dorsolaterally. Traces of the colour pattern form short, irregularly dispersed bands sub-parallel to the shell axis. This pattern can be derived from the previous one, but only short parts of zigzags are preserved. Whether the shell of this specimen was originally only slightly coloured or if the only slightly indicated colour pattern is a result of preservation bias is difficult to determine.

Type D. Transversal bands concordant with growth lines

Five specimens of *Phragmoceras dubium* Hedström, 1917 retaining original shell colouration are available for study

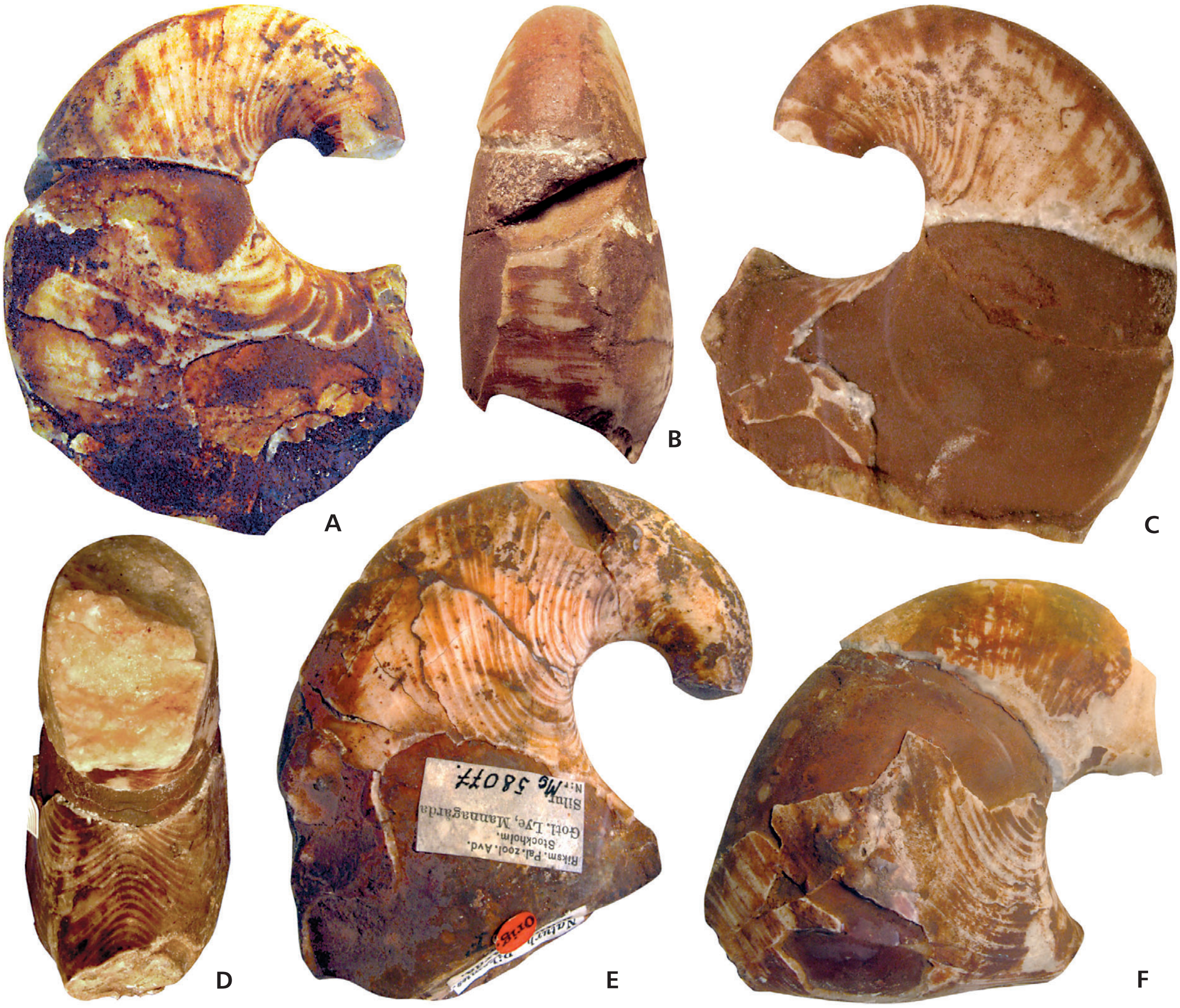

Figure 4. *Phragmoceras dubium* Hedström, 1917. Late Ludlow, locality Mannagärda, Gotland. • A–C – specimen Mo 58088, left lateral (A), dorsal (B) and right lateral views (C), × 1.5. • D, F – specimen Mo 167633, ventral and lateral views, × 0.8. • E – specimen Mo 58077, lateral view, × 1.2.

(RM Mo 52087, RM Mo 58077, RM Mo 58087–58088 and RM Mo 167633). All specimens listed above were found in locality Mannagärda, Gotland, late Ludlow in age, and are preserved in reddish fine-grained biomicritic limestone with common cephalopods.

The first specimen, Mo 58088, is an almost complete shell with open aperture, shell length is 47 mm, width 34 mm (Fig. 4A–C, see also pl. 7, figs 9, 10 in Hedström 1917). Brick-red colour bands, sometimes discontinuous, run around the entire circumference of the shell, conformably with growth lines, and they also follow growth lines in the apertural region. They are almost of the same width as the light grey interspaces separating them. Marked irregularities in the course of wide bands have been observed on convex dorsal side (RM Mo 58088, Fig. 4A–C), margins of bands are sometimes feathered. Pairs of bands sometimes fused to form broader bands.

The second specimen Mo 58077 is a shell with contracted aperture and missing apical part, shell length is 56 mm, width 46 mm, this shell exhibits the same colour pattern as the specimen mentioned below, the width of colour bands is however slightly lower (Fig. 4E).

Similar rather narrow colour bands are shown by the third specimen – a fragment of a phragmocone, Mo 52087 (Fig. 3D).

The fourth specimen (RM Mo 167633) is a contracted body chamber with part of a phragmocone, this specimen like that described above exhibits transversal bands concordant with growth lines, the shell colouration is well visible especially on the ventral side where narrow and dense bands are developed. The margin of colour bands is sharp, in one case two adjacent bands are converging into one (Fig. 4D). In addition, this specimen demonstrates development of colour bands around the constricted aperture (Fig. 4F). The subdorsally positioned apertural opening surrounded with colour bands suggesting that shell growth continued in the restricted area of the hyponomic opening after formation of the hyponomic sinus.

The final specimen, Mo 58087, is a small part of a phragmocone, the colour bands are well visible on the lateral side, and they are slightly narrower than on the above mentioned specimens.

Colour pattern in *Phragmoceras*

Two examined shells with preserved colour pattern in *Phragmoceras imbricatum* show a quite different colour patterns: broad sub-transversal bands versus a combination of narrow longitudinal and transversal bands (Fig. 8). While the first type is unusual among nautiloid, the second type of colouration is almost identical with the colour pattern observed in *Hexameroceras panderi* (Barrande, 1865). Both types of pattern also differ in the ratio between pigmented and unpigmented zones. The shell in the British specimen was originally markedly lighter than the shell of the specimen coming from Bohemia.

Phragmoceras eurystoma flexibile (from Gotland) exhibits narrow zig-zag bands (Fig. 8), a pattern so far known in representatives of Oncocerida, Tarphycerida and Orthocerida. Among four fragments only one shows a constricted aperture. Zig-zags disappear in middle part of the body chamber and in this character, this species resembles adult *Nautilus* with an unpigmented adapertural part of the body chamber. A similar situation has been found in oncocerid *Pentameroceras mirum* (see below).

All specimens of *Phragmoceras dubium* from Gotland having broad colour bands parallel with growth lines show very similar colour patterns, but the width of colour bands and their density vary slightly. Shell colouration in *P. dubium* strongly resembles the pattern described by Stridsberg (1985, p. 24) in *Octameroceras sinuosum* Stridsberg, 1985 and *O. rimosum* (Barrande, 1865). All these specimens come from the same locality and horizon. Both *Phragmoceras* and *Octameroceras* are endogastric brevicones with contracted aperture. Intensive colouring of the convex dorsal and dorsolateral sides in *Phragmoceras dubium* resembles colouring of convex ventral and ventrolateral regions of the shell in extant *Nautilus* and *Allonautilus.* Furthermore, the shell colouration in *Phragmoceras dubium* resembles colouration observed in Cretaceous nautilid *Eutrephoceras* Hyatt, 1894 illustrated by Mapes & Evans (1995) in which colour bands are subparallel with growth lines along the entire circumference of the shell. It represents a striking convergence in colour pattern development, although the living position of *Phragmoceras* compared to the above mentioned nautilids had to be quite different (see Manda 2008). In contrast to present-day nautilids, the fully-grown specimens of *P. dubium* also had intensively pigmented body chamber and contracted aperture.

Variations of colour pattern in Early Palaeozoic nautiloids

Barrande (1865–1877) did not observe different colouration types in any single species of Palaeozoic nautiloid. He therefore suggested very low intraspecific variability of colour pattern within this group. He examined in detail several dozens specimens of *Cyrtoceras parvulum* Barrande, 1866 from Ludlow of Bohemia and found only minor differences in colouration (expressed *e.g.* in width of colour bands). Foerste (1930) followed by later authors (*e.g.* Teichert 1964, Kobluk & Mapes 1989, Turek 2009) concluded that the colour pattern is usually a species-specific or even genus-specific feature in Early Palaeozoic nautiloids. Colour pattern polymorphism described in *Phragmoceras* herein is exceptional; some remarkable variations in colour pattern observed in Silurian nautiloids are discussed below.

Peismoceras pulchrum (Barrande, 1865) from Bohemia

An interesting variation in colour pattern has been documented in the Silurian lechritrochoceratid *Peismoceras pulchrum* from the early Ludlow (Gorstian) strata of Bohemia (Turek & Manda 2010). While some specimens show spiral bands on one lateral side and a zigzag-pattern on the opposite side of the shell, the majority display zigzags throughout the entire circumference of the shell. The passing of one type into the second one demonstrates that one pattern is derived from the other (Fig. 5).

Pentameroceras mirum (Barrande, 1865) from Gotland

Stridsberg (1985, fig. 25C, RM Mo 154005) illustrated a specimen assigned to this species, which display fine brownish, but very unequally developed transversal bands concordant with the growth lines. He interpreted these bands, resembling coloration in *Octameroceras* Hyatt, 1900, as colour patterns. However, these narrow bands in the shell seem quite likely to be a false colour pattern caused by diagenetic processes, and for that reason the authors of this paper do not consider this to be a true example

Figure 5. Shell colouration in the coiled barrandeocerid *Peismoceras pulchrum* (Barrande, 1865), Ludlow, early Gorstian, locality Butovice Na břekvici, Kopanina Formation, Bohemia. • A, C – specimen NM L 8055, right lateral (A) and left lateral (C) views, × 1.4. • B – specimen NM L 27401, body chamber, dorsal view, × 1.8. • D–F – specimen NM L 27400, right lateral (D), ventral (E), dorsal (F), and left lateral (H) views, × 1.4.

of colour pattern polymorphism. For a more detailed discussion of false colour pattern see Mapes & Davis (1996) and Klug *at al.* (2007).

In examining *P. mirum* from Gotland, we have found three specimens with very well developed chevron patterns. The best-preserved specimen (RM Mo152778, Fig. 6C–F) is a body chamber and part of a phragmocone. The aperture is contracted with characteristic five narrow lobes; maximum shell length preserved is 17 mm, diameter 11 mm. Information about the locality is missing, but the mode of preservation indicates that the specimen comes from locality Mannagärda (Ludlow in age). The specimen shows three well visible chevron colour bands, the fourth is preserved only in part. The bands are narrow and separated by a broad, unpigmented zone. The last chevron band is less intense than the others. The colour bands are restricted to the phragmocone and base of the body chamber; part of the body chamber close to the aperture is uncoloured, except for a darker grey band running around the aperture. As the specimen represents a mature individual, this band may be equivalent of black band deposited in the apertural region of mature specimens (comp. Ward 1987).

Two other specimens of *P. mirum* (RM Mo154295 and RM Mo154297) are preserved in grey argillite mudstone of Halla beds, locality Hörsne kanal, late Wenlock, Homerian, Wenlock. The first specimen (RM Mo154297, Fig. 6A) is a phragmocone with a preserved base of the body chamber, maximum length is 21 mm, and diameter increases from 5 to 15 mm. The shell is preserved in lateral sides. The shell wall is dark grey in colour. Four light-grey narrow bands are visible. The first and most apical band (width 0.5 mm) is straight. The next three bands are chevron-like and their amplitude and width (from 0.5 to 1 mm) increases toward the aperture. The last band occurs at the base of the body chamber. The second specimen (RM Mo 154295, Fig. 6B) is a fragment of a phragmocone and body chamber, length 20 mm and diameter 13 mm. The shell is dark-grey with one partly preserved, narrow, white zig-zag stripe.

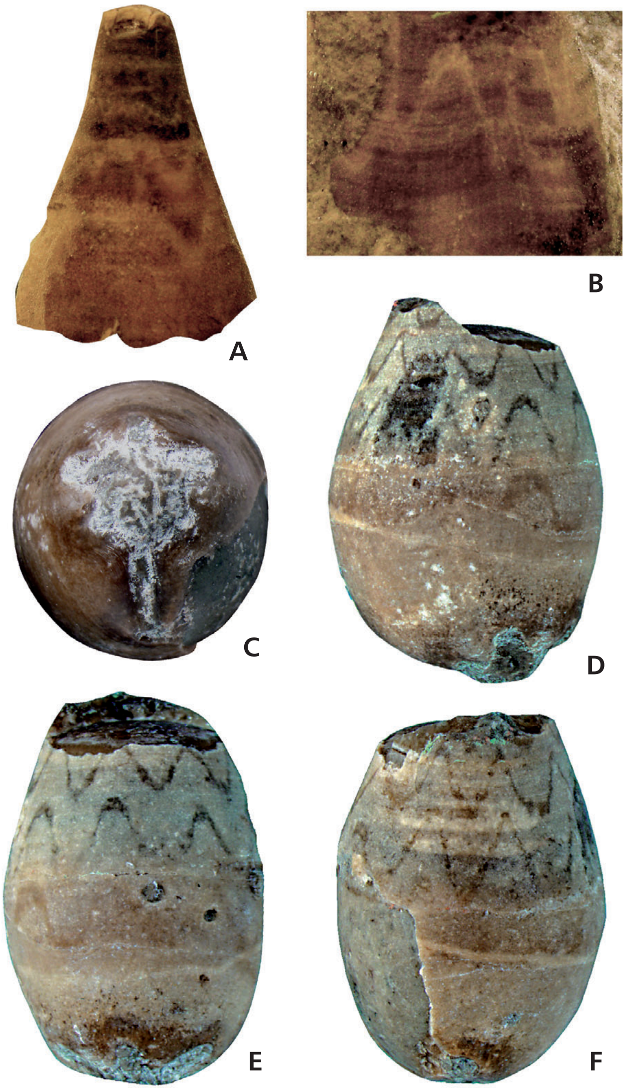

Figure 6. Shell colouration in the Silurian oncocerid *Pentameroceras mirum* (Barrande, 1865) from the Silurian rocks of Gotland. • A – specimen Mo 154297, late Wenlock, Homerian, Wenlock, Halla beds, locality Hörsne kanal, lateral view, × 1.8. • B – specimen Mo 154295, late Wenlock, Homerian, Wenlock, Halla beds, locality Hörsne kanal, detail of phragmocone, ventral view, × 2.5. • C–F – RM Mo 152778, late Ludlow, locality Mannagärda, Gotland, apertural (C), lateral (D), dorsal (E) and ventral (F) views, × 2.6.

The described variability of the colour pattern in oncocerid *Pentameroceras mirum* from Gotland expressed in intensity of colouration is not interpreted as a case of colour pattern polymorphism as the pattern is the same (Figs 6A–F, 8).

Hemiphragmoceratidae Foerste, 1926 from Gotland and Bohemia

The Hemiphragmoceratidae Foerste, 1926 group brevicone oncocerids with a slightly curved endogastric shell and thick subcentral siphuncle (*e.g.* Stridsberg 1985). Species of this family described by J. Barrande were originally placed in the genus *Phragmoceras*. Barrande (1870, pl. 429, figs 14–20) illustrated three specimens of *Hexameroceras panderi* (Barrande, 1865) from the late Ludlow of Bohemia in which the coloration is characterised by a combination of narrow longitudinal and transversal bands. The same colour pattern has been observed in several other specimens by the present authors. The variation in colour pattern is expressed in the density of longitudinal bands and their width, which is always lower than that of the interspaces between the bands (Fig. 5C–E). In addition, a specimen of *Tetrameroceras* sp. from latest Ludlow of Bohemia exhibits a quite similar shell colouration (unpublished data).

Stridsberg (1985, fig. 25B) illustrated the colour pattern in *Octameroceras rimosum* (Barrande, 1865) from Ludlow of Gotland. Distinct colour bands follow the growth lines and the longitudinal bands are not present. However, an interesting anomaly of colour pattern is visible on the dorsal (convex) side of the slightly endogastrically curved shell of *O. rimosum*. In a specimen illustrated by Stridsberg (1985, fig. 25B, RM Mo 56302), several transversal colour bands on the dorsal side of the phragmocone are disrupted (Fig. 7B). The colour pattern in this part of the shell consists of discontinuous longitudinal bands, similar to Bohemian *Hexameroceras panderi* (Fig. 7C–E).

Variability of colour pattern in nautiloids

Data concerning colour patterns in Tarphycerida, except for *Peismoceras* mentioned above, are so scarce that tracing the variation in colour patterns between individual genera is impossible. Nevertheless, narrow zigzag colour bands occurring in *Peismoceras* are known in some other nautiloids (oncocerids and discosorids) as well as in orthocerids (*e.g.* Foerste 1930, Turek & Manda 2010). The oldest known colouration in the Middle Ordovician nautiloid *Hoedstromoceras* Foerste, 1930 of uncertain position (Foerste 1930) has a similar character.

Three specimens of *Pentameroceras mirum* (Fig. 8) show similar colour patterns characterised by chevron bands. Nevertheless, there are distinct differences in their arrangement. A specimen from Mannagärda shows narrow pigmented bands; in contrast, two specimens from Hörsne kanal exhibit broad pigmented bands separated by narrow, unpigmented zones. It is a remarkable variability in colouration, but the type of the pattern is the same. It is hard to identify what might have influenced this variability. The differences in the environment may be one of the explanations. *Pentameroceras* with narrow pigmented bands comes from the Mannagärda locality which is situated on a shallow platform, while *Pentameroceras* from the Hörsne kanal locality inhabited the distal platform margin. The correlation between depth (*i.e.* off-inshore facies) and intensity of pigmentation needs to be checked in other nautiloids.

A similar colour pattern as has been observed in *Pentameroceras* is known in some other breviconic rizosceratids from the Silurian of Bohemia, especially *Cyrtoceras parvulum* Barrande, 1866 having broad, pigmented chevron bands (Barrande 1865–1877, Ruedemann 1921, Foerste 1930, Teichert 1964). Rizosceratidae and Trimeroceratidae are closely related families comprising short breviconic (straight or slightly curved) shells with thin ventral or sub-ventral empty siphuncle, but in the Trimeroceratidae the aperture is contracted (Sweet 1964, Stridsberg 1985). There is also striking similarity in the ontogenetic development of colour pattern. *Cyrtoceras parvulum* and *Pentameroceras mirum* from Hörsne kanal shared broad, pigmented bands separated by narrow, unpigmented (light) zones. The first unpigmented zone in the apical part of the shell is straight, others zones pass rapidly in chevron-like zones, in which their width and amplitude increases. Early shells of *Nautilus* exhibits coloration quite similar to latter growth stages, even before hatching time (see Stenzel 1964, fig. 64).

Hexameroceras and *Octameroceras* (Fig. 7) are closely related genera, as noted already by Stridsberg (1985), and they differ in the shape of contracted aperture in fully-grown specimens. Sweet (1964) even considered both genera congeneric. *Hexameroceras* from Bohemia exhibits a reticulate pattern consisting of a combination of narrow, transversal and longitudinal bands. *Octameroceras* from Gotland shows colour bands running parallel with growth lines. Nevertheless, on the ventral side is a zone in which narrow, longitudinal bands (as in *Hexameroceras*) are present. A similar pattern has been locally observed in present day *Nautilus pompilius*, in which similar anomalies appear just after repairing shell damage. This anomaly further confirms natural condition of colouration in *Octameroceras* from Gotland.

By analysing these cases, we can conclude that there existed remarkable variability in colour pattern in some early Palaeozoic nautiloids; other clear evidence of polymorphism, besides *Phragmoceras*, in species-genera level have not been found.

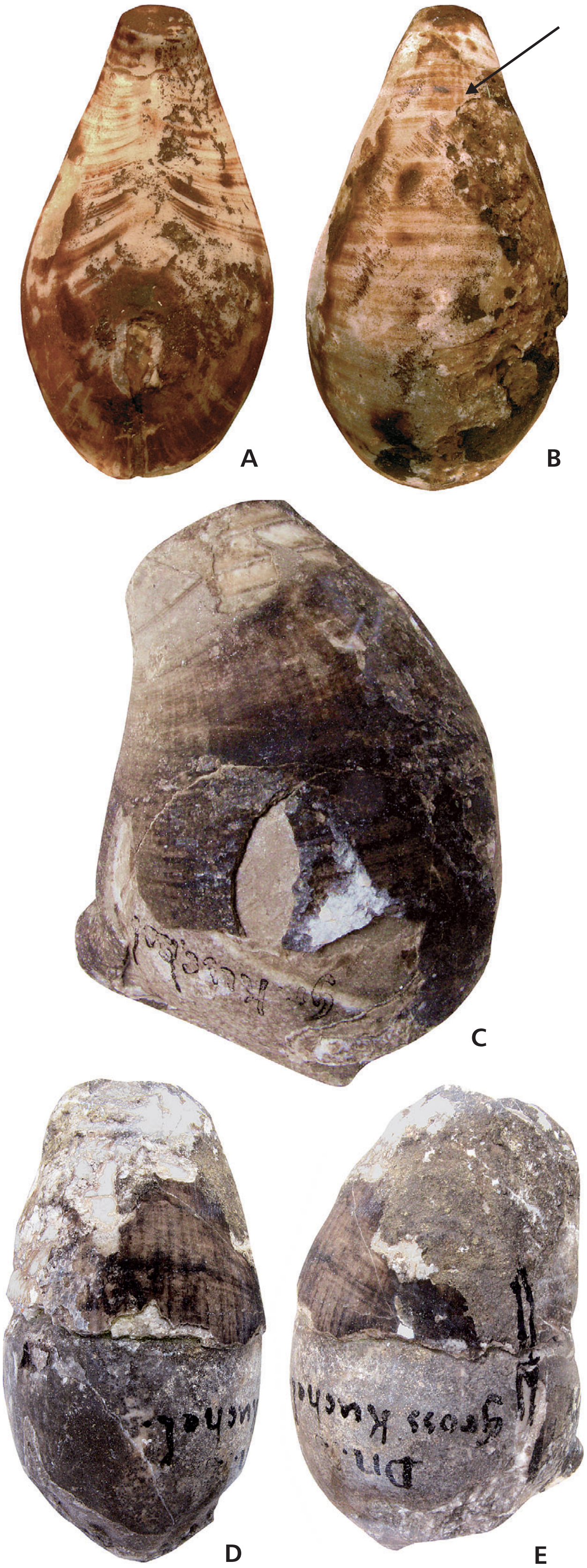

Figure 7. Colour pattern in the Silurian nautiloids of the family Hemiphragmoceratidae (Oncocerida). • A, B – *Octameroceras rimosum* (Barrande, 1865), RM Mo 56302, late Ludlow, locality Mannagärda, Gotland, ventral (A) and dorsal (B) views, × 2. • C–E –*Hexameroceras panderi* (Barrande, 1865), Ludlow, latest Ludfordian, locality Velká Chuchle, Bohemia; C, NM L 21205; specimen illustrated by J. Barrande (1870, pl. 429, fig. 16), lateral view, × 1; D, E – NM L 21306; specimen illustrated by J. Barrande (1870, pl. 429, figs 19, 20), Bohemia, dorsal (D) and lateral (E) views, × 0.7.

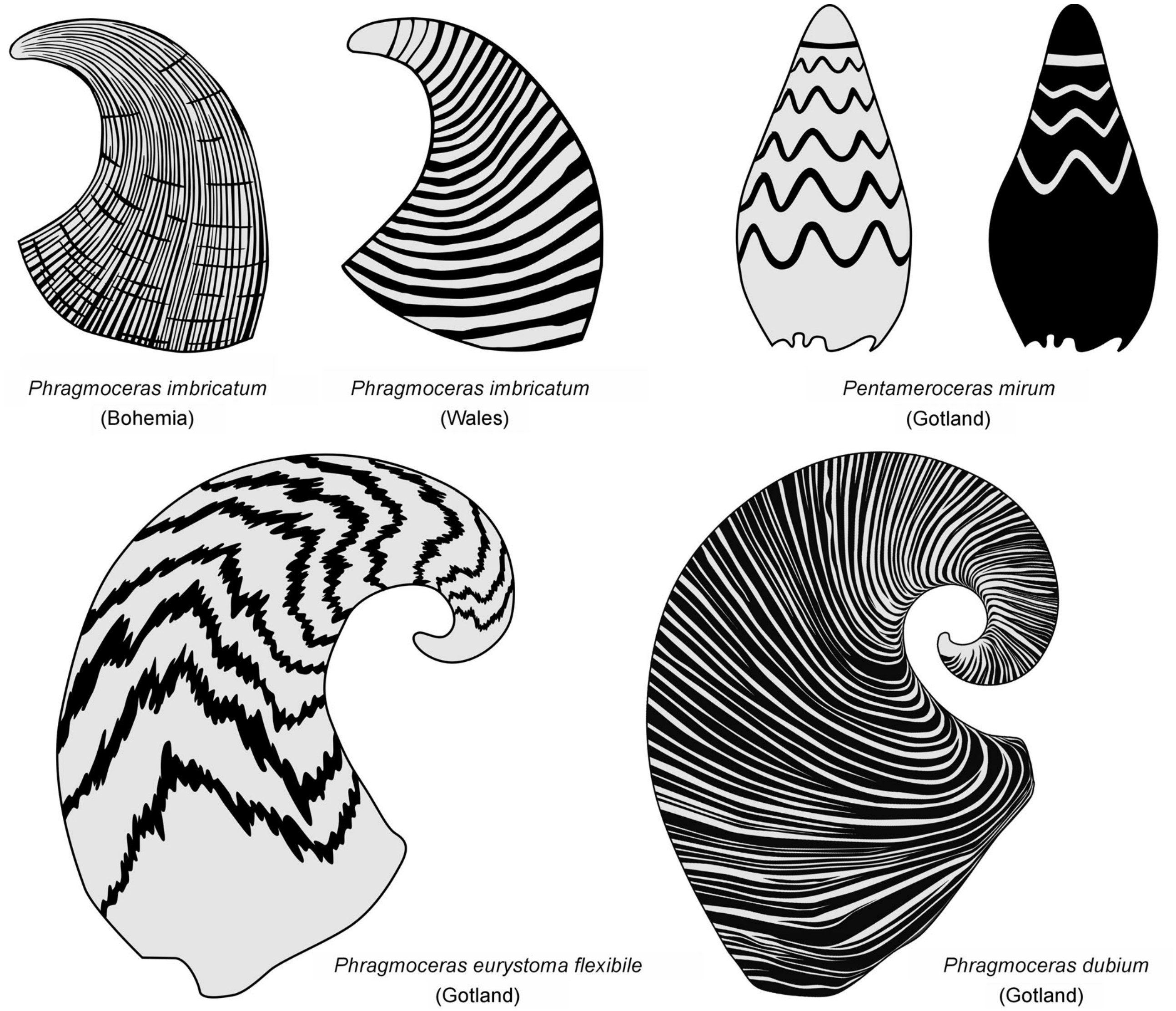

Figure 8. Schematic reconstruction of coloured shells of *Phragmoceras* (*Phragmoceras imbricatum* Barrande, 1865, *Phragmoceras eurystoma flexibile* Hedström, 1917, *Phragmoceras dubium* Hedström, 1917) and *Pentameroceras mirum* (Barrande, 1865). Not in scale.

Discussion

Ward *et al.* (1977) briefly described a variety of colour patterns in *Nautilus pompilius* and *N. repertus*. They mentioned two types of colour pattern in these species – a group showing brown stripes extending from the venter to umbilicus (typical for *N. pompilius*) and another group showing a brown patch on the umbilicus and strips extending from the venter to the middle of the lateral sides – a pattern characteristic for *N. repertus.* They also found a few transitional patterns between both variants. They have not found any correlation of these patterns with sex or depth. Despite this fact, shell colouration has been used as species or subspecies-distinctive feature (Habe & Okutani 1988, Saunders 1987). The general character of colour patterns in *Nautilus* species, however, is the same – transversal bands ventrally and ventrolaterally concordant with growth lines, sometimes with pairs of bands fused to form broader bands. Laterally, bands are sometimes bifurcating, running obliquely to growth lines. Two known species of *Allonautilus* exhibit ventrolaterally largely non-bifurcating colour bands coalescing across the venter, disappearing on the shoulder (Ward & Saunders 1997). The common feature of all fully mature specimens of living nautilids is white body chamber except the area near the umbilicus (*e.g.* Ward 1987).

Despite the fact that patterns of shell colour display a large diversity in Palaeozoic nautiloids and orthoceratoids, none of them show a colour pattern identical with the pattern characterising Recent *Nautilus* or *Allonautilus* (see Kobluk & Mapes 1989). Functions of colour pattern in fossil invertebrates have been widely discussed (see the references in Mapes & Davis 1996, Mapes & Schneck 1987). These authors summarized opinions concerning potential function of colour patterns. The shell colouration can be related to metabolism, vision, shell strength, light screening, thermoregulation or alternatively, according to Bauchau (2001) may be associated with the regulation of the growth of the shell to achieve developmental stability. As in Recent *Nautilus* (see Stenzel 1964, Cowen *et al.* 1973, Westermann 1998), colour patterns in fossil nautiloids disrupted the outline of the animal and served as a camouflage and thus as protection against predators. Such a function also seems to be most probable for Silurian *Phragmoceras*. Reliable explanation of remarkable colour polymorphism in *Phragmoceras* is, however, difficult. The number of specimens with preserved colour pattern is still very low. Precise data dealing with occurrence and stratigraphic level of British and some Swedish specimens are not available in necessary detail.

Colour pattern polymorphism in *Phragmoceras* can be connected with the temporary isolation of small populations, differences in latitude reflected in temperature of water, and perhaps depth and lighting of the inhabited environment. Despite some discrepancies in autecological interpretation of *Phragmoceras* among cephalopod students, all phragmoceratid species are morphologically very similar and consequently they probably have similar modes of life. However, *Phragmoceras* occurs in different facies and thus its adaptive potential was relatively high.

What really triggered colour polymorphism in *Phragmoceras*? Possible causes are given below. All other known cephalopods which possessing the same colour pattern as *Phragmoceras* and co-occurring with *Phragmoceras* are considered in discussion below.

Colour pattern *versus* depth inhabited

Depth inhabited may be an important agent of colour pattern development. It is important to emphasize that no colour polymorphism at the species-genus level has been found in one locality. All Silurian nautiloids inhabited relatively shallow water environment, not exceeding 150–200 m (Westermann 1998). Table 1 shows the distribution of colour pattern when compared to the depth zone. Shallow and deeper water settings are distinguished based on facies; shallow means light coloured limestones, grain-packstones, with highly diversified benthos and very rare pelagic elements; deeper facies comprise grey limestones, mostly wackestones, containing more pelagic elements and moderately diversified benthos.

It appears that only two colour patterns may be connected with depth zone: transversal-longitudinal narrow bands and bands parallel with growth lines. It is interesting that both patterns duplicate each other in phyletic lines. *Phragmoceras imbricatum* and *Hexameroceras mirum* from Bohemia shows transversal-longitudinal narrow bands. *Phragmoceras dubium* and *Ocameroceras sinuosum* and *O. rimosum* (*Octameroceras* is close related with *Hexameroceras*) from the Managarde locality exhibit bands parallel with growth lines.

Table 1. Colour pattern correlation with palaeogeographical setting and water depth at Silurian *Phragmoceras* and other nautiloids.

	Temperate	Tropical	
Colour pattern	Bohemia	England	Gotland
Phragmoceras			
Bands sub-parallel with growth lines	0	shallow	0
Bands parallel with growth lines	0	0	shallow
Transversal-longitudinal narrow bands	deeper	0	0
Zig-zags	0	0	deeper
Silurian nautiloids in generally			
Bands sub-parallel with growth lines	shallow-deeper	shallow	0
Bands parallel with growth lines	0	0	shallow
Transversal-longitudinal narrow bands	deeper	0	0
Zig-zags	shallow-deeper	0	deeper
Longitudinal bands	shallow-deeper	0	0
Undulating lines	shallow-deeper	0	0
Chevron pattern	shallow-deeper	0	shallow-deeper

Another probably depth related feature is represented by the ratio between pigmented (darker) and unpigmented (lighter) zones. Rather darker coloured shells occur in deeper water settings, it also seems valid in *Phragmoceras*. An interesting example is *Pentameroceras*, described above. Specimens from shallow water settings shows narrow coloured bands while specimens from deeper water mudstones exhibit broad pigmented bands, however, the colour pattern is the same (Fig. 9). It means that not only colour pattern polymorphism, but also proportion between parts of the pattern may the change visual characters of the shell.

Balinski (2010) summarised that marine invertebrates with colour-patterned shells essentially inhabit shallow water depths not exceeding 200 m. It represents an important fact in the reconstruction of depositional environment and palaecology because there is discussion about the bathymetric condition of some ancient biofacies. Coloured nautiloids from the Silurian cephalopod limestone biofacies in Bohemia thus may indicate a lower depth limit for this facies (see discussion in Miller & Furnish 1937 and Ferretti & Kříž 1995).

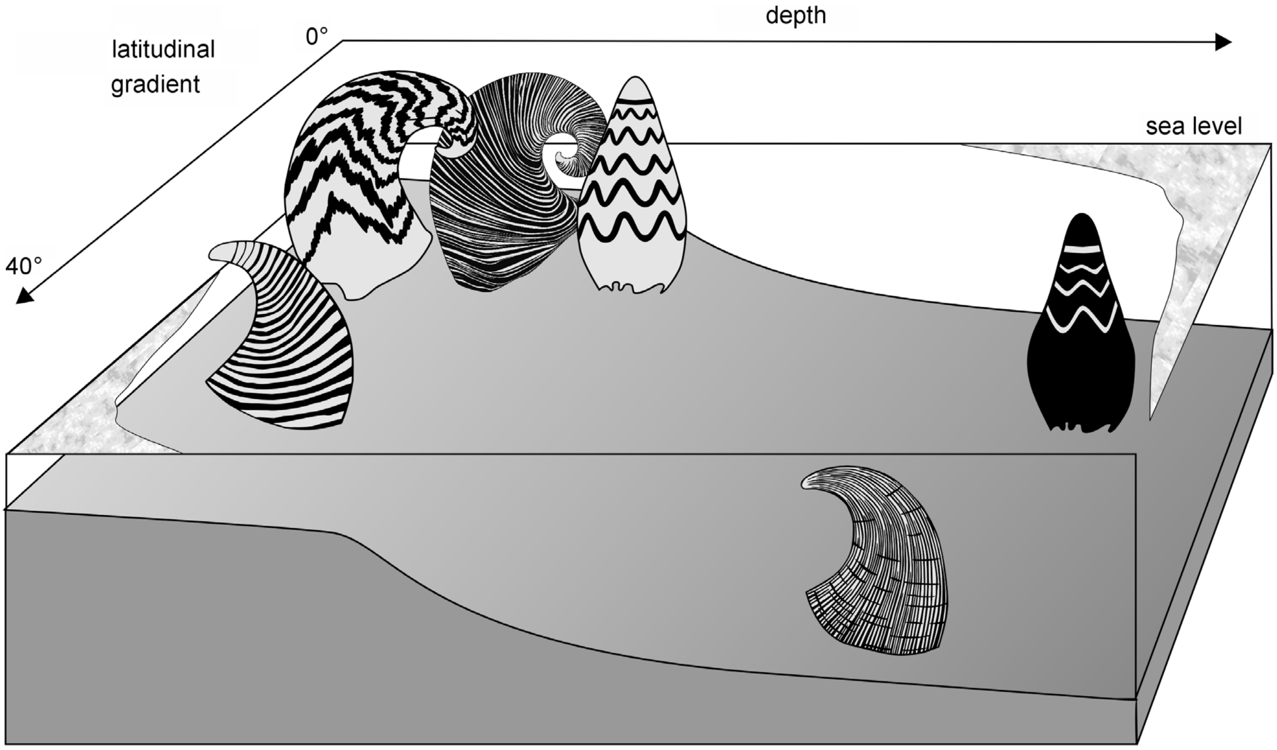

Figure 9. Colour pattern in the Silurian nautiloids *Phragmoceras* and *Pentameroceras* in relation to the depth and latitudinal position. Nautiloids inhabiting shallow water settings display rather lighter coloured shells in comparison with those that inhabited deeper water settings.

Colour pattern as a morphotype-specific feature?

The link between morphotype and colour pattern is still poorly understood, but a correlation between them sounds reasonable if the shell colouration functioned as a camouflage in nautiloids. Convergences in morphotype are common in Palaeozoic nautiloids (*e.g.* Manda & Turek 2009a) and may coincide with convergence in colour patterns (Manda & Turek 2009b). All *Phragmoceras* species shared similar shells. Some differences in shell flexure and shape of aperture probably affected the mode of life only slightly (Manda 2007, 2008; Manda & Frýda 2010). It suggests that in this case the colour pattern polymorphism is not related to morphotype and shell shape.

Colour pattern polymorphism as anti-predatory feature?

Shell shape and sculpture play an important role in buoyancy control and swimming quality (velocity, drag). Sculpture serves also a protective function against predators (Vermeij 1987). The colour pattern may be an analogous important agent in camouflage in both predator and prey (Kobluk & Mapes 1989, Cowen *et al.* 1973). Ordovician and Devonian cephalopods with preserved colour pattern are very rare. Consequently, evaluation of the possible trends in colour pattern evolution is still impossible, although remains as a promising task for future study, *e.g.*, of colour polymorphism in relation to diversity of predators. Nevertheless, all known types of colour patterns appeared at least by Silurian time, *i.e.* before the radiation of crushing predators in the Devonian (Signor & Brett 1984).

Fabrication noise, exaptation and shell coloration

Gould & Lewontin (1979) suggested that not all morphological features need an adaptive explanation. Many modern molluscs exhibits complicated colour patterns, although shell colouration is not visible during the life of an animal due to infaunal burrowing or covering of the shell by algae or epifauna. However, in cephalopods such as *Nautilus*, shell colouration is visible during life and thus influences the life of the animal. It is possible, that primary deposition of pigments in the shell served a different function (*e.g.* metabolic waste), and thus, the protective function of colouration represents in fact exaptation.

Boettiger *et al.* (2009) suggested that colour patterns in aquatic molluscs are a neurosecretory phenomenon and connected colour pattern with a neural model. They concluded that similar species could exhibit significantly different patterns, which means that the pattern differences cannot be the result of dramatic anatomical differences. According to Boettinger *et al.* (2009), pigmentation pattern may be change as a result of environmental disruptions. Shell colouration in *Phragmoceras* supports this explanation. However, it seems that specimens of species from populations inhabiting similar environment exhibit similar shell colouration. It supports assumption that the colour pattern functioned as camouflage in nautiloids, and thus, may be under selective control. Boettiger *et al.* (2009) also pointed out that colour patterns commonly degenerated during shell growth into a uniform pattern. It is not true in nautiloids, the pattern is archived during the entire life and even the apertural region of the shell may be unpigmented in fully-grown shells. It further supports the view that shell colouration functioned as an exaptation feature.

Evaluating the colour pattern polymporphism it should be taken in account that the effect of screening of a longitudinally banded shell and a shell with a combination of longitudinal and transversal bands would be probably the same in the photic zone as the effect of a transversally coloured shell. Nevertheless, the quality of vision of Silurian predators is unknown, future experiments with present day *Nautilus* may help there.

Shell coloration as a taxa specific feature?

In general, there exists correlation between colour pattern character and taxon in molluscs. Colour pattern in living gastropods is commonly species-specific and helps very much in specific recognition (Cox 1960). Concerning recent bivalves, Cox & Nuttall *in* Cox (1969) stated that certain types of colour patterns, or even the absence of coloration can be characteristic of particular families and genera, and may be extremely constant within a species. The latter authors, however, mentioned that many exceptions exist. In contrast with extant nautilids, some Recent molluscs, especially gastropods and bivalves exhibit remarkable polymorphism in colour pattern, expressed in quite different types of coloration (see Clarke 1978, Hoagland 1977, Reimchen 1978, Cook 1998). Within one species of some bivalves and gastropods there are present, *e.g.*, spots of many shapes and sizes, zigzag bands, and spiral stripes. Striking intrageneric and intraspecific colour pattern polymorphism ascertained in the Silurian discosorid *Phragmoceras* is reported in nautiloids for the first time. The cause of colour polymorphism may be an effect of taxonomic grouping. The specimens of *Phragmoceras imbricatum* would not really belong to the same species, and *Phragmoceras* including more than sixty species should be a cumulative genus. However, there is general agreement shared by many authors against this explanation.

Conclusions

Colour patterns are frequently supposed to be a species- or even genus-specific/diagnostic feature in ancient nautiloids. Present day *Nautilus* and *Allonautilus* are not exceptions (*e.g.* Foerste 1930, Kobluk & Mapes 1989, Turek 2009). However, colour pattern polymorphism has been documented in gastropods and bivalve molluscs. The first incontrovertible evidence for polymorphism in nautiloids is in Silurian *Phragmoceras.* Four different types of colour patterns on shells reflecting different mode of deposition of pigment by mantle margin have been found in this genus; two of these types even occur in a single species *Phragmoceras imbricatum.*

It is assumed that all species of *Phragmoceras* inhabited the photic zone and had a similar mode of life. Whether they were nectobenthic or rather active swimmers is not quite clear, but their body chamber, owing to the position of the centre of gravity of the animal, had to be situated almost vertically (Barskov 1989, Westermann 1998, Holland & Stridsberg 2004, Manda 2008). Shells of all specimens of *Phragmoceras* with preserved colour pattern are very similar in shell morphology; but they were found in different limestone facies and palaeogeographic position. No colour polymorphism was observed in shells from one locality. The primary function of the pigmentation pattern, however, is still subject to discussion (references see in Mapes & Davis 1986, Bauchau 2001). If it served as a form of crypsis, *e.g.* an effective strategy to avoid predation, then quite different types of colouration in *Phragmoceras* may indicate different solutions to this problem. Colour polymorphism may be related to depth zone, rather than latitudinal position. Differences in colouration probably also reflect distribution pattern of phragmoceratids with isolated local populations through time.

No other example of colour polymorphism in species-genus level was found, although distinct variability in colour patterns has been found in Silurian nautiloids *Pentameroceras* and *Peismoceras*. The relation between primarily pigmented and unpigmented areas occupying the surface of the shell varies among species and it may be influenced by depth inhabited (visually darker versus lighter shell). The partly unpigmented part of the body chamber – a feature clearly characterising Recent *Nautilus* or *Allonautilus*, is documented for the first time in fossil nautiloids in *Phragmoceras dubium erystoma* and *Pentameroceras*.

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The graptolite, conodont and sedimentary record through the late Ludlow Kozlowskii Event (Silurian) in the shale-dominated succession of Bohemia

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Abstract – The shale-dominated hemipelagic succession exposed in the southwestern part of the Prague Synform preserves the most complete Ludfordian graptolite record so far encountered from peri-Gondwanan Europe. Four graptolite biozones – the *Neocucullograptus inexpectatus*, *Nc. kozlowskii*, *Pseudomonoclimacis latilobus-Slovinograptus balticus* and *Pristiograptus fragmentalis* biozones – are recognised in the middle and late Ludfordian, between the *B. tenuis* Biozone and the base of the Přídolí Series. Conodont occurrences are restricted to scattered limestone beds, but enable tentative integration of the graptolite and conodont biozonal schemes. Particular attention was paid to faunal and sedimentary changes and the carbon isotope record across the middle Ludfordian Kozlowskii extinction Event. The Kozlowskii Event caused the almost simultaneous extinction of graptolites with ventrally curved rhabdosomes. The genera *Bohemograptus*, *Polonograptus* and *Neocucullograptus*, along with *Pseudomonoclimacis dalejensis*, disappeared from the fossil record. The off-shore conodont fauna recorded in the section was not strongly affected and similarly the pelagic orthocerids and nektonic *Ceratiocaris* passed unaffected through the extinction interval. The abundant and widespread pelagic myodocopid ostracod *Entomis*, however, became extinct. The late Ludfordian graptolite recovery gave origin to a novel fauna of Přídolí type as taxa that emerged or just reappeared above the Kozlowskii crisis. In Všeradice and elsewhere in the Prague Synform, the recovery, manifested by the appearance of *Pseudomonoclimacis latilobus* and *Slovinograptus balticus*, closely postdates the end of the isotope excursion but predates the FA of the conodont index *„Ozarkodina"snajdri*. Here the graptolite recovery was delayed relative to the recovery of the benthic fauna. A canalized intraformational limestone conglomerate corresponds with a gap in the sedimentary record above the Kozlowskii extinction and just below the graptolite recovery. The benthic faunas from the conglomerate matrix and pebbles permit correlation with the shallower part of the basin indicating a distinct fall in sea-level. The present data demonstrate the coincidence of the graptolite crisis with benthic faunal change and eustatic fall in sea-level manifested by facies change and the carbon isotope excursion. *Polonograptus chlupaci* sp. nov., from the *Nc. kozlowskii* Biozone, is described and several other graptolite taxa are redescribed.

Keywords: graptolites, conodonts, Silurian, biostratigraphy, Kozlowskii Event, extinction, peri-Gondwana.

1. Introduction

The Silurian was long considered to have been a period with a relatively stable greenhouse climate, devoid of significant extinction events (see Holland, 1991 and Calner, 2008 for summary). This view of an „idyllic Silurian" rapidly changed in the 1990s. Prominent extinction events were described among graptolites (Jaeger, 1991; Koren`, 1993; Urbanek, 1993; Loydell, 1994; Štorch, 1995*a, b*; Melchin, Koren` & Štorch 1998) and conodonts (Jeppsson, 1990, 1998; Jeppsson & Aldridge, 2000).

Later studies on carbon isotopes revealed that some extinctions correlate approximately with positive carbon isotope excursions and may have resulted from extraordinary perturbations in the carbon-ocean cycle (Munnecke *et al*. 2003; Lehnert *et al.* 2007*a*; Calner, 2008). In addition, oxygen isotopes suggest dramatic fluctuations in water temperature during the Silurian indicating recurrent periods with an ice-house climate (Lehnert *et al*. 2007*b*; Calner, 2008; Eriksson & Calner, 2008). Various climatic and oceanographic models have been proposed to explain extinctions and changes in chemistry in the Silurian oceans (Jeppsson, 1990; Bickert *et al.* 1997; Samtleben, Munnecke & Bickert, 2000). Nevertheless, there is as yet no generally accepted explanation (see discussion in Loydell, Jeppsson & Aldridge 2001 and Loydell, 2007). Particular debates have been devoted to high-resolution correlation. The correlation of graptolite extinctions in deeper water shale facies with those of conodonts in shallow water limestone facies, combined with correlation between different palaeogeographical settings, i.e. high and lower latitudes, is a difficult exercise. The timing, extent and selectivity of extinction in benthic groups are still poorly known (Talent *et al.* 1993; Kříž, 1998, 1999a, 2010*a*, *b*; Manda & Kříž, 2006; Eriksson *et al.* 2009). The question has been posed (Loydell, Jeppsson & Aldridge. 2001; Manda & Kříž, 2006; Loydell, 2007; Manda & Frýda, 2010): are extinctions in graptolites, conodonts and benthos coincident or do they represent separate events? Loydell (2007) presents evidence to indicate that the Wenlock graptolite and conodont extinction events are not coincident, but for some other events so far no adequate evidence has been provided.

The middle Ludfordian change in marine faunas is an example of such an extinction event. The Kozlowskii Event is considered to be one of the most significant graptolite extinction events, and has been recorded from Baltica, central-Asian terranes and peri-Gondwanan Bohemia (Koren, 1993; Urbanek, 1993; Štorch, 1995*a*, *b*; Manda & Kříž, 2007). A conodont extinction event, known as the Lau Event in Baltica, Laurentia and East Gondwana (Australia), is roughly coincident with the Kozlowskii Event, but detailed comparison is lacking (Jeppsson, 1990; Eriksson & Calner, 2008). A positive carbon isotope excursion, the largest in the Phanerozoic, has been identified close to both the Lau conodont extinction Event (Samtleben, Munnecke & Bickert, 2000; Calner & Eriksson, 2006; Stricanne, Munnecke & Pross, 2006; Kaljo *et al.* 2007) and the Kozlowskii graptolite extinction (Lehnert *et al.* 2007*a*). In Bohemia, the Kozlowskii Event is associated with prominent extinctions among benthic faunas (Manda & Kříž, 2006). Oxygen isotopes suggest progresive cooling accompanying an Icehouse period around the time of the extinction (for details see Lehnert *et al.* 2007*b*).

The Prague Synform (i.e. Barrandian area) of central Bohemia has long been considered a classic area for Silurian graptolite biostratigraphy and a reference area for correlation of the Early Palaeozoic of northwestern peri-Gondwana. Many graptolite biozones and index species were first distinguished and described from this area. The Llandovery, Wenlock and early Ludlow sedimentary rock sequence, composed largely of graptolite-bearing shales, provides an ideal opportunity for detailed study of the graptolite succession (Bouček, 1953; Přibyl, 1983; Štorch, 1994, 2006 and further references therein). Similarly, the Přídolí succession, composed of limestones interbedded with shales, has yielded graptolite assemblages permitting its division based upon graptolites (Přibyl, 1940; Kříž *et al.* 1986). In the limestone-dominated upper Ludlow strata of the Prague Synform, however, the graptolite biostratigraphy remained of rather poor resolution. The graptolite biozones established by Bouček (1936) and revised by Přibyl (1983) were defined inadequately and, in particular, there were no published descriptions of sections that had been measured and sampled in detail. Comparison between graptolite taxa based upon Bohemian type material preserved as internal moulds in skeletal limestones and specimens flattened in shales was inadequate and resulted in some confusion in stratigraphic correlation. Some of these graptolite taxa, described by Bouček (1931, 1936) and Přibyl (1943, 1983), are in need of revision.

The most detailed late Ludlow, Ludfordian, graptolite biozonal scheme was elaborated in Poland (Urbanek & Teller, 1997 and references therein) and partly applied in other parts of the Eastern European Platform (such as Podolia in Ukraine, Belarus, Latvia). Koren` and Sujarkova (1997, 2004) introduced a different biozonation in Central Asia. The graptolites collected from Kosov Quarry near Beroun (Štorch, 1995*a*) and from the present Všeradice Section enable correlation with both the Eastern European Platform and Central Asia.

In this paper, the shale-dominated succession comprising the middle Ludfordian Kozlowskii Event and post-extinction recovery is described for the first time both from Bohemia and peri-

Gondwana. The Všeradice section was exposed by trenches and measured and sampled bed by bed for graptolites. Isolated limestone beds were sampled for conodonts. The sedimentary succession was examined in detail and the carbon isotope record analysed in order to evaluate the depositional environment of the graptolite-bearing rocks and to recognize possible gaps in sedimentation. Scattered shelly faunas recovered from shales and some limestone beds enabled correlation between abundant benthic faunas of the limestone-dominated facies widespread in other Bohemian sections and the widely applicable graptolite biozones recognized herein.

2. Všeradice Section

In the Prague Synform, the middle and upper Ludfordian succession usually comprises carbonate rocks with poorly preserved and rare graptolites (Bouček, 1936; Kříž, 1992). The relatively deeper water, oxygen depleted hemipelagic shale facies, potentially rich in diverse graptolites, is restricted to the south-western closure and south-eastern flank of the Prague synform. There are only a few poorly exposed sections in the shale-dominated area, usually insufficient for detailed investigations (Horný, 1955, 1960). The single exception is the section along the field track near Všeradice village. This area is regarded as the deepest preserved part of the basin infill (Horný, 1960; Kříž, 1991, 1992).

2.a. Location and previous research

The Všeradice section is located on a gentle, south-facing slope along a field track running NNW from the Bykoš-Všeradice road, NW from Všeradice Village (Fig. 1). Rather discontinuous exposures and subcrops may be traced along the field track over a length of about 200 m. Close to the summit; bedrock becomes buried under thick drift deposits. The section represents the shale-dominated, relatively offshore facies of the Silurian succession in the Prague Synform, beginning with middle Wenlock and terminating with the lower part of Přídolí Series. Sedimentation here was little influenced by syn-sedimentary basalt volcanic activity, which left a significant record in most other Silurian sections of Bohemia (see e.g. Kříž *in* Chlupáč *et al.* 1998 for instance).

The first note on this important section was published by Horný (1960). Much later, Kříž (1992) presented a more detailed, but still incomplete log. His section started from marly shales high in the Homerian *Cyrtograptus lundgreni* Biozone and terminated with the middle Ludfordian intraformational conglomerate (bed no. 13 of this paper). Shale beds with the ostracod *Entomis migrans* and some bivalves, encountered just below the conglomerate, Kříž (1992) referred to the "*B. bohemicus tenuis* Interzone". Kříž *et al.* (1993) and later Kozłowska, Lenz & Štorch (2001) examined latest Wenlock (late Homerian) part of the section with particular emphasis on the Lundgreni Event and post extinction recovery. Piras (2006, and PhD Thesis, Universita degli Studi di Modena e Reggio Emilia, 2006) studied the lower Gorstian beds comprising the *N. nilssoni* and *L. progenitor* graptolite biozones. Budil, Collette & Manda (2010) studied the phyllocarid fauna from early Ludfordian.

In late 2008 and early 2009, excavations were conducted to expose the supposedly graptolite-rich, shale-dominated section through the upper Ludlow strata. Our data came from up to 2.5 m deep trenches VA and VB, excavated on both sides of the field track (Fig. 1). Trench VA and the upper part of trench VB exposed a *ca* 24 m thick middle and upper Ludfordian succession up to the base of the Přídolí Series.

2.b. Material and Methods

The shale-dominated Ludfordian was collected for graptolites in a similar way as the late Homerian interval studied by Kozłowska-Dawidziuk, Lenz & Štorch (2001). Isolated limestone beds and tuffitic intercalations enabled division of the 24 m thick succession into 37 arbitrary units of different stratigraphic thickness (beds 1–37 in ascending order, see Fig. 2). Shaly beds were further subdivided into 10–60 cm thick sub-units. Each sub-unit was sampled bed by bed down the section and all of its fossil samples were placed in the same sample bag(s). The majority of these sampling intervals were about 30 cm thick. Many intervals were rich in graptolites; some others were poor or barren. Every graptolite, at least tentatively determinable, was collected from the rock volume of about 0.03 m^3. The lower part of the section exposed by trench VB (see Fig. 2) lacks the arbitrary subdivision but fossils were collected in the same manner, in intervals (sub-units) of similar thickness. Only a few graptolites were found in the limestone and tuffitic beds.

The carbon isotope record of late Silurian carbonates coming from deeper water environments of the Prague Basin has never been studied, in contrast to the carbonates from more shallow environments (Lehnert *et al*. 2007*a*). The carbonates of the Všeradice section were sampled for determination of $\delta^{13}C_{carb}$ isotope evolution through the late Ludlow Kozlowskii Event. The isotopic composition of organic carbon from shales occurring between the carbonate beds was not studied due to the relatively high degree of weathering. The carbon isotope sampling of the Všeradice section (Fig. 2) started about 8.5 m below the late Ludlow Kozlowskii Event. The highest sample was collected from lowermost Přídoli beds (about 2 m above FA of *Neocolonograptus parultimus*). 15 samples were analysed for $\delta^{13}C$: 12 samples were taken from the Ludlow part of the section and 3 samples from the lowermost Přídolí. A few milligrams of rock powder (preferably micrite) were recovered with a dental drill from rock samples or polished slabs. Carbonate samples were decomposed in a vacuum by 100% phosphoric acid at a temperature of 25 degrees Celsius. The carbon and oxygen isotopic composition of the released CO_2 was measured with a Finnigan Mat 251 mass spectrometer. All values are reported in ‰ relative to V–PDB by assigning a $\delta^{13}C$ value of +1.95 ‰ and a $\delta^{18}O$ value of 2.20 ‰ to NSB 19. Accuracy and precision were controlled by replicate measurements of laboratory standards and were better than ±0.1‰ for both carbon and oxygen isotopes.

Conodont samples were collected from the majority of limestone beds and nodules uncovered in both trenches across the interval from Ludfordian to the lowermost Přídolí. A total of 28 samples of average weight between 3–5.5 kg was taken mostly from the entire thickness of each limestone bed (bulk samples). The rock was broken into approximately 5 cm large pieces and processed using standard acid techniques with 10–15 % acetic acid. Residues were washed through calibrated double sieves of 2.24 mm (upper) and 90 µm (lower) meshes. Wet residues were washed with acetone and dried. Dried, relatively voluminous residues (of up to 250 ml), with a prevalence of pyrite, goethite and complex silicates (e.g. nagashimalite, macfallite) were concentrated using the heavy liquids diiodomethane (density 3.3 g/cm^3) and tribrommethane. Conodonts were obtained from only 9 of the limestone beds; no conodonts were extracted from nodules. The conodont material was documented directly in aluminium cells using a Leica D160 digital camera and a Leica MZ7s stereomicroscope and SEM images of selected conodont elements (coated with gold) were made by using a Cameca SX100 electron microscope.

Graptolites are housed in the collection of Petr Štorch in the Czech Geological Survey. Non-graptolite macrofauna is deposited in collection of Štěpán Manda in the Czech Geological Survey (unnumbered specimens in locality collection, prefix SM Všeradice section). The conodont material is temporarily stored in the collection of Ladislav Slavík at the Institute of Geology, Academy of Sciences, Czech Republic and will be later deposited as a part of a larger collection in the National Museum, Prague.

2.c. Sedimentary succession, benthic fauna and depositional environment

The lower part of the section consists of light grey laminated calcareous shale (beds 1–10, *B. tenuis*–*Nc. kozlowskii* biozones). Graptolites and pelagic ostracods (*Entomis migrans* Barrande, *Bolbozoe bohemica* Barrande) are the most common faunal elements, but their abundance is strongly variable. Pelagic orthocerids (*Parakionoceras originale* Barrande, *Michelinoceras michelini* Barrande, *Kopaninoceras* sp., *Arionoceras* sp.) and the phyllocarid *Ceratiocaris* sp. occur only in some beds. Flattened smooth atrypids are present occasionally, but on some bedding planes they occur abundantly. Bivalves are rather rare: *Cardiola docens* Barrande, *C*. aff. *docens* Barrande, *C*. cf. *pectinata* Barrande, *C*. aff. *foma* Barrande, *Butovicela migrans* (Barrande) and *Tenka aspirans* (Barrande). Shale bed no. 3 yielded the trilobite *Cromus beaumonti* Barrande. Up to 20 cm thick beds of grey argillitic, usually laminated, mudstones occur throughout this part of the section. Limestones contain occasional graptolites and cephalopods, in one case graptolites were found to be oriented by currents and wrapped around a cephalopod shell lying obliquely to the bedding plane – a so-called "comet" (Ferretti & Kříž, 1995). Limestone nodules rich in pyrite, with a maximum diameter of 20 cm occur sporadically. Thin, 1–3 mm thick lenticular laminae of mudstone are common in the shales. Seven beds of yellow grey, upward fining tuffites, 5 to 25 cm thick, were found in this part of the section. Rare trilobite debris (*Otarion* sp. and unidentified taxa) was found in some tuffites. In addition, tuffitic bed no. 4 contains close to its base small rounded intraclasts of rusty cephalopod packstone with small cephalopod fragments (*Michelinoceras michelini*, *Pseudocycloceras* sp., *Kopaninoceras* sp., *Ophioceras simplex* Barrande), common disarticulated bivalves (*Cardiola docens*), and rare rhynchonellid brachiopods.

The shale-dominated sequence suggests an offshore hemipelagic environment. Some light coloured laminae contain brachiopods and bivalves, which indicates the occasional activity of weak bottom currents ventilating the otherwise anoxic conditions close to the sea bottom. Deposition of shales was interrupted by that of tuffite layers, that also include skeletal fragments derived from shallow water environments (e.g. intraclasts of cephalopod limestone, trilobite fragments).

The shale-dominated sequence ends with a thin bed of fine-grained mud-wackestone overlain by bioturbated tuffitic shale (bed nos 11 and 12), but no body fossils were found.

The section continues with a large lens, up to 160 cm thick, formed of inverse graded intraformational conglomerate (bed no. 13). The matrix consists of coarse, light grey crinoidal grainstone, which passes upward into fine-grained wackestone (Fig. 3). Crinoid ossicles are abraded only in the lower part. Brachiopods are usually disarticulated, but well preserved including fine growth structures in shells. *Atrypa evenida* Havlíček is the most common: from 126 collected shells, 72 are ventral valves, 53 are dorsal valves, and only one shell is articulated (for complete list of brachiopods see Kříž, 1992). Fragments of trilobites, *Ananaspis fecunda* (Barrande), proetids, odontopleurids, corals and gastropods are also present. Pebbles are usually rounded; their abundance and size (maximum diameter is about 25 cm) increase from the base of the bed upward. Pebbles include four lithological types that differ also in their fossil content: (1) Small rounded pebbles of dark-grey wackestone with cephalopods and the bivalve *Cheiopteria glabra* Goldfuss (which indicates a latest *Nc. kozlowskii* Biozone age; see Kříž, 1999a; Manda & Kříž, 2006); (2) Rounded pebbles of brachiopod-trilobite wackestone with the trilobite *Ananaspis fecunda*; (3) Small angular intraclasts of rusty fine-grained packstone with ostracods, the brachiopod *Atrypa* sp. and trilobite *A. fecunda*; (4) Intraclasts that represent probably exhumed limestone nodules with *Entomis migrans* (i.e. *S. linearis*-*Nc. kozlowskii* Zone in age; see Kříž, 1999a). The conglomerates are overlain by an up to 10 cm thick bed of dark-grey mudstone with some cracks on the upper bedding plane.

The intraformational conglomerate probably represents a canalised debris-flow because it forms large lenses in the shale and shows clear inverse grading (e.g. Einsele, 2000, p. 214). The fauna preserved in the matrix of the conglomerate suggests transport from a nearby shallow water locality.

The overlying sedimentary succession comprises dark-grey mudstones (particularly nodular) intercalated with dark-grey laminated shale (bed nos 14–20, *Ps. latilobus*-*Sl. balticus* Biozone). The shale contains common graptolites and rare cephalopods (e.g. *Parakionoceras originale, Michelinoceras michelini, Arionoceras* sp.), phyllocarids (*Ceratiocaris* sp.), and a few benthic remains including scolecodonts, brachiopods (*Plectodonta* sp.), smooth ostracods and juvenile gastropods. Higher up a distinct tuffitic bed is present. The tuffite is locally eroded and filled with cross-stratified, rusty, upward fining grainstone with cohesive shale intraclasts (bed nos 21–22). The grainstone contains crinoids, trilobites, corals, ostracods, cephalopods and other fossils (see Table 1). This limestone is overlain by a thin bed of tuffite (bed no. 23) and, higher up, shale (bed no. 24). The succeeding strata comprise a mudstone bed overlain by a tuffitic bed (bed nos 25–26).

The sequence above the intraformational conglomerates was deposited at the margin of a bathymetric high, as indicated by the shales with benthic fauna and limestone beds. The skeletal limestone filling the depressions in the tuffite probably represents storm event deposits with cross stratification, normal grading, and shale intraclasts (see Fig. 3). Brachiopods are usually disarticulated and large brachiopods and trilobites are broken into small fragments (Tab. 1). The brachiopod assemblage is dominated by the shallow water brachiopod *Kirkidium* sp. accompannied by the rather deeper water *Jarovathyris canaliculata* (see Havlíček & Štorch, 1990); this suggests mixing of two distinct depth-related communities during transport.

The upper part of the studied section (beds 27–43, *P. fragmentalis* and *Ne. parultimus*-*Ne. ultimus* biozones) is developed as calcareous shale and platy argillite mudstone, but the shale dominates. One thin bed (no. 36) of grey, upward fining crinoidal wackestone is present. It contains common, minute fragments of brachiopods (atrypids, orthids, leptaenids and strophomenids), trilobites (*Otarion* sp. and *Prionopeltis striata* Šnajdr) and disarticulated ostracods. Shale beds yielded graptolites and rare pelagic cephalopods. Bed no. 27 contains also pyritised shells of juvenile cephalopods and gastropods. A thin level with accumulations of the flattened atrypid *Lissatrypa* sp. was observed in mudstone bed no. 30.

This part of the succession was deposited during deepening, which corresponds with that interpreted in other coeval sections of the Prague Synform (Horný, 1955; Kříž *et al.* 1986; Kříž 1991; Manda & Kříž, 2006). The sparse or absent benthic fauna suggests usually anoxic conditions at bottom. Bed no. 36, of fine-grained skeletal limestone, probably reflects a storm event as indicated by its sharp base and upward fining. Rounded crinoid debris and small fragments of disarticulated atrypid brachiopods indicate a significant amount of transport.

2.d. Gaps in sedimentation and source area of conglomerates

The Všeradice Section is located in the Western Segment (Kříž, 1992) of the Prague Synform. This is characterised by off-shore hemipelagic sedimentation throughout the Silurian as indicated by the shale-dominated sequence ranging from the lowest Llandovery to the Ludlow (Horný, 1955, 1960). Common tuffite beds throughout the Ludlow succession indicate nearby volcanic activity and deposition of reworked volcaniclastic material. Tuffites in the upper *Ps. latilobus-Sl. balticus* Biozone are the youngest known manifestation of volcanic activity in the Silurian strata of the Prague Synform, although coeval basalt effusives are unknown. More limestones (wacke-mudstone and gravity deposits) appear in the middle and upper Ludfordian parts of the succession, which is consistent with basin-ward extension of shallow water sedimentation into the Western Segment of the Synform (Horný, 1955, 1960). This proliferation of carbonates is correlatable with the latest Ludlow lowstand well documented in coeval limestone sequences elsewhere in the Prague Synform (Horný, 1955; Kříž 1991, Kříž *in* Chlupáč *et al.* 1998; Manda & Kříž, 2006). Earlier lowstands (those in the late Wenlock and early Ludfordian) are not distinguishable in the sedimentary log in the Všeradice section and elsewhere in the Western Segment (Horný, 1955, 1960). Kříž (1991) suggested that intense subsidence occurred in this part of the basin in the Ludlow. However, a relatively thin sedimentary succession, including limestones in the latest Ludlow, probably indicates reduced accommodation space. Canalised debris-flow deposits indicate the appearance of nearby shallow water environments (although these are not preserved in the rock record) within the Western Segment, which was isolated from the main shallow platforms located farther to the North. Although corresponding with the lowstand recorded in coeval limestone strata, eustatic sea-level oscillation cannot explain fully the appearance of this local shallow water area, i.e. a small-scale carbonate domain surrounded by shale deposition. The submarine high was most probably associated with local, synsedimentary uplift. Sea-level drawdown, associated with the middle Ludfordian Kozlowskii and/or Lau Event initiated only a debris flow from the neighbouring submarine high. Slopes were probably relatively steep, as suggested by the exhumed limestone nodules with ostracods in the debris flow. These nodules (but no surrounding matrix) contain fine framboidal dolomite, which directly documents the early diagenetic origin of the dolomite.

The stratigraphically significant shelly fauna preserved in the limestone debris-flow (intraformational conglomerate), the lenticular cross section of the conglomerate body and the much reduced thickness of the post-Kozlowskii Ludfordian indicate prominent erosion and a gap in sedimentation in the Všeradice Section, when compared to coeval strata in the limestone-dominated sections of the Prague Synform.

The temporal and spatial extent of the gap connected with these canalised debris-flow deposits is evident from analysis of faunas in the matrix and pebbles (i.e. it spans the interval between the LA of *Nc. kozlowskii* until at least the FA of the index trilobite *A. fecunda*). However, allochthonous fauna from both intraclasts and matrix make correlation with coeval carbonate sequences of the Prague Synform possible (see discussion in correlation section).

2.e. Conodont fauna

The late Silurian conodont biozonation was developed by Walliser (1964), who included the conodont data from the Prague Synform into his first biozonal framework. Schönlaub (*in* Chlupáč, Kříž & Schönlaub, 1980 and *in* Kříž *et al.* 1986) furnished crucial conodont data from sections in the late Ludlow and Přídolí of the Prague Synform and demonstrated taxon ranges. Schönlaub *in* Kříž *et al.* (1986) made an extensive summary of conodont faunas obtained from samples from numerous sections and localities that were sampled and studied by him or by previous authors. He recognized a succession of Walliser's biozones for the Ludlow and Přídolí – *A. ploeckensis*, *P. siluricus*, *E. latialata*, "*Oz.*" *snajdri*, "*Oz.*" *crispa* and "*Oz.*" *eosteinhornensis*. The Ludlow part of this biozonation is in use without large changes; the “*Oz.*” *eosteinhornensis s.s.* and “*Oz.*” *detorta* biozones suggested for the Přídolí by Jeppsson (1988) are problematic or inapplicable (see discussions in Carls, Slavík & Valenzuela-Ríos, 2007).

The conodont faunas of the Všeradice Section (Fig. 4) are studied for the first time in this paper. The conodont sampling was successful only in one third of the samples, which yielded ca 350, mostly fragmented conodont elements. The conodont faunas are rather poor regarding taxonomic diversity and are of low abundance in general with the exception of the intraformational conglomerate (bed 13) and grainstone bed no. 22 where the numbers of conodont elements exceed 80. A relatively rich conodont sample was obtained from bed no. 28 with more than 70 conodont elements. The composition of conodont faunas in all samples is well-balanced and variable regarding the size of the elements; also the frequent presence of tiny, simple-cone elements suggests that assemblage composition was not strongly affected by hydrodynamic sorting of particles. The depositional characters of some carbonate layers (i.e. intraformational conglomerate, presence of intraclasts and grainstone fillings) described in the text above suggests the likelihood of stratigraphical mixing of conodont elements, but evidence for conodont redeposition was not found.

The preservation of conodonts in samples is good. Apart from long ranging simple cones (e.g., belodellids, *Panderodus*), the conodont material obtained enables recognition of the following conodont genera: *Delotaxis*, *Kockelella*, *Ozarkodina*, *Polygnathoides* and *Wurmiella*. Due to fragmentation, some taxonomic assignments are only to generic level, but several stratigraphically important taxa were recognized and enabled delimitation of the *P. siluricus*, “*Oz.*” *snajdri* and “*Oz*”. *crispa* conodont biozones in the middle–late Ludfordian (see Fig. 4). The stratigraphically lowest evidence for the *P. siluricus* Biozone is the presence of *Kockelella maenniki* Serpagli and Corradini in bed no. 2. This species, erected in Sardinia (Serpagli & Corradini, 1998, 1999*a*), is confined to the lower–middle part of the *P. siluricus* Biozone. Representatives of the genus *Kockelella* were found also in beds nos 4 and 9. Following the reconstruction of the origin and phylogeny of the genus given by Serpagli and Corradini (1999), *Kockelella absidata sardoa* (see Serpagli & Corradini, 1999) found in bed 4 ranges into the lower *P. siluricus* Biozone; Pa elements of the long ranging *Kockelella absidata* group were found in beds nos 2 and 9. The record of *K. absidata* ssp. together with *P. siluricus* points to the highest stratigraphical occurrence of the *K. absidata* group (Branson & Mehl, 1933). The distribution of several taxa of the genus *Kockelella* and their stratigraphic relations within the *P. siluricus* Biozone are shown in Slavík, Kříž & Carls (2010) from the Požáry section.

The interval from bed no. 11 to bed no. 19 yielded mostly representatives of the genus *Wurmiella* [*W. excavata excavata* (Branson & Mehl) and *Wurmiella inclinata* (Rhodes)], and *Ozarkodina typica* Branson & Mehl (= *Hindeodella confluens* Jeppsson). *Oz. typica* particularly shows high intra-specific variability as regards denticulation of the blade, variation in "cockscomb" structure and proportions of the Pa element (length and width of the unit). The stratigraphical evaluation of the changing morphology of the Pa element of *Oz. typica*, however, requires more material with precise stratigraphical control. The *E. latialatus* Biozone could have been expected to be found within this interval, but there is no direct evidence for this biozone and there is also no proof that the coniform element of *Acodina*? sp. may truly belong to the apparatus of *Pedavis* Klapper & Philip.

The “*Oz.*” *snajdri* Biozone is directly documented by several Pa elements of the name–bearer taxon in bed no. 22. Transition Pa elements between "*Ozarkodina*" *snajdri* and "*Ozarkodina*" *crispa* were obtained from bed no. 28. The element on Figure 4r exhibits already a large undulated platform like that seen in typical “*Oz.*” *crispa*, but the termination of the blade within the platform is in question. The taxa overlap considerably stratigraphically, however, “*Oz.*” *snajdri* appears at a lower stratigraphical level in the Prague Synform (Walliser, 1964; Schönlaub *in* Chlupáč, Kříž & Schönlaub, 1980). Accordingly, the base of the “*Oz.*” *crispa* Biozone can be expected to lie close to this stratigraphical level. The generic name of these biozonally diagnostic taxa is placed in quotation marks because of the ambiguity of the generic assignment as explained in Murphy Valenzuela-Ríos & Carls (2004). Bed 36 is the highest bed that yielded conodonts, although these are of no biostratigraphical value, the Přídolí age of this level being indicated by graptolites only.

2.f. Graptolite fauna

Graptolite rhabdosomes are uncommon in this hemipelagic, shale-dominated offshore succession, if compared to the rich early Silurian and even early Ludlow taphocenoses. Diversity is moderate to low.

Twenty graptolite taxa have been identified from the middle and late Ludfordian and earliest Přídolí. Despite the relative scarcity, however, graptolites are still playing a dominant role in the preserved pelagic macrofauna, being associated by myodocopid ostracodes before the Kozlowskii Event. Shale beds with few graptolite rhabdosomes are rich in ostracodes (accompanying cephalopods) and *vice versa*. The principal graptolite taxa are figured in Figures 5, 6, and 7. All biozones applied in this paper are interval zones defined as an interval between two biohorizons (see *International Stratigraphic Guide* edited by Salvador, 1994).

The lower part of the succession described in this paper was exposed in the upper part of the VA trench, on the western side of the field track. It is developed in the form of partly bleached, brownish calcareous shales with *Pristiograptus dubius* (Suess) *s.l.*, *Pseudomonoclimacis kosoviensis* (Bouček) and *Bohemograptus tenuis* (Bouček), and referred to the uppermost part of the lower–middle Ludfordian *B. tenuis* Biozone. The same lithology, but intercalated with several muddy limestone and tuffitic-carbonate beds, continues through the succeeding *Neocucullograptus inexpectatus* and *Neocucullograptus kozlowskii* biozones.

The lower part of the 8.7 m thick *Nc. inexpectatus* Biozone was exposed in the overlapping parts of the neighbouring trenches VB and VA. Small, long-ranging *P. dubius*, *Pseudomonoclimacis dalejensis* (Bouček), *B. tenuis*, large rhabdosomes of *Ps. kosoviensis* (Bouček), and the biozonal index species *Neocucullograptus inexpectatus* (Bouček) are common in the shale. Uncommon *Linograptus posthumus* (R. Richter), *Bohemograptus praecornutus* Urbanek, and *Polonograptus chlupaci* sp. nov. have been collected from the upper part of the *inexpectatus* Biozone on the eastern side of the track – in the VA trench.

Higher in the VA trench *Nc. inexpectatus* is replaced by a more derived form – *Neocucullograptus kozlowskii* Urbanek – which is the index species of the next biozone. Apart from the different index graptolite, the 3.2 m thick *kozlowskii* Biozone contains an assemblage similar to that of the *inexpectatus* Biozone. *Polonograptus podoliensis* Přibyl – a prominent but uncommon element in the assemblage of the *N. kozlowskii* Biozone in Kosov Quarry near Beroun (Štorch, 1995*a*) and a few other sections (Přibyl, 1983), has not been recovered from the Všeradice Section.

The continuous graptolite record and sedimentation were interrupted at the base of limestone bed no. 11 and graptolites reappeared only above the intraformational conglomerate (Figs 2–3, bed no. 13).

The mass extinction of the middle Ludfordian graptolite fauna at the top of the *kozlowskii* Biozone has been described and discussed by Urbanek (1970, 1993). Although all graptolites with ventrally curved rhabdosomes (*Bohemograptus*, *Neocucullograptus* and *Polonograptus*) vanished, some generalists such as *Pristiograptus dubius*, *Linograptus posthumus* and *Pseudomonoclimacis kosoviensis* reappeared soon after the extinction, together with several newcomers of rather cryptic origin.

Graptolites appearing in the first shale intercalations within the limestone dominated interval immediately above the intraformational conglomerates belong to a new, post-extinction assemblage of the *Pseudomonoclimacis latilobus-Slovinograptus balticus* Biozone. The assemblage, dominated by *Ps. latilobus* (Tsegelnjuk), comprises also *Sl. balticus* (Teller), *L. posthumus*, *Ps. kosoviensis*, and a slender form of *P. dubius*.

Higher in the succession *Sl. balticus* has been replaced by the more slender, weakly S-shaped *Sl.* cf. *balticus* (Teller) accompanied by *Pseudomonoclimacis* aff. *kosoviensis*, *Crinitograptus*? sp. and the long ranging *L. posthumus* and *P. dubius*. Rare finds of *Pristiograptus fragmentalis* (Bouček) in bed 27 enable recognition of a specific *P. fragmentalis* Biozone in the interval between the last joint occurrence of *Ps. latilobus* and *Sl. balticus* and the first occurrence of *Neocolonograptus parultimus* (Jaeger), the latter indicating the base of Přídolí Series.

In the uppermost shale beds exposed in the trench (beds no. 35–41), *Ne. parultimus* is accompanied by *Neocolonograptus ultimus* (Perner), *Formosograptus formosus* (Bouček), *Crinitograptus*? sp., *L. posthumus*, the last *P. fragmentalis* and a slender form of *P. dubius*.

2.g. Carbon isotopes

The $\delta^{13}C_{carb}$ values from the Všeradice section range from –2 to 2‰ and in contrast to earlier studied sections of the Prague Basin (Lehnert *et al.* 2007*a*) no distinct positive $\delta^{13}C$ shift was observed above the level of the Kozlowskii Event. The lack of this $\delta^{13}C$ positive excursion as well as the relatively low

$\delta^{13}C_{carb}$ values in the Všeradice section (frequently close to or just below zero) may suggest an absence of sedimentary record equivalent to beds with the high positive $\delta^{13}C$ values and/or a slight diagenetic overprint. A high content of organic carbon in the shale-dominated succession could cause a lowering of the $\delta^{13}C_{carb}$ values during diagenetic processes. The decomposition of organic matter yields isotopically light carbon, which can then be precipitated as carbonate, which pushes the $\delta^{13}C_{carb}$ values down in organic-rich carbonates. Because of that we cannot determine whether the measured low $\delta^{13}C$ values represent the primary isotopic composition of the studied micrites or values that have been slightly secondarily lowered by diagenetic overprint, or both. The only positive $\delta^{13}C$ values were recorded in an interval just above the late Ludlow Kozlowskii Event roughly to a level about 4.5 m below the FA of "*Ozarkodina*" *snajdri*. However, no distinct positive $\delta^{13}C$ shift was found in the carbonates from the Všeradice section (Fig. 8).

Previous studies (Lehnert *et al.* 2003, 2007*a*) revealed a distinct positive shift of the $\delta^{13}C_{carb}$ values from the carbonate platform of the Prague Basin. The most complete isotopic peak was recorded from the Kosov Section (Fig. 8) where the positive $\delta^{13}C$ shift starts at level of the late Ludlow Kozlowskii Event (Fig. 8). The values in the subsequent part of the Kosov Section (between 6.7 and 8 ‰) show no indication of a decrease in $\delta^{13}C$. Another, earlier studied section, the Mušlovka Quarry Section, clearly shows that this $\delta^{13}C$ positive excursion ends before the FA of "*Oz.*" *snajdri*. The level of the late Ludlow Kozlowskii Event was confidently indicated biostratigraphically in the Všeradice Section; however, determination of the FAD of "*Oz*". *snajdri* is less cetain because only a few conodont elements of the latter conodont species were found. The true FA of "*Oz*". *snajdri* may thus be lower in the section than shown (Fig. 2).

In the Všeradice Section the level of the late Ludlow Kozlowskii Event is just below the intraformational conglomerate (bed no. 13), which probably corresponds to the prominent gap in the sedimentary record (Fig. 2). The absence of a distinct positive shift of the $\delta^{13}C$ values at the Všeradice Section likely suggests an absence of sedimentary record equivalent to beds with the high positive $\delta^{13}C$ values in the Kosov Section (Fig. 8).

3. Graptolite biozones and correlation

Graptolite biozones are used as the primary correlation tool as the conodonts from the section are not sufficient to compose a precise zonal scheme. Whenever possible the shelly fauna and its potential for correlation are commented upon.

3.a. The *Bohemograptus tenuis* Biozone

Přibyl (1983) designated an interval between the demise of the saetograptids and the first occurrence of *Neocucullograptus inexpectatus* (Bouček) as the "*Pristiograptus longus*" Biozone with, at its top, the *Bohemograptus bohemicus* Bed. "*Pristiograptus longus* (Bouček)" is considered herein to be a junior synonym of *Pristiograptus dubius* (Suess) *sensu lato*. *Bohemograptus bohemicus* (Barrande) is considerably outnumbered by its evolutionary offshoot *Bohemograptus tenuis* (Bouček) in this level. We prefer to define the entire interval between the last saetograptids and the first *Neocucullograptus* as the *Bohemograptus tenuis* Biozone. This interval is probably coeval with the *Bohemograptus bohemicus-Neolobograptus auriculatus* biozones erected by Teller (1969) and Urbanek (1970) in the subsurface Silurian rocks of Poland and further updated by Urbanek & Teller (1997). Holland & Palmer (1974) used the *B. tenuis* Biozone to designate strata with a monospecific bohemograptid fauna overlying the *S. leintwardinensis* Biozone in the Welsh Borderland (see *Bohemograptus* proliferation Zone in Zalasiewicz *et al.* 2009). The present *B. tenuis* Biozone is correlatable also with the *B. tenuis* Interzone sandwiched between the *S. linearis* and *Polonograptus podoliensis* biozones in Tien Shan, Kyrgyzstan (Koren` & Sujarkova, 2004). *Saetograptus linearis* is a biozonal index graptolite in Bohemia and *Polonograptus podoliensis* (Přibyl) is an important component in assemblages of the *Nc. inexpectatus* and *Nc. kozlowskii* biozones (Přibyl, 1983; Štorch, 1995*a*). Finally, in Bohemia the *B. tenuis* Biozone is used to name the interval between the late *S. leintwardinensis* Biozone mass extinction and the subsequent development of the new neocucullograptid and polonograptid fauna. The uppermost part of the *B. tenuis* Biozone, overlain by the FA of *Neocucullograptus inexpectatus* (Bouček), is shown in the lowermost part of the section illustrated by Figure 2.

3.b. The *Neocucullograptus inexpectatus* Biozone

The *Nc. inexpectatus* Biozone of this paper corresponds to the lower part of the *N. inexpectatus* Biozone of Přibyl (1983). The stratigraphically lowest neocucullograptid rhabdosomes define the base of the biozone, whereas its top is defined by the first appearance of *Nc. kozlowskii*. Apart from *Nc. inexpectatus inexpectatus* (Bouček, 1931), Urbanek (1970) recognized the more advanced subspecies *Nc. inexpectatus supernus* that certainly occurs in the upper part of the biozone at Kosov Quarry (Štorch, 1995*a*). Preservation of the specimens found in Všeradice Section, however, is not good enough to enable separation of the two subspecies. Limestone nodules in tuffite bed no. 4 contain the conodont *Ozarkodina fundamentata* that indicates the *P. siluricus* Biozone. In addition, a bivalve assemblage with *Cardiola docens* occurs in the limestone nodules (bed no. 4). This bivalve assemblage is used in correlations of carbonate sequences in peri-Gondwanan Europe; it ranges from the *S. linearis* Biozone up to the *Nc. inexpectatus* Biozone (Kříž, 1998, 1999*a, b*, 2010*a, b*).

3.c. The *Neocucullograptus kozlowskii* Biozone

Přibyl (1983) did not recognize the *Neocucullograptus kozlowskii* Biozone in Bohemia; hence the upper part of his *Nc. inexpectatus* Biozone correlates with the *Neocucullograptus kozlowskii* Biozone *sensu* Štorch (1995*a*) and the present paper. The *Nc. kozlowskii* Biozone comprises an interval between the FA and LA of its name giving species. The present conception of the *Nc. kozlowskii* Biozone matches well that introduced for the East European Platform by Urbanek (1970) and further elaborated by Urbanek & Teller (1997). The same neocucullograptid biozones are probably applicable in Podolia, although Tsegelnjuk (1976, 1981) did not use a *Nc. inexpectatus* Biozone. A limestone bed just above the base of the *Nc. kozlowskii* Biozone yielded the index conodont *Polygnathoides siluricus*. The direct correlation between *Nc. kozlowskii* Biozone and upper part of the *P. siluricus* Biozone has been previously documented in Kosov Quarry only (Lehnert *et al.* 2007*a*). The upper limit of the *Nc. kozlowskii* Biozone is defined by the sudden extinction of the bohemograptid–polonograptid-neocucullograptid fauna, defined as the Kozlowskii Event by Urbanek (1993). Graptolite extinction and facies change indicating shallowing were identified also in Kosov Quarry near Beroun (Štorch, 1995*a, b*). There, however, graptolites are missing in the supposed post extinction recovery interval.

Limestones and intraformational conglomerates that occur just above the graptolite extinction level in the Všeradice section suggest that the extinction coincides with the beginning of shallowing as suggested by Urbanek (1993) and Melchin, Koren` & Štorch (1998). Apart from graptolites, the ostracod *Richteria migrans* disappeared (similarly as elsewhere in the Prague Synform, see Manda & Kříž, 2006). This is a striking feature because this ostracod is a common component of pelagic faunas in peri-Gondwanan basins starting from the lower Ludfordian *S. linearis* Biozone (Siveter, Vannier & Palmer, 1991; Kříž, 1999*a*). *Bolbozoe* disappeared from shales in the *Nc. inexpectatus* Biozone. Note that no pelagic ostracods appeared during the post-extinction recovery. Pelagic orthocerids pass through the Kozlowskii extinction Event and *Parakionoceras, Kopaninoceras, Arionoceras* and *Michelinoceras* occur throughout the section. Conodonts found in limestone just above the Kozlowskii Event are the same as in the lowest *Nc. kozlowski* Biozone except for *P. siluricus*. This suggests that the deeper water conodont assemblage consists mainly of long-ranging taxa and that the extinction thus affected rather shallow water conodont faunas (see also Slavík *et al.* 2010). This should be taken into account when correlating deeper water limestones.

Manda & Kříž (2006) concluded that the Kozlowskii Event correlates roughly with the conodont extinction known as the Lau Event (Jeppsson, 1993). However, no section with adequately combined graptolite and conodont records is known. Consequently, high-resolution correlation of the graptolite and conodont extinctions is doubtful. Moreover the Lau Event is not clearly manifested in the conodont faunas in the Prague Synform and its lower part is entirely missing in the sections (Slavík, Kříž & Carls, 2010).

In the Kosov Section the LA of *P. siluricus* (defining the Lau Event) is drawn below the LA of *Nc. inexpectatus* and *B. tenuis*. Conodonts are, however, rare in this section. The late Ludfordian carbon isotope excursion which is commonly ascribed to Lau Event (Saltzman, 2001; Maartma *et al.* 2005; Lehnert *et al.* 2007*a*) started in the Kosov Section close to the level of the graptolite extinction.

3.d. The *Pseudomonoclimacis latilobus-Slovinograptus balticus* Biozone

The graptolite assemblage recovered from shaly intercalations within the post-*kozlowskii* limestone suite is dominated by the two biozonal index species, *Pseudomonoclimacis latilobus* (Tsegelnjuk, 1976) and *Slovinograptus balticus* (Teller, 1966), both widespread in the East European Platform (e.g. Tsegelnjuk, 1976; Paškevičius, 1979 and Urbanek, 1997). Přibyl (1983) described these two species under the junior synonyms "*Saetograptus insignitus*" and "*Monograptus abhorrens*", respectively, from a temporary trench in Velký Vrch hill near Koněprusy. He recognized a distinctive "*S. insignitus*" Biozone also in Kosov Quarry and in a water supply gallery in Praha-Podolí. We are not surprised to find these graptolites in relatively more offshore facies in the Všeradice Section. The *Ps. latilobus-Sl. balticus* Biozone of this paper is an interval between the last occurrence of *Nc. kozlowskii* at the base and last joint occurrence of *Ps. latilobus* and *Sl. balticus* at the top.

The intraformational conglomerate just below the lowest occurrences of *Ps. latilobus* and *Sl. balticus* contains trilobites and other shelly fossils of relatively inshore provenance corresponding with the former *Ananaspis fecunda* Horizon (Horný, 1955). Benthic fossils recovered from both matrix and pebbles of the conglomerate belong to the *Ananaspis fecunda-Cyrtia postera* Assemblage, which therefore predated the *Ps. latilobus-Sl. balticus* graptolite assemblage. The relict graptolite fauna that survived the maximum low stand (shallow water limestones with *Ananaspis fecunda* overlie deeper water shale and mudstone in the Kosov and Mořina areas) was subsequently joined by the new association of *Ps. latilobus* and *Sl. balticus*. Although in the Všeradice Section the interval between the Kozlowskii extinction and the FA of *Ps. latilobus* is only about 2.5 m thick, in Kosov Quarry it comprises at least 10 m of strata. This indicates that the post-extinction interval with strongly impoverished or missing graptolites was remarkably long and the recovery of graptolites was delayed after the benthic faunal recovery. Finally, the limestone sequence with the *Ananaspis fecunda-Cyrtia postera* Assemblage (*A. fecunda* Horizon of Horný, 1955) developed across the basin, correlates with the *Ps. latilobus-Sl. balticus* Biozone as used here.

Pseudomonoclimacis latilobus and *Slovinograptus balticus* range together higher up the succession, close to the FA of *Neocolonograptus parultimus* (Jaeger) – the biozonal index of the lowermost Přídolí. The graptolite assemblage of the present *Ps. latilobus-Sl. balticus* Biozone is quite similar to that of the homonymous zone applied by Urbanek (1997) in Poland. It is uncertain, however, how precisely the two *latilobus-balticus* biozones correlate. The index taxa of the three succeeding biozones, i.e. *Uncinatograptus acer* Tsegelnjuk, *Uncinatograptus protospineus* Urbanek and *Uncinatograptus spineus* Tsegelnjuk, which overlie the *Ps. latilobus-Sl. balticus* Biozone in Poland (Urbanek, 1997), are missing in the Všeradice Section and elsewhere in peri-Gondwanan Europe. The lack of these biozones may be explained by the palaeogeographical isolation of peri-Gondwanan Europe in the latest Ludlow. In the Všeradice section, however, some gaps in sedimentation should be also considered since the 2.5 m between the LA of *Ps. latilobus* and the FA of *N. parultimus* corresponds witha ca 120 m thick sequence in Poland (see Urbanek, 1997, fig. 3). Přibyl (1983) recognized a monospecific "*Pristiograptus*" *fecundus* Biozone above his "*insignitus* Biozone" in Kosov Quarry and some other sections of the Prague Synform. "*Pristiograptus*" *fecundus* (Přibyl), which is probably a descendant of *Pseudomonoclimacis latilobus*, has not been recovered from the Všeradice Section.

Limestone bed no. 22, containing „*Oz.*" *snajdri* and other conodont taxa (Fig. 2), immediately overlies the last occurrence of *Ps. latilobus*. The FA of "*Oz.* " *snajdri* is therefore above the FA of *Ps. latilobus*.

3.e. The *Pristiograptus fragmentalis* Biozone

Instead of distinctive range biozones we can apply only another interval biozone, named after the presumably long ranging *Pristiograptus fragmentalis* (Bouček) and defined as an interval between the highest joint occurrence of *Ps. latilobus* and *Sl. balticus* and the FA of *Neocolonograptus parultimus*. *Pristiograptus fragmentalis* (Bouček, 1936) is a robust form having a weakly ventrally curved to almost straight most proximal part of its rhabdosome and considerably overlapping, pristiograptid distal thecae. Our specimens (Figs 5p, 7j, k) are identical with forms figured by Kříž *et al.* (1986), Urbanek (1997, pl. 15, figs 5–6) and, in part, by Koren` & Sujarkova (1997, pl. 1, figs 1–6; text-fig. 7A–G).

Pristiograptus fragmentalis Biozone is the uppermost graptolite biozone of the Ludlow in Bohemia (Bouček, 1936). Bouček (1936, p. 13) noted that *P. fragmentalis* occurs in cephalopod limestones with the trilobites *Cromus intercostatus* Barrande and *Cerauroides hawlei* (Barrande), below the first appearance of *Ne. ultimus* at the Lochkov locality. *Cr. intercostatus* and *C. hawlei* form part of the distinct *Denckmanites-Cromus* trilobite Assemblage established by Chlupáč (1987). This assemblage is known only from a few sections near Lochkov village where it is restricted to a single thin bed. Šnajdr (1985) noted that the latter assemblage occurs 11–14 cm below the FA of *Ne. parultimus* in the Orthoceras Quarry Section. Kříž *et al.* (1986) reported *P. fragmentalis* from the uppermost Ludlow just below the FA of *Ne. parultimus* (in the Koledník and Karlštejn sections). New data from the Všeradice Section suggest that the FA of *P. fragmentalis* in Bohemia falls immediately after the LA of *Ps. latilobus*.

The Všeradice Section seems to be either condensed or interrupted by a discrete unconformity in this interval, since *Ne. parultimus*, the index of the basal Přídolí, makes its first appearance less than 1 m above the last *Sl. balticus*. As in other Bohemian sections (Kříž *et al.* 1986), *Ne. parultimus* is accompanied by *Formosograptus formosus* in the Všeradice Section. In the East European Platform (Paškevičius, 1979; Urbanek & Teller, 1997), Arctic Canada (Lenz & Kozłowska-Dawidziuk, 2004) and Tien Shan (Koren & Sujarkova, 1997) *Formosograptus formosus* appears much lower and even gives its name to a combined biozone in the latest Ludfordian. Similarly, *Pristiograptus fragmentalis* appears in Poland earlier, it co-occurs with *Ps. latilobus*, but disappeared already before the LA of *Ps. latilobus*.

4. Conclusions

Although late Ludfordian graptolites have rarely left a fossil record sufficient for detailed biostratigraphy and high-resolution correlation, their better understanding is of crucial importance as correlation of the Silurian System relies primarily on graptolite biozones. Benthic faunas and sequence boundaries can be used in correlations within individual basins, especially in stratigraphical intervals where conodont biozones lack the precision of those based on graptolites. Here, four graptolite biozones are distinguished in the latest Ludlow between the *B. tenuis* Biozone and the base of Přídolí Series.The Všeradice Section provides the most complete graptolite record in the peri-Gondwanan realm. The late Ludlow graptolite biozonation previously applied in Bohemia and other parts of peri-Gondwanan Europe resulted rather from uncertain correlations between isolated partial sections.

The Kozlowskii extinction Event and subsequent recovery is recorded for the first time from both Bohemia and peri-Gondwana; this also represents first record of the event in higher latitudes outside the tropical zone. The Všeradice section is unique also in its sedimentary record. Although situated in an offshore, open sea setting, it enables correlation with benthic and particularly conodont faunas, because it was situated close to a small shallow water area with carbonate sedimentation, which was colonized by benthic assemblages closely related to those inhabiting the carbonate platform situated to the north.

The Kozlowskii Event caused extinction of many graptolite lineages as previously suggested. Bohemograptids, neocucullograptids and *Polonograptus* all vanished from the fossil record. It is noteworthy that the pelagic orthocerids and nektonic *Ceratiocaris* passed through the extinction interval (Fig. 9). The pelagic ostracod *Entomis*, however, became extinct. Although a single taxon, its extinction is of note because it is a widespread, long-ranging generalist. Similarly, the conodont faunas in these deeper water settings were affected only slightly (see also Slavík, Kříž & Carls, 2010). Data from Všeradice section further support the earlier thoughts of Lehnert *et al.* (2007*b*) and Eriksson & Calner (2008) that the Kozlowskii extinction Event coincides with a drop in sea level and period of Ice House climate.

The interval between the graptolite extinction and subsequent recovery and radiation was relatively long (based on sedimentary rock thickness). Eroded shale and the intraformational conglomarate in the Všeradice section indicate a prominent gap in sedimentation in this time. The benthic faunas from the conglomerate (matrix and pebbles of different age), nevertheless, make correlation possible with coeval shallow-water carbonate strata (Figs 8–10).

In terms of eustatic sea-level oscillations, the graptolite recovery recorded in the Prague

Synform coincides with a period of rising sea level after major eustatic drawdown. It was delayed far behind the recovery of benthic fauna. The graptolite recovery started after the end of the positive carbon isotope excursion and before the FAD of "*Oz". snajdri*. The post-Kozlowskii Event graptolite recovery gave origin to a novel graptolite fauna of Přídolí type. Some graptolite taxa that emerged or reappeared above the Kozlowskii Event crisis are likely ancestors to substantial elements of Přídolí graptolite assemblages (e.g. *Sl. balticus* gave rise to *Sl. beatus* (Koren', 1983 and Jaeger in Kříž *et al.* 1986) and *Ps. kosoviensis* may have evolved into *Ps. transgrediens*). In turn, *Ne. parultimus,* although remarkably similar to *Ps. latilobus*, has been derived from other, less specialized ancestor after Urbanek (1997).

The latest Ludlow *F. formosus* and/or *Uncinatograptus acer*, *U. protospineus* and *U. spineus* biozones, distinguished in Baltica and elsewhere in lower palaeolatitudes, are missing in Bohemia and indeed in the whole of peri-Gondwana. *F. formosus,* which makes its lowest occurrence in middle Ludfordian strata in Poland, Lithuania, Kyrgyzstan, Kazakhstan and Arctic Canada, is unknown from below the *Ps. ultimus-Ps. parultimus* Biozone of the basal Přídolí Series in Bohemia and there are some discrepancies in stratigraphical ranges of some other taxa (e.g. *P. fragmentalis*). Differences may result from temporary palaeobiogeographical separation rather than an incomplete fossil record in peri-Gondwana due to a condensed or missing sedimentary rock record.

Precise correlation of late Ludlow conodont and graptolite biozones is not yet possible from published data. Consequently the correlation of the graptolite Kozlowskii and conodont Lau events is still unknown in detail, although that the two events are approximately coincident is suggested from their position at the beginning of the positive carbon isotope excursion.

5. Systematic palaeontology (by Petr Štorch)

All graptolite taxa previously unknown under the correct name from Bohemia, new species and new combinations are described. Illustrated and described specimens are housed in the official collection of Czech Geological Survey, Prague (prefix PŠ); type specimens prefixed L are housed in the National Museum, Prague.

Pseudomonoclimacis kosoviensis (Bouček, 1931)

Figures 5i; 6g–j; 7s

1931 *Monograptus kosoviensis* n. sp.; Bouček, pp. 2, 15; text-fig. 1c, d.
1936 *Monograptus kosoviensis* Bouček 1931; Bouček, pp. 10–11, pl. 2, fig. 10; text-fig. 1g–k.
1943 *Pristiograptus kosoviensis* (Bouček, 1931); Přibyl, pp. 24–25, pl. 3, figs 14, 15.
1997 *Pristiograptus dubius* cf. *frequens* Jaekel, 1889; Rickards & Wright, pp. 219, 221–222; text-fig. 9i, j.

Material. 26 flattened rhabdosomes from bed nos 1a, 1b, 3, 10 and 16 of the Všeradice section (see Fig. 2), several rhabdosomes from the middle part of trench VB below the present log, and the type material figured by Bouček and Přibyl.

Lectotype. Designated by Bouček (1936): specimen no L 19940 figured by Bouček (1931, text-fig. 1d); from the level corresponding with the *tenuis* Biozone of the present biozonal scheme; Koledník Quarry near Beroun, Bohemia.

Description. The sicula is straight or gently ventrally curved, 1.2–1.7 mm long, its apex attaining a level at or below the aperture of th 2. The sicular aperture is concave, 0.22–0.28 mm wide, furnished with a short and slender virgella. The nema is robust, 0.4 mm wide in mature specimens, and extending as much as 30 mm beyond the distalmost thecae. The rhabdosome gradually widens from 0.45–0.6 mm at the apertural margin of th 1, through 0.7–0.8 mm at th 3, 0.85–1.1 mm at th 5, 1.2–1.7 mm at th 10 and 1.55–1.95 mm at th 20 to a maximum of 2.5–2.7 mm attained 40–50 mm from the sicula. Isolated distal fragments are 2.8 mm wide. Proximal thecae are slightly geniculate and overlap for one–third their length. More or less prominent hook-like secondary apertural additions are developed in proximal thecae of mature rhabdosomes with a more than 30–40 mm long thecate part

(Fig. 6i). Details are not seen due to inadequate preservation. The 2TRD increases from 1–1.35 mm at th 2 and 1.1–1.45 mm at th 5 to 1.3–1.7 mm at th 10 and then gradually until 2.1–2.3 mm attained most distally. Proximal thecae number 12–13 in 10 mm; long, simply tubular distal thecae number 9.5–8.5 in 10 mm and overlap for almost three-quarters of their length. Distal thecal apertures are perpendicular to the thecal axis or are slightly everted.

Remarks. Our specimens agree in all dimensions with Bouček`s (1931) type material, especially in their distal dorso-ventral width and thecal spacing. The sicular part of the rhabdosome is described for the first time and shows that this species is similar to *Pseudomonoclimacis contumax* (Bouček, 1936) and "*Monograptus*" sp. of Rickards & Palmer (1977). The apertural overgrowths observed in our mature rhabdosomes of *Ps. kosoviensis* (Bouček, 1931) are equally developed in „*Monograptus*" sp. (of Rickards & Palmer, 1977), which may be distinguished solely by its larger, up to 2.5 mm long sicula attaining a level above the aperture of th 2. *Pseudomonoclimacis contumax* differs from stratigraphically younger *Ps. kosoviensis* in having a less robust rhabdosome with a straight to slightly dorsally curved proximal part and more closely spaced thecae. Small apertural outgrowths have been found in one mature specimen of *Ps. contumax*.

Jaeger (1978) demonstrated that the hook-like apertural structures in „*Monograptus*" sp. of Rickards & Palmer (1977) are secondary structures formed during the late astogenetic or gerontic stage of colony development. He also reported similar secondary outgrowths in *C. colonus*, *S. chimaera* and *M. haupti*. The tendency to thecal isolation and development of lateral apertural lobes, however, may represent, at least in part, natural variability rather than gerontic growth because of its occurrence in immature rhabdosomes.

Although the resemblance of the proximal and mesial thecae of *Ps. kosoviensis* to *Monoclimacis* thecae is commonly enhanced by flattening, the distinct thecal geniculation, hook-like apertural growth additions in the proximal thecae of mature rhabdosomes, very rigid nema and proximal part of the rhabdosome lacking ventral curvature clearly differentiate these graptolites from the *Pristiograptus dubius* Group, including *Pristiograptus frequens* Jaekel figured by Jaeger (1991, pl. 25, figs 9, 11, 15). *M. kosoviensis* Bouček and related taxa are best assignable to the genus *Pseudomonoclimacis* (Mikhaylova, 1976) *sensu* Koren` (1986), Urbanek (1997) and Lenz & Kozłowska-Dawidziuk (2004).

Pseudomonoclimacis aff. *kosoviensis* (Bouček, 1931)
Figures 6l; 7r

Remarks. Nine rhabdosomes found in the *fragmentalis* Biozone can be distinguished from typical *Ps. kosoviensis* by their relatively robust proximal part and lesser distal maximum width (2.1 mm). Thecae are equally overlaping and exhibit the same tendency to develop hook-like apertural outgrowths proximally. Thecae are wider and slightly more widely spaced (2TRD th 10 = 2.1 mm). This stratigraphically distinctive form is left in open nomenclature referring to its close similarity to *Ps. kosoviensis* until more material is available.

Pseudomonoclimacis latilobus (Tsegelnjuk, 1976)
Figures 5d, e, j, r, s; 7q

1976 *Colonograptus latilobus* n. sp.; Tsegelnjuk, p. 109, pl. 29, figs 9–11.
1983 *Saetograptus* (*Colonograptus*) *insignitus* n. sp.; Přibyl, p. 160, pl. 1, figs 3–8; pl. 4, figs 11–13.
1988 *Ludensograptus latilobus* (Tsegelnjuk); Tsegelnjuk, p. 82, text-fig. 3.
1988 *Monograptus latilobus* (Tsegelnjuk); Koren`, Rinenberg & Lytochkin, p. 17, text-figs 9–10.
1997 *Pseudomonoclimacis latilobus* (Tsegelnjuk, 1976); Urbanek, pp. 161–165, pls 17–19, text-figs 45–47.
1997 *Monograptus latilobus* (Tsegelnjuk, 1976); Koren` & Sujarkova, pp. 75–77, pl. 4, figs 3–4; text-fig. 11g–n.

Material. 22 flattened rhabdosomes from bed nos 14, 16 and 20 of the Všeradice Section (see Fig. 2) and several rhabdosomes from Velký Vrch near Koněprusy, including topotypical specimens of „*S. insignitus*“ collected by Alois Přibyl.

Holotype. Specimen no N 1788/11 figured by Tsegelnjuk (1976) on pl. 29 as fig. 11; from the “? *leintwardinensis* Biozone” of the Gushcha borehole, Volynia, Ukraine.

Description. The dorsal wall of the medium-sized, 20–30 mm long rhabdosome is straight or slightly ventrally curved in the proximal part. The sicula is also ventrally curved. It is *ca* 2.0 mm long, including rarely recognizable slender prosicular part. The readily visible metasicular portion is 1.4–1.5 mm long. Sicular aperture is 0.4 mm wide in profile, deeply concave, furnished with a *ca* 0.1 mm long dorsal lobe. The first theca initiates 0.2–0.3 mm above the sicular aperture. Th 1 is roughly triangular in outline, with a slightly everted aperture provided with more or less developed, ventrally directed, and paired lateral lobes. Distinct ventro-lateral apertural lobes are present on each theca throughout the rhabdosome. Thecae appear slightly geniculated due to a gentle excavation on the ventral thecal wall. Flattened thecae exhibit somewhat isolated and introverted apertures with the lateral lobe separated by a notch from the ventral wall of the next theca. The ventral part of the apertural margin is either acuminate, when preserved in profile, or lobate, when obliquely flattened. Distal thecae are 2.1–2.4 mm long, straight, and inclined at an angle of 40–50° to the rhabdosome. The rhabdosome is 0.85–0.95 mm wide at the th 1 aperture, 1.15–1.3 mm wide at th 3, 1.3–1.5 mm wide at th 5, and 1.6–1.8 mm wide at th 10. Maximum distal width of the rhabdosome, 2–2.1 mm, is attained by *ca* 14th theca. Two-thecae repeat distance (2TRD) increases from 1.3–1.45 mm at th 2, to 1.5–1.7 mm at th 10 and then to the distal maximum 1.75–1.95 mm, i.e. the distal thecae number 10.5–11.5 in 10 mm of rhabdosome length.

Remarks: The present material matches the typical specimens illustrated by Tsegelnjuk (1976, 1978) and Urbanek (1997). A morphologically less advanced and stratigraphically younger morphotype, described and illustrated by Urbanek (1997, pl. 19) is similar to *Pseudomonoclimacis fecundus* (Přibyl, 1943), which can be distinguished by its poorly developed apertural lobes and less robust most proximal part of the rhabdosome.

Polonograptus chlupaci sp. nov.

Figures 5o; 7o; 11a, b

1995*a* *Polonograptus egregius* (Urbanek, 1970); Štorch, p. 74–75, pl. 4, figs 1–5; text-figs 4d; 6f, i, j, l.

Name. After the late Prof. Ivo Chlupáč, distinguished Czech stratigrapher and palaeontologist.

Material. Eight complete and four incomplete flattened rhabdosomes and several fragments from Kosov Quarry and two incomplete rhabdosomes from the Všeradice section.

Holotype. Specimen no PŠ 631, figured by Štorch (1995*a*, pl. 4, fig. 3; text-fig. 6i) and refigured herein on fig. 8a, from the middle Ludfordian *Nc. kozlowskii* Biozone at Kosov Quarry near Beroun, Bohemia

Diagnosis. Rhabdosome regularly ventrally coiled, almost circular. Sicula 1.3–1.7 mm long; the apex reaches about two–thirds up the 1.2–1.7 mm long th 1. Relatively short th 1 followed by considerably longer (2.4–3.6 mm) th 2. Thecae slender tubes terminated by simple apertures with gentle lateral apertural elevations. 4.4–4.9 mm long distal thecae overlap for about two–thirds their length.

Discussion. This unusual taxon was described by Štorch (1995*a*) from the *kozlowskii* Biozone of the Kosov Quarry as *Polonograptus egregius* (Urbanek, 1970). Two almost circular rhabdosomes encountered from the same level in the Všeradice Section exhibit the same parameters medially and distally whereas their proximal parts are broken. The specimen shown on Figures 5o and 7o seems to have an incomplete th 1 and the sicula and initial bud are missing.

Urbanek (1970) erected „*Monograptus*“ *egregius* upon fragmentary material from the *kozlowskii* Biozone of the Mielnik Borehole in eastern Poland. The holotype is a distal fragment comprising four thecae and the paratype is a sicula with a very incomplete first theca. Urbanek (1970, pl. 42, fig. f) published a hypothetical complete development of the first theca based on isolated fragments, but subsequently this “reconstruction” was used as the most essential part in the generic diagnosis of *Egregiograptus* Rickards & Wright, 1997. Koren` & Sujarkova (2004) encountered a rich and moderately well preserved egregiograptid fauna in Tien-Shan (Kyrgyzstan) and considered the extremely long th 1 a principal diagnostic feature of *Egregiograptus.* Accordingly, Koren` & Sujarkova referred Bohemian specimens with overall egregiograptid morphology combined with a short th 1 to a new, so far undescribed species of *Polonograptus*. This form, which is named *Polonograptus chlupaci* sp. nov. in this paper, can be barely distinguished from egregiograptids when its proximal part with its short th 1 and long th 2 is broken, since the mesial and distal parts of its rhabdosome match *Egregiograptus rinellae* Koren & Sujarkova 2004, or *Egregiograptus egregius* Urbanek as illustrated by Tomcyzk *et al.* (1990). The most similar polonograptid – *Polonograptus aloisi* Koren` & Sujarkova, 1997 – differs from *P. chlupaci* in having an arcuately curved and more rapidly widening rhabdosome with strongly inclined, shorter and less overlapping thecae.

Slovinograptus balticus (Teller, 1966)

Figures 5b, f, g, k–n; 7l, p

1966 *Monograptus balticus* n. sp.; Teller, pp. 556–558, pl. 1, figs 6–11; text-fig. 4a, b.
1974 „*Monograptus*“ *balticus* Teller; Paškevičius, p. 126, pl. 15, figs 1–5; pl. 19, figs 4–11; pl. 20, figs 1–2.
1976 *Wolynograptus balticus* (Teller); Tsegelnjuk, pp. 111–112, pl. 33, fig. 5.
1979 *Monograptus balticus* Teller; Paškevičius, pp. 168–169, pl. 12, figs 4–8; pl. 28, figs 1–12.
1983 „*Monograptus*“ *balticus* Teller; Tsegelnjuk, pl. 145, fig. 34.
1983 *Monograptus* (*Wolynograptus*) *abhorrens* sp. n.; Přibyl, p. 159–160, pl. 2, figs 5–9; pl. 4, figs 5–9.
1988 *Monograptus balticus* Teller; Koren`, Lytochkin & Rinenberg, p. 17, fig. 1.
1997 *Monograptus balticus* Teller, 1966; Koren` & Sujarkova, p. 71, pl. 1, figs 9–10; text-fig. 9e–h, (?a)

Material. 20 rhabdosomes; mostly flattened. Several specimens are pyritized, either with periderm or preserved as internal moulds. An additional four flattened specimens originate from Velký Vrch (type locality of “*Monograptus* (*Wolynograptus*) *abhorrens* Přibyl”).

Holotype. The specimen figured by Teller (1966, pl. 1, fig. 6) and refigured by Koren` & Sujarkova (1997, text-fig. 9G) from the late Ludfordian of the Łeba 3 borehole in northern Poland.

Description. The otherwise straight rhabdosome is slightly dorsally curved in its slender proximal part. The sicula is 1.35–1.45 mm long, and gently ventrally recurved. Its apex reaches *ca* two-thirds up th 1. The sicular aperture is concave in outline, 0.18–0.22 mm wide, furnished with a weakly developed dorsal lobe and short virgella. Slender, 1.25–1.45 mm long th 1 diverges at about 5° from the rhabdosome axis with its origin 0.25–0.4 mm above the sicular aperture. Thecal aperture is covered by tightly appressed, transversely extended hood. The succeeding thecae are slender, very gently inclined, straight or gently S-shaped tubes with prominent apertural hoods that may be responsible for the common subscalariform mode of rhabdosome preservation. A thecal length of 2.25 mm was measured in th 10 which overlaps for one–half of the succeeding theca (see also specimen on Figure 5n). The rhabdosome widens gradually from 0.45 mm at the level of the first thecal aperture, to 0.6–0.7 mm at th 3, and 0.7–0.85 mm at th 5. A width of 0.85–1.2 mm is attained by about th 10 and is maintained in the distalmost parts of the present, still not fully mature rhabdosomes. The 2TRD is 1.7–2.0 mm at th 2, and 1.7–2.4 mm more distally.

Discussion. Tsegelnjuk (1976) assigned *Monograptus balticus* Teller, 1966 and other three species to his new genus *Wolynograptus*. He chose *Wolynograptus valleculosus* Tsegelnjuk, 1976 as the type species. This choice turned out unfortunate since *W. valleculosus* differs from other species included in this genus in having hooked metathecae without characteristic tightly appressed, globular and transversely extended apertural hoods. Its rhabdosome and described thecal morphology resemble *Uncinatograptus acer* (Tsegelnjuk, 1976) instead. Urbanek (1997) included slender wedge-shaped Ludfordian monograptids with thecal apertures covered by tightly appressed hoods to a new subgenus *Slovinograptus*. Morphological distinctiveness of its sigmoidally curved thecae and close affinities to *M. beatus Koren*' and *M. microdon* R. Richter (see Jaeger 1986) lead us to promote *Slovinograptus* to a genus. A successive series leading from Ludfordian *Sl. balticus* (Teller) through *Sl. beatus* (Koren') of Přídolí to Lochkovian *Sl. microdon* (R. Richter) has been suggested by Koren' (1983).

Flattened specimens of *Slovinograptus balticus* figured by Teller (1966) and Paškevičius (1974, 1979) differ from the present material in their more abrupt widening within the first 5–7 thecae, when measured without the apertural hoods. This apparent difference may be explained by the largely box-like mode of flattening of Polish and Lithuanian specimens, as suggested by pressed-through interthecal septa. The Bohemian specimens, by contrast, have been partly pyritized in calcareous shale and argillitic limestone. Specimen PŠ 2015 (Figure 5n) is a pyritized internal mould preserved in relief. It is obvious that the dorsal rhabdosome curvature, missing in the specimens of "*Monograptus abhorrens* Přibyl, 1983" and specimens of *Sl. balticus* studied by Urbanek (1997, pl. 3, figs 2, 4–5) is partly due to natural intraspecific variation and, in part, due to the subscalariform orientation of the rhabdosomes. No Bohemian specimen exhibits such pronounced and ventrally extended apertural hoods as does the rhabdosome figured by Koren` & Sujarkova (1997, text-fig. 9A). *Sl. balticus* either varies in its rhabdosomal curvature and apertural hood development or still comprises several palaeogeographically isolated populations of so far unrecognized taxonomic status. The type material of "*Monograptus abhorrens*" has been missing for at least twenty years. Due to the considerable morphological variability caused by different preservation, observed already within our material from Všeradice section, we have retained all material in a single species.

Slovinograptus cf. *balticus* (Teller, 1966)

Figures 6e; 7f

Remarks. This form is slender, gently S-shaped or almost straight except for a slightly dorsally curved proximal part comprising 2–3 initial thecae. The DVW increases from 0.45 mm at th1, through 0.6 mm at th 3 and 0.75 mm at th 5, to 0.85 mm at th 10. The 2TRD of 1.9–2.1 mm is constant throughout the rhabdosome.

Sl. beatus (Koren`, 1983) can be differentiated by its wider, more robust proximal part. *Sl. balticus* is distinguishable by its ventrally curved to almost straight, more rapidly widening proximal part and by its interthecal septa which are inclined to the rhabdosome axis. Eleven rhabdosomes of *Slovinograptus* cf. *balticus* from the upper *fragmentalis* and *parultimus-ultimus* biozones in the Vseradice section help to fill a stratigraphical gap between the late Ludfordian slovinograptids (*Sl. hamulosus* and *Sl. balticus*) and forms ranging from the late Přídolí [*Sl. beatus* (Koren`), *Sl. aksajensis* (Koren`)] through to the earliest Devonian *M. uniformis* Biozone [*Sl. microdon* (R. Richter)].

The narrow wedge-shaped rhabdosomes, ventral thecal walls parallel to the rhabdosome axis or sloping slightly inwards, and dorsal thecal walls terminated by apertural hood transversely extended into tabular or semicircular roof make this group of graptolites fairly distinctive.

Crinitograptus? sp.

Figures 6f; 7h

Remarks. About 20 dorsally arcuate, slender rhabdosomes of nearly uniform width were collected from a restricted interval of the uppermost *fragmentalis* and lowermost *parultimus-ultimus* biozones. Material is poorly preserved but obviously represents a distinctive form previously unknown from Bohemian sections. It is readily recognizable by its prominent apertural hoods combined with long and slender prothecae with ventral wall parallel to the rhabdosome. Short metathecae terminate with ventrally to proximo-ventrally directed apertural hoods which, in some specimens, appear to be transversely extended. Dorso-ventral width is 0.4–0.5 mm across the parallel-sided part of the theca and *c.* 0.85 mm across the apertural hood. 2TRD is 2.3–2.55 mm in the majority of our specimens that are, however, either incomplete or just fragments. The proximal end is barely recognizable and the sicula is not preserved.

A similar taxon, designated as *Crinitograptus* cf. *operculatus* (Münch), has been encountered by Lenz & Kozłowska-Dawidziuk (2004) from the lowermost Přídolí of the Arctic Islands of Canada. The Canadian specimens are broader (0.6–0.7 mm without hoods and 1.0–1.2 mm across the hoods) and their thecae are more widely spaced (3 thecae in 5 mm). Until better specimens are available, the Všeradice material has also been tentatively assigned to *Crinitograptus* due to the nearly uniform rhabdosome width, slender thecae with ventral walls parallel to the rhabdosome axis, and apertural hoods. The hooded apertural structure and prothecae parallel to the rhabdosome, however, suggest that this taxon may have evolved from *Slovinograptus* instead.

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Figure and table captions

Figure 1. Position of the area studied within the Czech Republic (a), distribution of the Silurian rocks of the Prague Synform (b) and detailed position of the Všeradice section on a topographic map.

Figure 2. Chronostratigraphy and lithology of the Všeradice section. Ranges of graptolites, conodonts and selected other fossils are included.

Figure 3. Microfacies of the carbonate gravity deposits from the Všeradice section. (a) Coarse grained grainstone with an intraclast of dark gray mudstone with dolomite, bed no. 13. (b) Coarse grained grainstone with crinoids, trilobites and rugose coral, small rounded intraclasts (wackestone with spongies and ostracod fragments and fine grainded wacke-grainstone), bed no. 13. (c) Partly pyritised rugose coral with partly damaged wall preserved in grainstone, bed no. 13. (d) An intraclast of mudstone with ostracods, smaller ostracod is filled with pyrite, bed no. 13. Intraclastic crinoidal grainstone with cohesive intraclasts of shale and a fragment of tabulate coral, bed no. 22. (e) Detail of contact of matrix with cohesive intraclasts, bed no. 22. Scale bars 2 mm, in d 0,5 mm.

Figure 4. Conodonts from the Všeradice section (SEM images). All images are at the same magnification (scale bar represents 500 µm). (a) *Kockelella maenniki* Serpagli & Corradini, oral view of Pa element, bed no. 2. (b) *Kockelella* cf. *a. absidata*, lateral view of Pa element, bed no. 2. (c) *Kockelella absidata sardoa* Serpagli & Corradini, lateral view of Pa element, bed no. 4. (d) *Kockelella absidata* ssp., lateral view of Pa element, bed no. 9. (e) *Polygnathoides siluricus* Branson & Mehl, oral view (ea) and lateral view (eb) of incomplete Pa element from bed no. 9. (f) *Wurmiella inclinata* (Rhodes), lateral view of Pa element, bed no. 13. (g) *W. inclinata*, lateral view of Pa element from the base of bed no. 13. (h) *W. inclinata*, lateral view (ha) and oral view (hb) of Pa element from base of bed no. 13. (i) *Wurmiella excavata excavata* (Branson & Mehl), lateral view (ia) and oral view (ib) of Pa element from base of bed no. 13. (j) *W.* cf. *excavata*, lateral view of Pa element, bed no. 2. (k) *Ozarkodina typica*, lateral view (ka) and oral view (kb) of Pa element, bed no. 9. (l) *Ozarkodina typica* Branson & Mehl, lateral view (la) and oral view (lb) of Pa element from the base of bed no. 13. (m) *O. typica*, lateral view (ma) and oral view (mb) of Pa element from the base of bed no. 13. (n) *O.* cf. *typica*, lateral view (na) and oral view (nb) of Pa element, bed no. 22. (o) *Oz. typica*, lateral view (oa) and oral view (ob) of Pa element from the base of bed no. 13. (p) *Oz. typica*, lateral view (pa) and oral view (pb) of Pa element from the base of bed no. 13. (q) *Delotaxis* sp., lateral view of incomplete element from the base of bed no. 13. (r) "*Ozarkodina*" *snajdri–crispa* transition, oral view of incomplete Pa element, bed no. 28. (s) *Oz. typica*, lateral view of Pa element, bed no. 22. (t) "*Ozarkodina*" *snajdri* or *crispa*, lateral view of Pb element, bed no. 22. (u) *Oz. typica*, lateral view of Pb element from the base of bed no. 13. (v–z) "*Ozarkodina*" *snajdri* Walliser, lateral views (va–vz) and oral views (vb–vz) of Pa elements from bed no. 22.

Figure 5. Middle and late Ludfordian graptolites from the Všeradice section. (a) *Neocucullograptus kozlowskii* Urbanek: PŠ 2028, upper part of bed no. 10; (b, f, g, k–n) *Slovinograptus balticus* (Teller): (b) PŠ 2020, (f) PŠ 2011, (g) PŠ 2018, (k) PŠ 2016, (l) PŠ 2017-1, (m) PŠ 2017-2, (n) PŠ 2015, bed no. 20; (c) *Linograptus posthumus* R. Richter: PŠ 2029, lowermost part of bed no. 7; (d, e, j, r, s) *Pseudomonoclimacis latilobus* (Tsegelnjuk): (d) PŠ 2004, (e) PŠ 2023, (j) PŠ 2001, (r) PŠ 2006, (s) PŠ 2003, (d, j, r, s) bed no. 14, (e) bed no. 20; (h) *Pristiograptus dubius* (Suess): PŠ 2024, bed no. 31; (i) *Pseudomonoclimacis kosoviensis* (Bouček): PŠ 2009, bed no. 16; (o) *Polonograptus chlupaci* sp. nov.: PŠ 2030, lowermost part of bed no. 7; (p) *Pristiograptus fragmentalis* (Bouček): PŠ 2031, bed no. 27; (q) *Pseudomonoclimacis dalejensis* (Bouček): PŠ 2027b, bed no. 10. Vertical scale bars represent 1 mm.

Figure 6. Middle and late Ludfordian and basal Přídolí graptolites from the Všeradice section. (a, b) *Formosograptus formosus* (Bouček): (a) PŠ 2025, (b) PŠ 2303, bed no. 37; (c, d) *Neocolonograptus parultimus* (Jaeger): (c) PŠ 2026, (d) PŠ 2302, bed no. 37; (e) *Slovinograptus* cf. *balticus* (Teller): PŠ 2307, bed 33; (f) *Crinitograptus*? sp.: PŠ 2308, bed 33; (g-j) *Pseudomonoclimacis kosoviensis* (Bouček): (g) PŠ 2244; (h) PŠ 2114, (i) PŠ 2101, (j) PŠ 2110a, lowermost part of section VB; (k) *Neocucullograptus inexpectatus* (Bouček) ssp.: PŠ 2100, lowermost part of the section designated VB; (l) *Pseudomonoclimacis* aff. *kosoviensis* (Bouček): PŠ 2304, bed 27; (m) *Pristiograptus fragmentalis* (Bouček): PŠ 2309, bed no. 27; (n) *Neocolonograptus ultimus* (Perner): PŠ 2310, bed 39. Vertical scale bars represent 1 mm.

Figure 7. Middle and late Ludfordian and basal Přídolí graptolites from the Všeradice section. (a) *Neocucullograptus inexpectatus* (Bouček) ssp.: PŠ 2100, lowermost part of the section designated VB; (b) *Linograptus posthumus* R. Richter: PŠ 2029, lowermost part of bed no. 7; (c) *Formosograptus formosus* (Bouček): PŠ 2303, bed 37; (d) *Neocolonograptus parultimus* (Jaeger): PŠ 2302, bed 37; (e) *Neocolonograptus ultimus* PŠ 2310, bed 39; (f) *Slovinograptus* cf. *balticus* (Teller): PŠ 2307, bed 33; (g) *Bohemograptus tenuis* (Bouček): PŠ 2098, lowermost part of section VB; (h) *Crinitograptus*? sp.: PŠ 2308, bed 33; (i) *Pseudomonoclimacis dalejensis* (Bouček): PŠ 2027b, bed no. 10; (j, k) *Pristiograptus fragmentalis* (Bouček): (j) PŠ 2309, (k) PŠ 2031, bed no. 27; (l, p) *Slovinograptus balticus* (Teller): (l) PŠ 2018, (p) PŠ 2016, bed no. 20; (m) *Neocucullograptus kozlowskii* Urbanek: PŠ 2028, upper part of bed no. 10; (n) *Pristiograptus dubius* (Suess): PŠ 2024, bed no. 31; (o) *Polonograptus chlupaci* sp. nov.: PŠ 2030, lowermost part of bed no. 7; (q) *Pseudomonoclimacis latilobus* (Tsegelnjuk): PŠ 2006, bed no. 14; (r) *Pseudomonoclimacis* aff. *kosoviensis* (Bouček): PŠ 2304, bed 27; (s) *Pseudomonoclimacis kosoviensis* (Bouček): PŠ 2110a, lowermost part of section VB; All specimens x 5, vertical scale bar represents 1 mm.

Figure 8. Correlation of the Všeradice section with a shallow water succession exposed in the New Kosov Quarry section showing lithology, ranges of selected fossils, relative eustatic oscillation, and carbon isotope curve. Note that conodonts are not included because conodonts have not been studied in Kosov Quarry. The grey field indicates the interval of a sedimentary break in the Všeradice section. Data from Kosov Quarry are adopted from Kříž (1992) and Lehnert *et al.* (2007).

Figure 9. Kozlowskii Event: graptolite crisis recorded by Bohemian sections. Note that all ventrally curved graptolites dissapeared from the fossil record. Most species recorded for the first time from the *Pr. fragmentalis* Biozone suggest striking evolutionary links between Ludfordian and Přídolí graptolite faunas.

Figure 10. Correlation of late Ludlow graptolite and conodont biozones, bivalve communities and trilobite horizons in Bohemia with conodont biozones and formations in Gotland (including eustatic oscilation and climatic state as sugested by Lehnert *et al.* 2007*a*). Gaps in discussed Bohemian sections are indicated.

Figure 11. Type material of *Polonograptus chlupaci* sp. nov.; (a) holotype PŠ 631, (b) paratype PŠ 667/1; *Nc. kozlowskii* Biozone, Kosov Quarry, x 5. Scale bar represents 1 mm.

Table 1. Fauna and selected taphonomic features recorded in the limestone bed no 22 (late Ludfordian, *Pseudomonoclimacis latilobus-Slovinograptus balticus* Biozone). Sample weight is *c*. 15 kg. Abbreviations: S – number of specimens, D and A – number of disarticulated/articulated specimens in brachiopods, C and P – numbers of cephalons/pygidia in trilobite remains. S and D mean deeper/shallow-water faunal elements respectively. This taphocoenosis is composed of two different faunas mixed together in a gravity flow deposit. The respective faunas originated from relatively shallow and deeper slope settings.

Species	**S**	**D**	**A**	**C**	**P**	
Lissatrypa postfumida	27	20	7	-	-	
Jarovathyris canaliculata	21	8	13	-	-	D
Tabulata	15					S
Kirkidium sp.	14	14	-	-	-	S
Septatrypa aff. *verna*	11	5	6	-	-	
Atrypa sp.	10	9	1	-	-	S
Bryozoa indet.	9	-	-	-	-	S
Aulacoporida indet.	9	-	-	-	-	S
Rugosa indet. (slender form)	5	-	-	-	-	
Michelinoceras sp.	5	-	-	-	-	D
Janiomya aff. *flexa*	5	5	-	-	-	
Cromus aff. *bohemicus*	5	-	-	-	5	
Treptostomata indet.	3	-	-	-	-	S
Strophomenacea indet.	3	3	-	-	-	
Otarion sp.	3	-	-	3	-	
Orhoria sp.	3	3	-	-	-	
Navispira sp.	3	3	-	-	-	D
Euophalompterus sp.	3	-	-	-	-	S
Cryptophyllus copelandi	3	3	-	-	-	
Salopina sp.	2	2	-	-	-	
Ryckholtia cf. *ryckholti*	2	-	-	-	2	S
Rhynchonellidina indet.	2	2	-	-	-	
Resserella sp.	2	2	-	-	-	
Hyolithes sp.	2	-	-	-	-	
Arionoceras sp.	2	-	-	-	-	D
Pseudocycloceras sp.	1	-	-	-	-	
Plectodonta sp.	1	1	-	-	-	D
Platyceras sp.	1	-	-	-	-	
Orbiculoidea sp.	1	1	-	-	-	
Lyocelia sp.	1	-	1	-	-	
Lingulida indet.	1	1	-	-	-	
Isorthis aff. *tomyris*	1	1	-	-	-	S
Interproetus sp.	1	-	-	1	-	
Cheirurina indet.	1	-	-	1	-	
Harpetida indet.	1	-	-	1	-	
Decoroproetus sp.	1	-	-	1	-	
Ceratiocaris sp.	1	-	-	-	-	D
smooth ostracods	c	c	r	-	-	

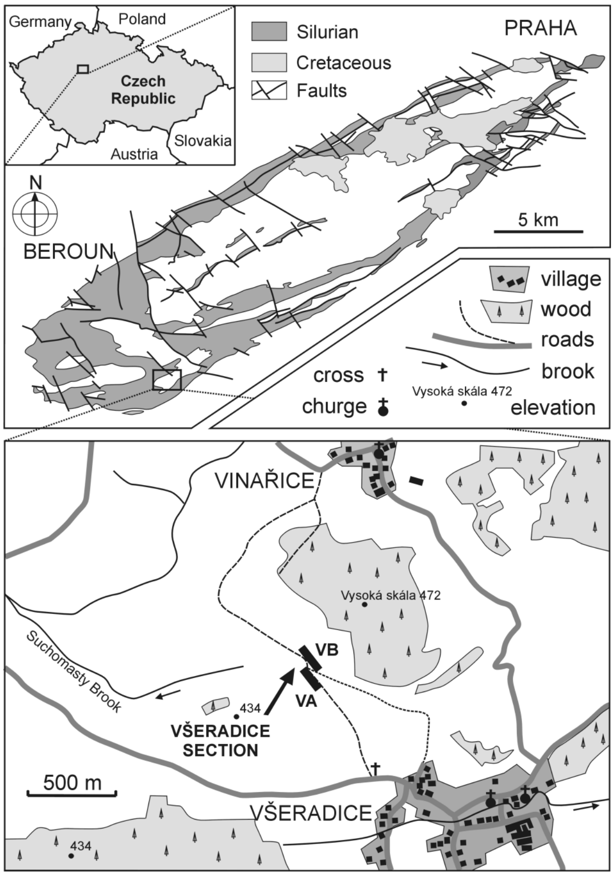

Germany
Poland
Czech Republic
Austria
Slovakia
Silurian
Cretaceous
Faults
PRAHA
N
BEROUN
5 km
village
wood
roads
brook
cross
churge
Vysoká skála 472
elevation
VINAŘICE
Vysoká skála 472
VB
VA
434
VŠERADICE SECTION
Suchomasty Brook
500 m
VŠERADICE
434

Fig. 1

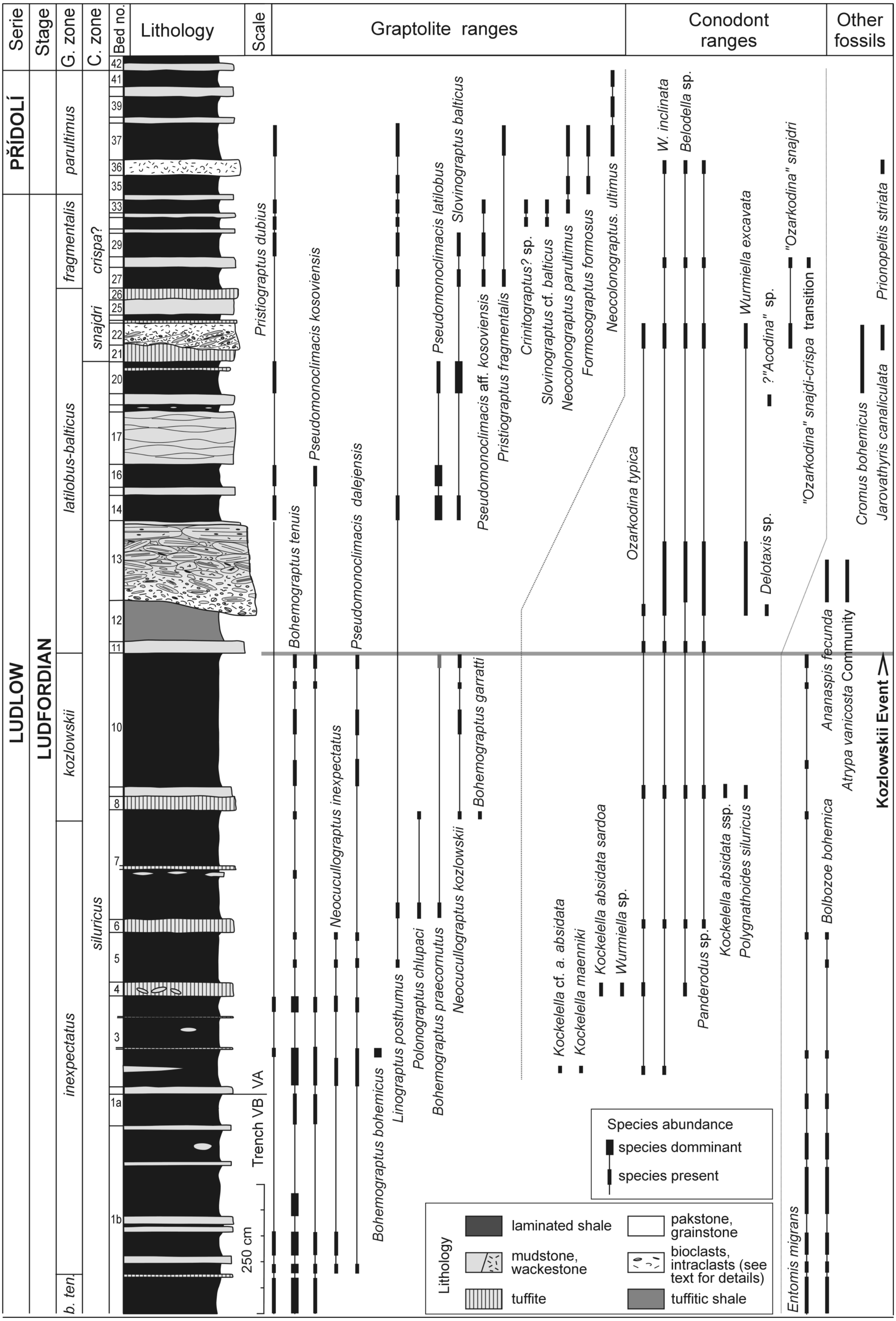

Serie
Stage
G. zone
C. zone
Bed no.
Lithology
Scale
Graptolite ranges
Conodont ranges
Other fossils
PŘÍDOLÍ
LUDLOW
LUDFORDIAN
parultimus
fragmentalis
latilobus-balticus
kozlowskii
inexpectatus
b. ten.
crispa?
snajdri
siluricus
42
41
39
37
36
35
33
29
27
26
25
22
21
20
17
16
14
13
12
11
10
8
7
6
5
4
3
1a
1b
Trench VB
VA
250 cm
Pristiograptus dubius
Pseudomonoclimacis kosoviensis
Pseudomonoclimacis latilobus
Slovinograptus balticus
Pseudomonoclimacis aff. kosoviensis
Pristiograptus fragmentalis
Crinitograptus? sp.
Slovinograptus cf. balticus
Neocolonograptus parultimus
Formosograptus formosus
Neocolonograptus. ultimus
Bohemograptus tenuis
Pseudomonoclimacis dalejensis
Neocucullograptus inexpectatus
Bohemograptus bohemicus
Linograptus posthumus
Polonograptus chlupaci
Bohemograptus praecornutus
Neocucullograptus kozlowskii
Bohemograptus garratti
W. inclinata
Belodella sp.
Wurmiella excavata
"Ozarkodina" snajdri
?"Acodina" sp.
"Ozarkodina" snajdri-crispa transition
Ozarkodina typica
Delotaxis sp.
Kockelella cf. a. absidata
Kockelella maenniki
Kockelella absidata sardoa
Wurmiella sp.
Panderodus sp.
Kockelella absidata ssp.
Polygnathoides siluricus
Prionopeltis striata
Cromus bohemicus
Jarovathyris canaliculata
Ananaspis fecunda
Atrypa vanicosta Community
Kozlowskii Event
Bolbozoe bohemica
Entomis migrans
Species abundance
species dominant
species present
Lithology
laminated shale
mudstone, wackestone
tuffite
pakstone, grainstone
bioclasts, intraclasts (see text for details)
tuffitic shale

Fig. 2

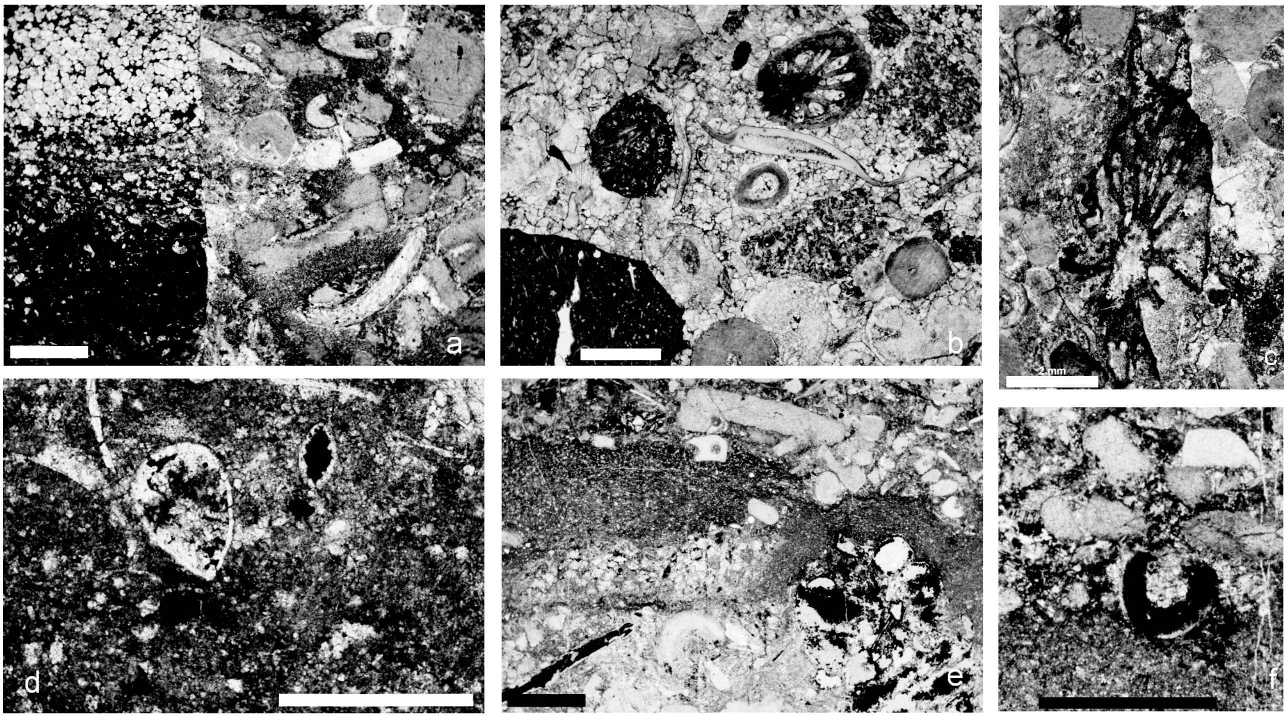
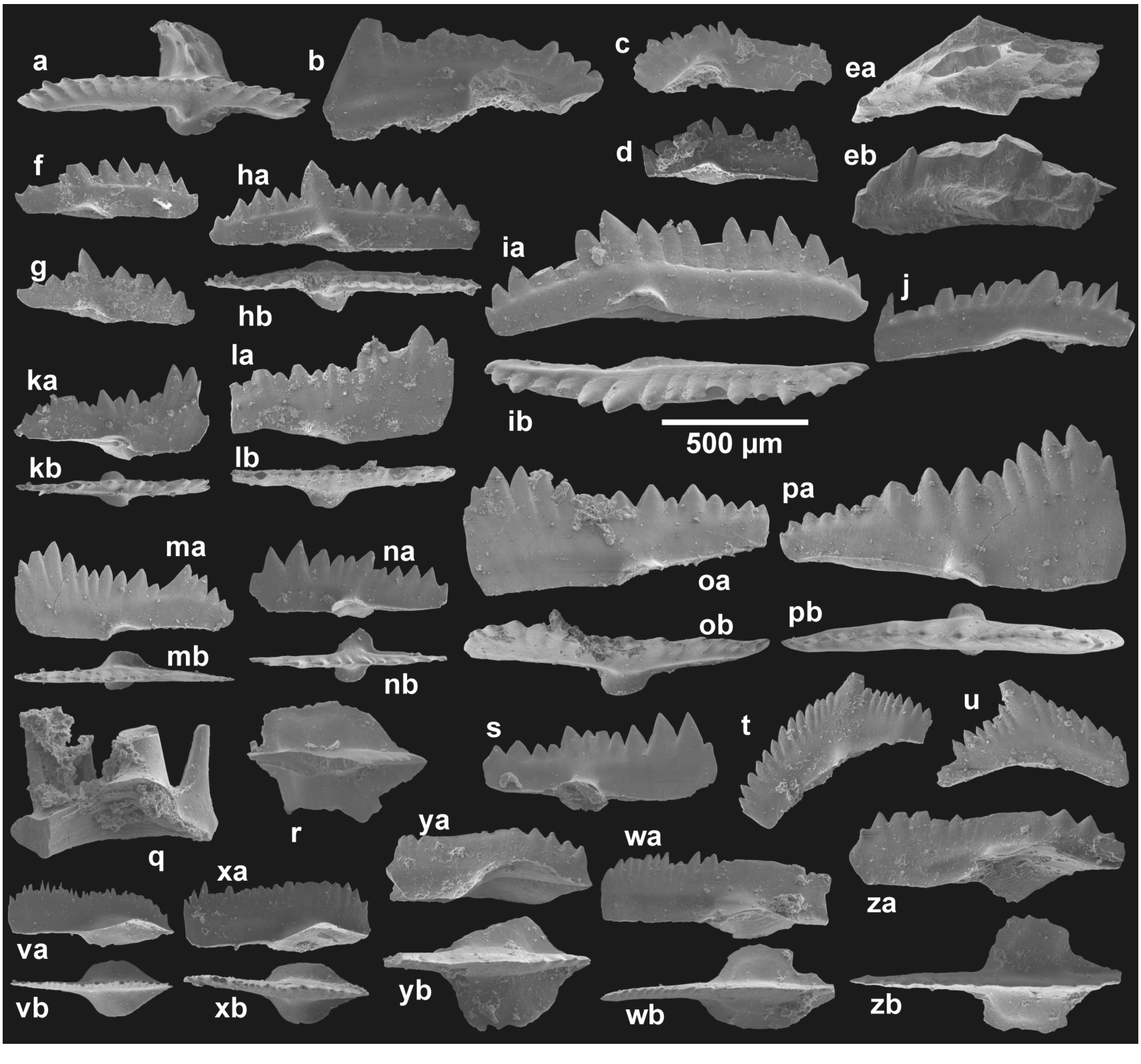

a
b
c
2 mm
d
e
f

Fig. 3


a
b
c
ea
d
eb
f
ha
g
hb
ia
j
ib
ka
la
kb
lb
500 µm
ma
na
oa
pa
mb
nb
ob
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q
r
s
t
u
ya
wa
za
va
xa
vb
xb
yb
wb
zb

Fig. 4

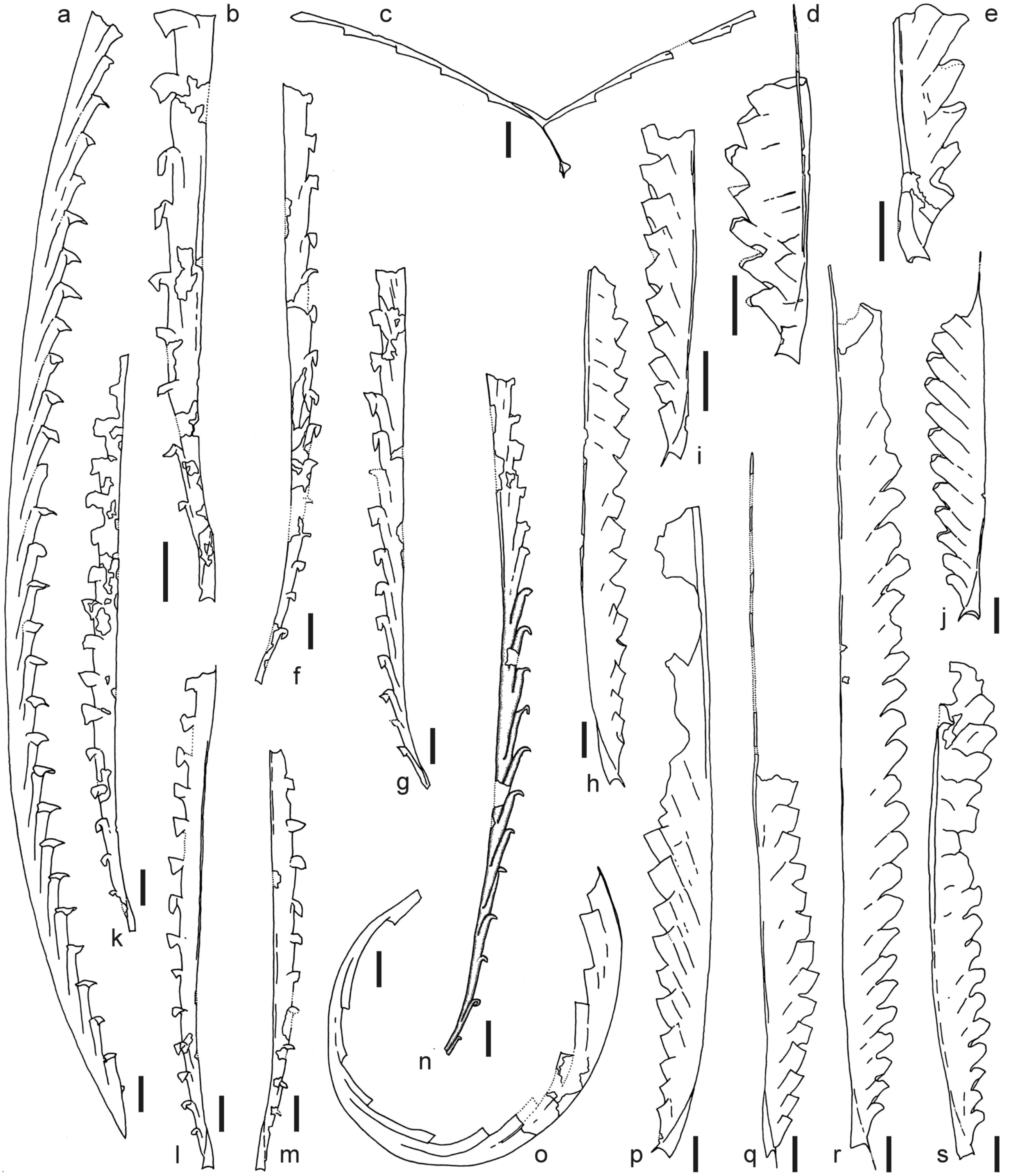


Fig. 5

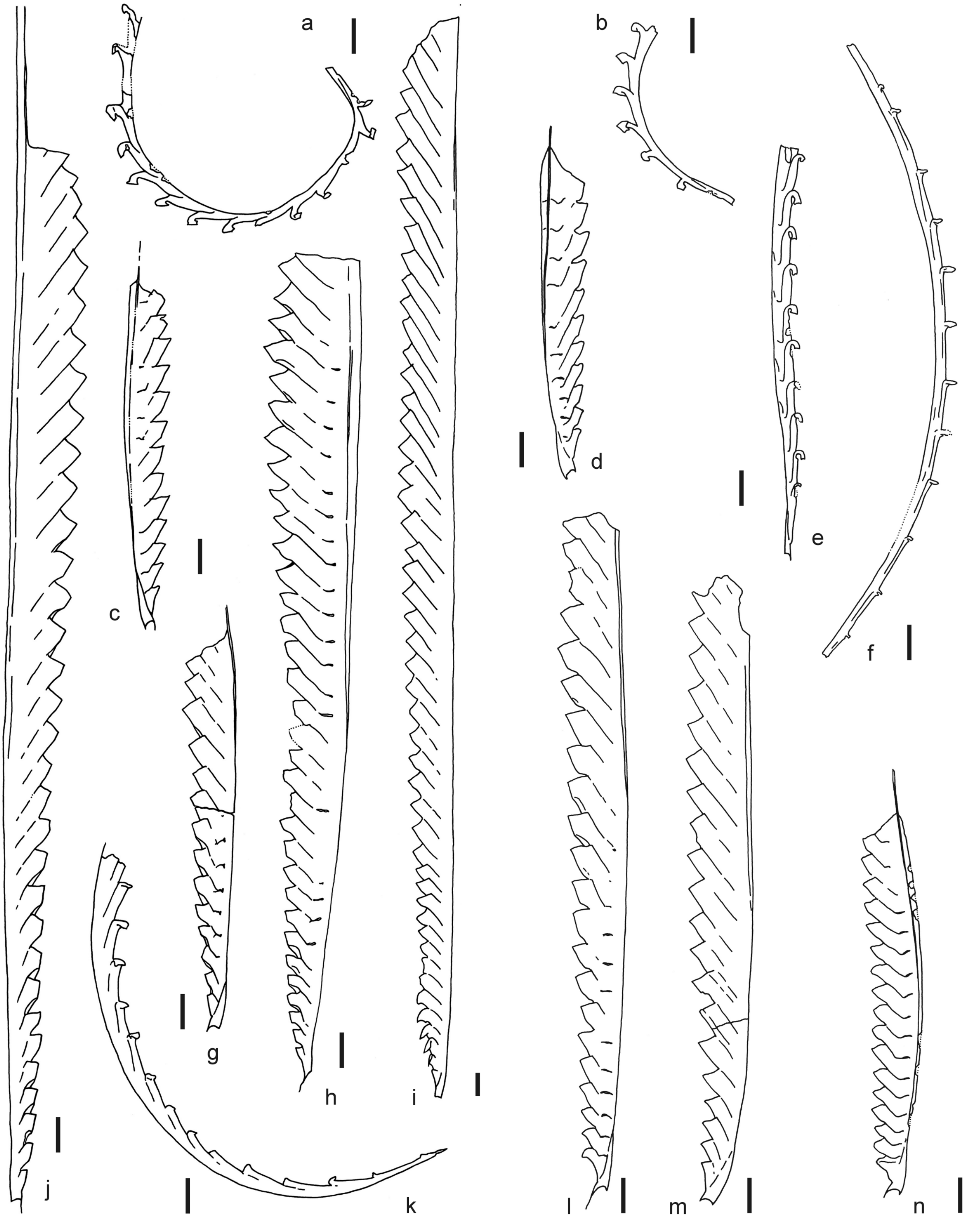


Fig. 6

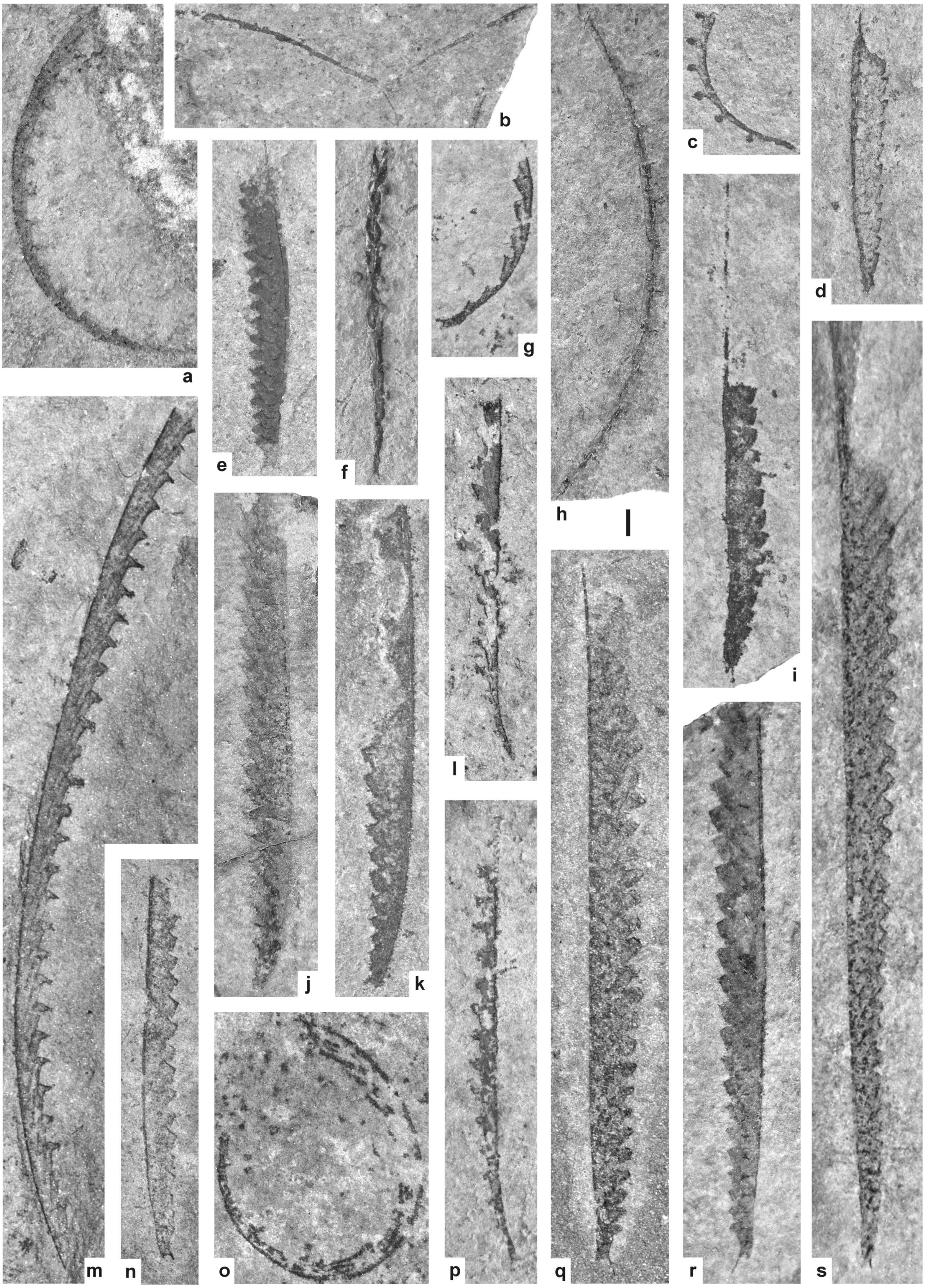


Fig. 7

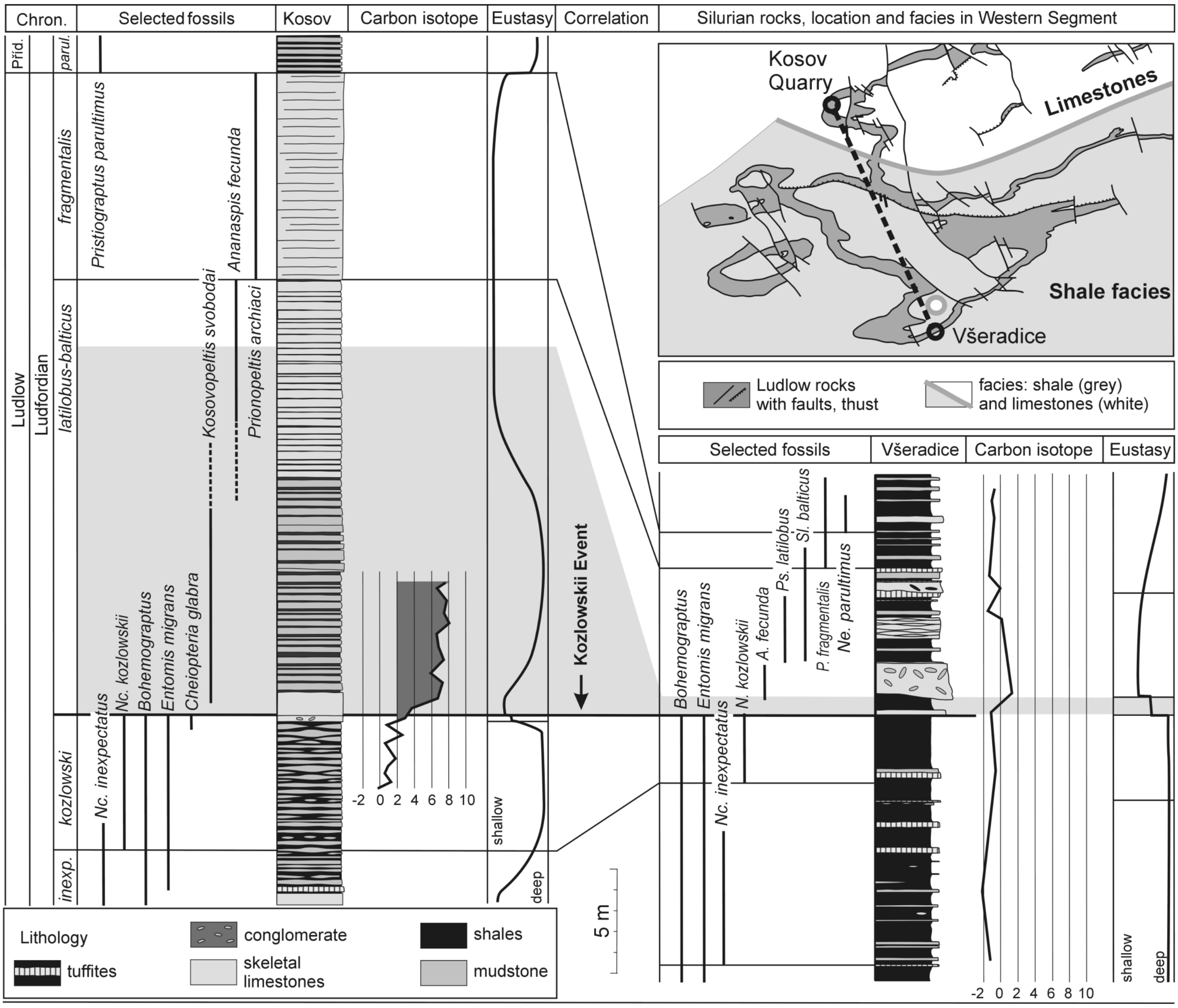

Chron.
Selected fossils
Kosov
Carbon isotope
Eustasy
Correlation
Silurian rocks, location and facies in Western Segment
Přid.
parul.
Ludlow
Ludfordian
fragmentalis
latilobus-balticus
kozlowski
inexp.
Pristiograptus parultimus
Ananaspis fecunda
Kosovopeltis svobodai
Prionopeltis archiaci
Cheiopteria glabra
Entomis migrans
Bohemograptus
Nc. kozlowskii
Nc. inexpectatus
Kozlowskii Event
-2 0 2 4 6 8 10
shallow
deep
Kosov Quarry
Limestones
Shale facies
Všeradice
Ludlow rocks with faults, thust
facies: shale (grey) and limestones (white)
Selected fossils
Všeradice
Carbon isotope
Eustasy
Bohemograptus
Entomis migrans
Nc. inexpectatus
N. kozlowskii
A. fecunda
Ps. latilobus
Sl. balticus
P. fragmentalis
Ne. parultimus
-2 0 2 4 6 8 10
shallow
deep
5 m
Lithology
tuffites
conglomerate
skeletal limestones
shales
mudstone

Fig. 8

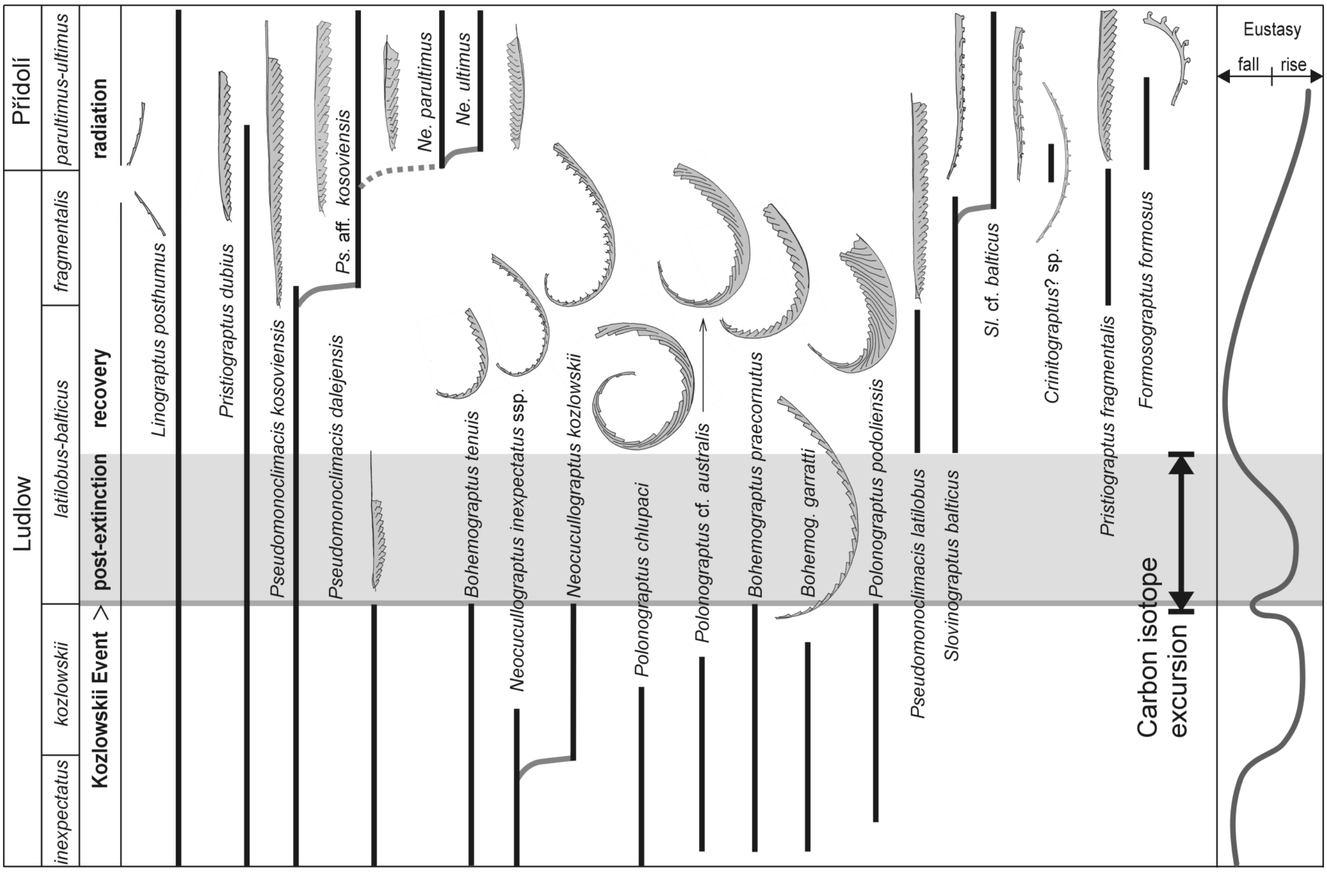
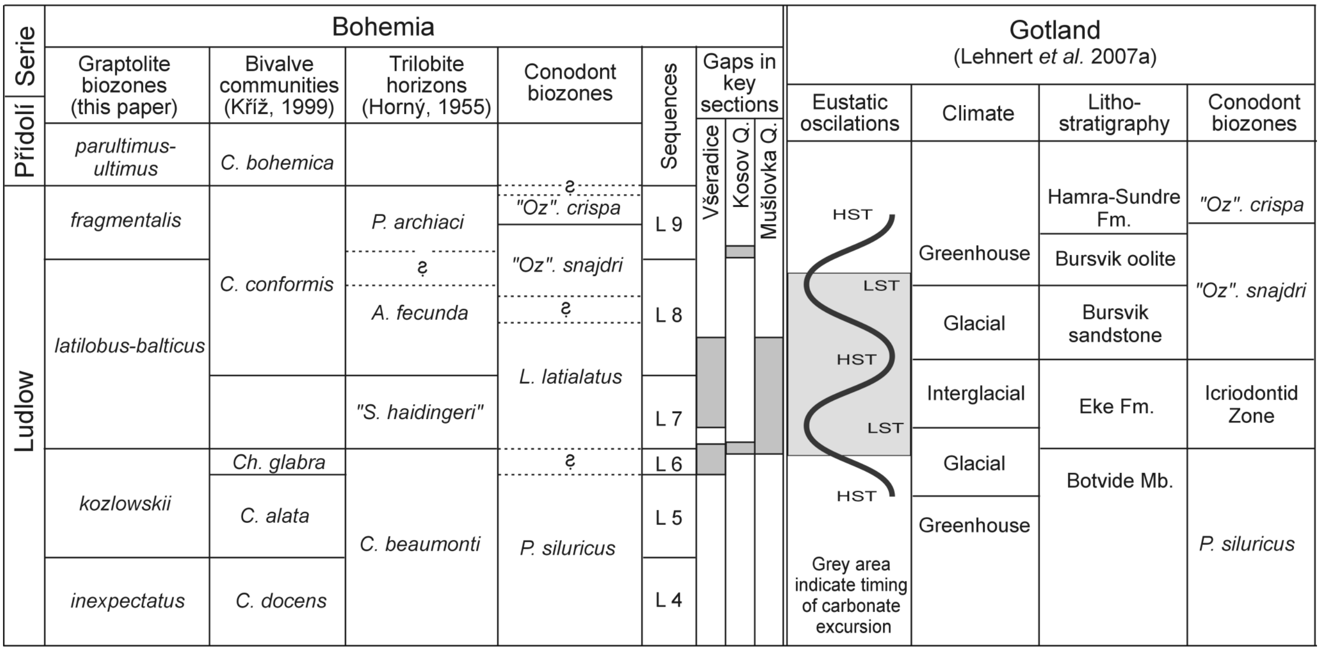


Fig. 9



Serie	Bohemia: Graptolite biozones (this paper)	Bivalve communities (Kříž, 1999)	Trilobite horizons (Horný, 1955)	Conodont biozones	Sequences	Gaps in key sections: Všeradice	Kosov Q.	Mušlovka Q.	Gotland (Lehnert *et al.* 2007a): Eustatic oscilations	Climate	Litho-stratigraphy	Conodont biozones
Přídolí	*parultimus-ultimus*	*C. bohemica*		?								
Ludlow	*fragmentalis*	*C. conformis*	*P. archiaci*	"*Oz*". *crispa*	L 9				HST	Greenhouse	Hamra-Sundre Fm.	"*Oz*". *crispa*
			?	"*Oz*". *snajdri*					LST		Bursvik oolite	"*Oz*". *snajdri*
	latilobus-balticus		*A. fecunda*	?	L 8				HST	Glacial	Bursvik sandstone	
			"*S. haidingeri*"	*L. latialatus*	L 7				LST	Interglacial	Eke Fm.	Icriodontid Zone
	kozlowskii	*Ch. glabra*	*C. beaumonti*	?	L 6				HST	Glacial	Botvide Mb.	*P. siluricus*
		C. alata		*P. siluricus*	L 5					Greenhouse		
	inexpectatus	*C. docens*			L 4				Grey area indicate timing of carbonate excursion			

Fig. 10

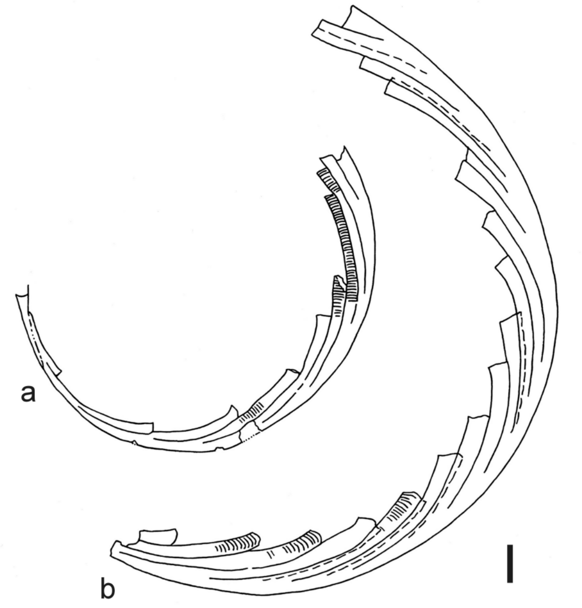


Fig. 11

PŘÍLOHA 13

Práce v tisku

Manda, Š., Turek, V. Přijato. Late Emsian Rutoceratoidea (Nautiloidea) from the Prague Basin, Czech Republic: morphology, diversity and palaeecology. Palaeontology.

LATE EMSIAN RUTOCERATOIDEA (NAUTILOIDEA) FROM THE PRAGUE BASIN, CZECH REPUBLIC: MORPHOLOGY, DIVERSITY AND PALAEOECOLOGY

by ŠTĚPÁN MANDA* *and* VOJTĚCH TUREK†

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Abstract: Nautiloids of the superfamily Rutoceratoidea from the late Emsian (late Early Devonian) of the Prague Basin (Czech Republic) are commented upon. Species recognized include the hercoceratids *Hercoceras mirum*, *H.*? *transiens*, *Ptenoceras proximum*, *P. nudum*, *P. minusculum* and *Anomaloceras anomalum*, as well as the rutoceratids *Adelphoceras bohemicum*, *Homoadelphoceras devonicans*, *Pseudorutoceras bolli* and *Goldringia*? *devonicans*. In addition, four new species are described: *Parauloceras regulare* sp. nov., *Roussanoffoceras chlupaci* sp. nov., *Otomaroceras* sp. nov. and *Goldringia* sp. nov. Morphology and distribution patterns of Pragian and late Emsian rutoceratoid faunas from the Prague Basin are compared. They show that an increased diversity was accompanied by a higher level of specialization of rutoceratoids, which manifested itself in low abundance, increased facies dependence and greater variation in shell size during the Early Devonian. The evolution of sculpture and a contracted aperture, both regarded as protective-adaptive features, was also examined, but no adaptive trend towards more pronounced sculpture and constriction of the aperture was found to have occurred in the Early Devonian. A more distinctive sculpture was, however, observed in shallow-water assemblages of *P. proximum* in comparison with deeper-water faunules, and two additional cephalopod species were examined in order to obtain comparative data. The presence of distinct sculpture patterns in coeval shallow- and deeper-water assemblages suggests limited migration between them and consequently reflects some degree of territoriality in Devonian nautiloids. New data on early shell development in *P. proximum* are presented. During the Chotreč Event, rutoceratoid generic diversity dropped dramatically, one family became extinct and the Early Devonian diversification of the group came to an end. The recovery of nautiloid faunas was slower than that of other cephalopods and associated, unrelated invertebrates. The absence of change in abundance patterns between Pragian and late Emsian rutoceratoid faunas, i.e. prior to and subsequent to ammonoid radiation, suggests that the appearance and radiation of the latter group in the early Emsian did not affect the structure of nautiloid assemblages, i.e. these two clades did not occupy the same niches.

Key words: Rutoceratoidea, taxonomy, shell morphology, palaeoecology, intraspecific variability, Devonian, Choteč Event, new taxa.

CEPHALOPODS are significant predators in Recent seas; in fact, they already were so as far back as the Early Ordovician. The composition and structure of cephalopod faunas changed substantially during their geological history. The relative stability in cephalopod faunas after the Ordovician radiation ended in the Devonian when these faunas changed markedly and ammonoids, nautilids and many nautiloid families appeared. However, changes in the Devonian marine ecosystems are still poorly understood and many models-explanations have been put forward. Among these is the hypothesis of a 'Middle Palaeozoic Revolution', as suggested by Signor and Brett (1984), which has often been discussed subsequently (e.g. Brett 2003; Kröger 2005; Klug 2007; Klug *et al.* 2008, 2009). The last-named authors collective explained some changes in morphology and abundance of invertebrates as due to an increased diversity and abundance of durophagous predators. The increasing diversity amongst nautiloids, with highly elaborated sculpture, was presented as an example. Without exception, all well-sculptured Devonian nautiloids are assigned to the Rutoceratoidea, which thus represents a model group for testing the present hypothesis. However, the majority of known taxa were described in the late nineteenth century and therefore are insufficiently documented and in need of revision.

The rutoceratoids (superfamily Rutoceratoidea Hyatt, 1884) comprise oncocerid nautiloids with curved and coiled exogastric shells and usually with highly elaborate sculpture, characterized by distinct outgrowths (wings, spines, nodes and collars). High disparity in shell form and growth structure patterns as well as a wide range of intraspecific variation is exceptional amongst nautiloids. Rutoceratoids include both species with small shells as well as the largest of known Palaeozoic nautiloids. With twenty-seven genera and in excess of a hundred described species, they represent the second most diversified group of Devonian nautiloids, the most diverse being the oncocerid family Entimoceratidae Zhuravleva, 1974.

Rutoceratoids arose close to the Lochkovian/Pragian boundary, disappeared in the early Frasnian (for summary see Manda and Turek 2009*a*) and formed a characteristic component of the temperate-water faunas of the Early–Middle Devonian Old World (e.g., Zhuravleva 1974, Dzik and Korn 1992, Turek 2007) and Middle Devonian Eastern American realms (Flower 1945, 1957). The Prague Basin (central Bohemia) represents one of the classic areas of fossiliferous Devonian strata and a long tradition of research and fossil collecting (for summary see Chlupáč 1993, 1998, 1999). Highly refined litho- and biostratigraphic subdivisions and extensive collections thus provide an extraordinary opportunity fordetailed studies. Large collections of rutoceratoids have been made from the Pragian Praha Formation and the late Emsian Třebotov Limestone. The Pragian rutoceratoids have recently been revised by Turek (2007) and Manda and Turek (2009*a*).

Our current knowledge regarding late Emsian rutoceratoids from the Daleje-Třebotov Formation is summarised and evaluated in the present paper and four new species are described. Morphology, distribution patterns and evolution of rutoceratoids in the Early Devonian are discussed.

TERMINOLOGY AND MATERIAL

The morphological terminology is adopted largely from Teichert (1964). The terms height, width and length are used as defined by Stridsberg (1985). For the terminology of growth structures reference is made to Manda and Turek (2009*a*).

The subclass Nautiloidea is used as defined by Teichert (1988), i.e. including the orders Discosorida, Oncocerida, Tarphycerida and Nautilida. According to this concept, straight-shelled cephalopods of the order Orthocerida, previously placed within the Nautiloidea, are excluded from nautiloids and placed in a separate subclass, Orthoceratoidea. Consequently, the nautiloids comprise cephalopods with similar general morphology, embryonic development and ontogeny as the Recent genus *Nautilus*, whereby we use the term ‘nautiloids’ to have the usual meaning in relation to palaeobiological studies and examination of long-term evolutionary trends (see Manda 2008; Kröger and Zhang 2009; Manda and Turek 2009*b*).

All specimens, except those figured in Plate 1, figures 1–7, 10–14 and Text-fig. 3A–C, E, F–G, were coated with ammonium chloride prior to photography.

Institutional abbreviations. NM L, National Museum (Prague); CGS, Czech Geological Survey Prague; in particular Š. Manda (prefix SM), I. Chlupáč (ICH) and ‘Palaeontological’ collections (CGS p); MCZ, Museum of Comparative Zoology, Harvard University (Cambridge).

CEPHALOPODS FROM THE LATE EMSIAN TŘEBOTOV LIMESTONE: AN OVERVIEW

In Barrande’s (1965*a*) concept, the ‘Etage G-g3’, which includes the Třebotov Limestone (late Emsian) and Choteč Limestone (Eifelian), yielded in addition to goniatitid ammonoids, an unusually diversified fauna of nautiloids and orthoceratoids. The vast majority evidently came from the upper part of the Třebotov Limestone (Text-fig. 1); only a few may have been collected from the Choteč Limestone. Barrande (1856, 1865*b*–1877) erected thirty species of *Orthoceras* Bruguière, 1789, twelve of *Phragmoceras* Broderip *in* Murchison, 1839, eleven of *Cyrtoceras* Goldfuss, 1833, eight of

Gomphoceras Sowerby *in* Murchison, 1839, four of *Gyroceras* Koninck, 1844, two of *Nautilus* Linnaeus, 1758, one of *Trochoceras* Barrande, 1848, plus three new genera: *Nothoceras* Barrande, 1856, *Hercoceras* Barrande, 1865*b* (each with one species) and *Adelphoceras* Barrande, 1870 (with two species).

The taxonomic assignment of some of Barrande´s species was subsequently discussed by Hyatt (1884, 1894, 1900), Foerste (1926), Flower (1938, 1945, 1950*a–b*, 1955), Flower and Teichert (1957), Zhuravleva (1972, 1974, 1978), Dzik (1984), Turek and Marek (1986), Dzik and Korn (1992), Manda (2001), Turek (2007, 2009) and Manda and Turek (2009*a*). Fourteen genera have been established based on Barrande's species from this stratigraphical level: *Anomaloceras* Hyatt, 1884, *Tripleuroceras* Hyatt, 1884, *Triplooceras* Hyatt, 1884, *Blakeoceras* Foerste, 1926, *Conostichoceras* Foerste, 1926, *Bolloceras* Foerste, 1926, *Homoadelphoceras* Foerste, 1926, *Paracleistoceras* Foerste, 1926, *Paraconradoceras* Foerste, 1926, *Poteriocerina* Foerste, 1926, *Turnoceras* Foerste, 1926, *Metaphragmoceras* Flower, 1938, *Piratoceras* Zhuravleva, 1974 (which is a subjective synonym of *Hercoceras*; see Turek 2007) and *Pseudorutoceras* Manda and Turek, 2009. Šulc (1932) described juvenile orthoceratids from the uppermost Třebotov Limestone at Prague-Holyně, while Turek (2007, 2009) studied the variability, early ontogeny and colour pattern in the genera *Hercoceras* and *Ptenoceras*.

Some of these species have not been revised since Barrande's time. Their modern generic assignment is in some cases unclear, especially in view of their state of preservation. Specimens were usually affected by post-depositional deformation. Moreover, they are often badly corroded, being generally preserved as internal moulds, occasionally with shell remains. However, internal features such as septa and siphuncle are frequently very well preserved. Despite the fact that the number of described species may exceed the real number of species that existed (for discussion see Dzik 1984, Turek and Marek 1986), the diversity of late Emsian non-ammonoid cephalopods in the Prague Basin was relatively high, as an outline by Zhuravleva (1972, 1974, 1978) illustrates.

Chlupáč (1959) and Chlupáč *et al.* (1979) published data on the stratigraphic range of some of Barrande's species, although the status of certain taxa mentioned is in need of revision. The great majority of nautiloids from the Třebotov Limestone have largely been incorrectly considered in the literature to be of Middle Devonian age (e.g., Kummel 1964; Zhuravleva 1972, 1974; Teichert *et al.* 1980; Kröger 2005), which has had an impact on conclusions concerning diversity and macro-evolutionary trends amongst nonammonoid cephalopods close to the Early/Middle Devonian boundary. Barrande's 'etage G-g3' includes the Třebotov Limestone (late Emsian) and Choteč Limestone (Eifelian) as currently defined (Chlupáč 1983*a*). The lithological characteristics of specimens preserved in light-grey micritic limestone (exceptionally in dark red micritic limestone) as well as remarks in Barrande's field books (see Chlupáč 1983*a*, 1999) testify to the fact that nautiloids assigned to 'Hlubočep G-g3' and 'Holyn G-g3' originate from the Třebotov Limestone and thus are of late Emsian age. The age of a few specimens preserved in dark grey micritic limestone of Barrande's 'etage G-g3' remains questionable; they may have come from the basal portion of the early Eifelian Choteč Limestone (Text-fig. 2).

NOTES REGARDING LATE EMSIAN RUTOCERATOIDEA FROM THE PRAGUE BASIN

Barrande (1865*b*–1877) described eleven species which subsequent authors referred to the rutoceratoids, from the lower part of his 'etage G-g3', which corresponds to the late Emsian, Daleje-Třebotov Formation (see Chlupáč 1998). Ten of these are considered valid and each of them is briefly discussed below. Species which have never been previously photographed, are now illustrated in that way. *Anomaloceras anomalum* is redescribed and the generic diagnosis emended. Four new species are described in the systematic section, but only two of them are formally named.

Family Hercoceratidae Hyatt, 1884

Hercoceras mirum Barrande, 1865*b*. The lectotype, NM L 242 (designated and refigured by Turek 2007), was illustrated by Barrande (1865*b*, pl. 42, figs 3, 4). It is from the Třebotov Limestone at Prague-Hlubočepy. This species is the commonest late Emsian rutoceratoid in the Prague Basin, with more than 600 specimens known. It was already described in detail by Barrande (1865*b*, 1867). Hyatt (1884, 1894, 1900) assigned the genus *Hercoceras* Barrande, 1865*b* to his family Hercoceratidae. Turek (2007) studied the shell variability of *H. mirum* (including in his concept the variety *Hercoceras mirum*? var. *irregularis* Barrande, 1865*b*) and described its juvenile shell. New data concerning the contracted aperture are included in the present paper (see chapter „Apertural modifications in rutoceratoids“ bellow).

Hercoceras? *transiens* (Barrande, 1865*b*). Holotype, by monotypy, is NM L 8061, which was originally assigned to the genus *Trochoceras* and illustrated by Barrande (1865*b*, pl. 30, figs 13–17) from the Třebotov Limestone at Prague-Hlubočepy (see Pl. 1, figs 3–4). The specimen is an internal mould, only moderately affected by deformation, but strongly corroded. In the plane-coiled shell, with two whorls, the adapertural part of the last whorl markedly diverges. The aperture is slightly contracted. Hyatt (1894) considered *T. transiens* to be assignable to *Hercoceras*. The absence of lateral outgrowths in *T. transiens* is probably due to poor preservation, but the general morphology of the shell is clearly identical with *Hercoceras*. Zhuravleva (1974) supported Barrande’s original combination. Nevertheless, *Trochoceras transiens* differs from *T. davidsoni* Barrande, 1865*b* (early Devonian, Pragian of Bohemia) in having a markedly depressed cross section and in lacking intrasiphonal deposits and lateral outgrows near the aperture.

Ptenoceras proximum (Barrande, 1865*b*). Holotype, by monotypy, is NM L 10085, originally assigned to the genus *Gyroceras*, illustrated by Barrande (1865*b*, pl. 103, figs 12–14) from the Třebotov Limestone at Prague-Hlubočepy. The specimen is a corroded internal mould, of which the ventral surface was superficially artificially abraded to expose the siphuncle; the embryonic shell is preserved. In addition to the holotype, about 60 specimens were available for study; these are mostly undeformed internal moulds, but occasionally shell remains are preserved. The diameter of fully-grown specimens ranges between 30 and 50 mm. This is an easily recognized species due to the characteristic whorl section and sculpture on the border area between the dorsal and ventral sides and one pair of small lateral processes near the aperture in adult specimens.

Hyatt (1894) was the first to place this fairly common species in his newly established genus *Ptenoceras* (type species: *Ptenoceras alatum* of Pragian age) in the family Hercoceratidae. Although Barrande (1865*b*) figured only a single specimen, about 60 specimens are available for study (National Museum and Czech Geological Survey collections).

Ptenoceras nudum (Barrande, 1865*b*). Three specimens of *Gyroceras nudum* were illustrated by Barrande (1865*b*, pl. 43, figs 8–9 [NM L 9085], figs 10–11 [NM L 9088] and fig. 12 [NM L 9086]); all from the Třebotov Limestone at Prague-Hlubočepy. Due to the preservation of Barrande’s specimens, it was not possible to determine with certainty if all specimens do belong to the same species. They differ especially in the shape of shell and cross section. The largest specimen (NM L 9085) is an internal mould, strongly affected by deformation. In its strongly depressed shell and shell size, it resembles *Hercoceras mirum*, although no traces of ventrolateral outgrows are visible. An artificially abraded fragment of a shell (NM L 9086) displays the siphuncle. Its systematic position is questionable especially in view of its extreme lateral expansion rate. Specimen NM L 9088 illustrated by Barrande (1865*b*, pl. 43, figs 10, 11) is designated lectotype herein. It is not deformed; the only slightly superficially artificially abraded shell represents the fully-grown stage with an enrolled adapertural part of the body chamber. A pair of ventrolateral nodes is preserved. As far as shell morphology is concerned, it is similar to a well-preserved specimen illustrated by Turek (2009, fig. 3a), which preserves the colour pattern. In total, four specimens are known (National Museum, CGS p4912).

Gyroceras nudum was considered to belong to *Hercoceras* by Hyatt (1894). Turek (2009) transferred it to *Ptenoceras* on account of its similarity both to the type species of that genus, *P. alatum*, and to *P. proximum.* Turek (2007) and Manda and Turek (2009) pointed out that *Ptenoceras* and *Hercoceras* may be distinguished not only on general shell shape and cross section, but also on the appearance of lateral outgrowths rather than the mode of coiling or character of outgrowths (wings *vs* spines); in *Ptenoceras* one or two pairs of outgrowths appear just before the end of shell growth (wings or spines), while in *Hercoceras* outgrowths (spines, rarely wings) are already visible on the first whorl. However, on internal moulds these features are frequently poorly visible or even missing.

Ptenoceras minusculum (Barrande, 1865*b*) comb. nov. Holotype, by monotypy, is NM L 8060. The type specimen, originally assigned to *Gyroceras*, was illustrated by Barrande (1865*b*, pl. 30, figs 18–21) from the Třebotov Limestone at Prague-Hlubočepy (see Pl. 1, fig. 2). A strongly corroded internal mould, ventrally artificially abraded to expose the empty siphuncle. The position of the siphuncle was noted to be eccentric by Barrande (1865*b*), but this cannot be confirmed. The shell is loosely coiled, expands moderately and is strongly depressed. A pair of lateral outgrowths (not shown in Barrande's original figure) is present near the aperture and there is a faint indication of a node sinistrally. Their shape was similar to those in *P. proximum* and *P. nudum*. All these features indicate a close relationship between this species and the genus *Ptenoceras*. In addition to the holotype, only two additional specimens are known (CGS SM 338, National Museum collections).

Family Rutoceratidae Hyatt, 1884

Adelphoceras bohemicum Barrande, 1870. Holotype, by monotypy, is NM L 21496, illustrated by Barrande (1870, pl. 459, figs 1–4) from the Třebotov Limestone at Prague-Hlubočepy. *Adelphoceras* Barrande, 1870 is a monospecific genus, its type species being poorly known. The holotype, which is the sole specimen known, represents half of the last whorl and is preserved as a slightly deformed internal mould (Pl. 1, figs 11, 12, 14). Hyatt (1884, 1894) classified the latter genus within the Rutoceratidae and this assignment was largely accepted (Flower 1950*a*; Ruzhencev *et al.* 1962; Kummel 1964; Zhuravleva 1972; Dzik 1984 and others). Although the aperture in the holotype is moderately contracted, the apertural margin is not preserved and Barrande's reconstruction with a T-shaped aperture cannot be considered anything else than hypothetical (Dzik 1984). Flower (1945) mentioned actinosiphonate deposits; however, this observation has not been confirmed. The apparently slightly torticonic shell of *A. bohemicum* mentioned by Furnish and Glenister (*in* Kummel 1964) may be a reflection of diagenetic processes.

'Adelphoceras' secundum (Barrande, 1877). Holotype, by monotypy, is NM L 21897, illustrated by Barrande (1877, pl. 461, figs 4–6; pl. 474, fig. 1) from Hlubočepy G-g3. The holotype is a deformed internal mould preserved in dark grey micritic limestone which corresponds to either the upper portion of the Třebotov Limestone or the basal levels of the Choteč Limestone. It represents half a whorl; the diameter of the whorl is 163 mm, the maximum height and width 54 mm and 93 mm, respectively. The shell is convolute, exogastric, in cross section strongly depressed, with a shallow, broad impressed zone; the siphuncle is slightly shifted from the ventral side. We have been unable to observe the growth lines and recurrent growth ridges with a shallow, broad ventral lobe and lateral lobes which are so clearly shown in Barrande's illustrations. Barrande (1877) originally assigned this species to *Adelphoceras*, which, however, is characterized by an irregularly coiled shell, nodes, contracted aperture and growth structures without lateral lobes. No diagnostic feature of rutoceratoids is visible in '*A.*' *secundum*.

Goldringia? *devonicans* (Barrande, 1866) comb. nov. The holotype, NM L 15414, was illustrated by Barrande (1866, pl. 240, figs 1, 2, as *Cyrtoceras devonicans*); it is from the Třebotov Limestone at Prague-Hlubočepy (see Pl. 1, fig. 1). The specimen is an internal mould of the body chamber with a single phragmocone chamber. In spite of strong corrosion, conspicuous longitudinal ribs combined with distant transverse ribs are clearly visible. The length of the longitudinal ribs is markedly less than that of the transverse ones. Thus, the surface sculpture is reminiscent of that of the Early–Middle Devonian genus *Goldringia* Flower, 1945, in particular of the Givetian *G. cyclops* (Hall, 1861) from New York State (see Hall 1892, pl. 54, fig. 1). The siphuncle is very probably situated close to the ventral side but the internal structure is unknown. On account of the very poor preservation, taxonomic assignment remains uncertain although its assignment to the family Rutoceratidae is well supported.

Homoadelphoceras devonicans (Barrande, 1866). Holotype, by monotypy, is NM L 10320. Barrande (1866, pl. 240, figs 16, 17) illustrated it from the Třebotov Limestone at Prague-Hlubočepy (Pl. 1, figs 5, 10). The specimen is an internal mould of the phragmocone with incomplete body chamber which is obliquely longitudinally dislocated, preserved in light grey biomicritic limestone, with the phragmocone being strongly deformed by compaction. The diameter of the shell is 36 mm, its maximum length and width being 53 mm and 70 mm, respectively. The planispirally coiled, depressed shell appears expand laterally rapidly, but the apical angle may have been considerably influenced by deformation and corrosion. The body chamber was probably less coiled than the phragmocone so that the shape of the shell was probably similar to that in *Adelphoceras*. Six rows of prominent tubercles (two lateral on each side and one ventral pair) are the most characteristic feature of the sculpture seen on the corroded surface of the internal mould. They were probably situated on transverse ribs. The first artificially abraded preserved phragmocone chamber revels a ventrally situated siphuncle with radial plates within the septal foramen. Flower (1950*a*) placed *Homoadelphoceras* in the family Rutoceratidae and this assignment has been largely accepted (Ruzhencev *et al.* 1962; Kummel 1964; Zhuravleva 1972 and others). According to Dzik (1984), the type specimens of *H. devonicans* and *A. bohemicum* are conspecific. Due to poor preservation of both specimens we can neither confirm nor refute this opinion. With the exception of the extreme expansion rate in *H. devonicans*, which may in part be the result of secondary diagenetic processes, we have not found any important difference between *H. devonicans* and *A. bohemicum*.

Pseudorutoceras bolli (Barrande, 1877). Lectotype (designated by Manda and Turek 2009*a*) is NM L 24212 as illustrated by Barrande (1865*b*, pl. 42, figs 3, 4, as *Cyrtoceras bolli*) from the Třebotov Limestone at Prague-Hlubočepy. This species is the type of *Pseudorutoceras* Manda and Turek, 2009*a*; the surface sculpture (undulating frills) which resembles a colour pattern was recently discussed by Turek (2009). In total, four shells of *P. bolli* are known, all of them being figured types.

SYSTEMATIC PALAEONTOLOGY

Subclass NAUTILOIDEA Agassiz, 1847
Order ONCOCERIDA Flower, 1950*a*
Superfamily RUTOCERATOIDEA Hyatt, 1884
Family PARAULOCERATIDAE Manda and Turek, 2009

Genus PARAULOCERAS Manda and Turek, 2009

Type species. Cyrtoceras pupus Barrande, 1877, designated by Manda and Turek, (2009*a*), Early Devonian (Pragian), PragueBasin.

Discussion. To date, *Parauloceras* is known only from Early Devonian strata of the Prague Basin where it is represented by an evolutionary lineage containing two closely related species, *Parauloceras pupus* (Barrande, 1877) from the early-middle Pragian (Dvorce-Prokop and Loděnice limestones) and *P. regulare* sp. nov. from the late Emsian (Třebotov Limestone).

Parauloceras regulare sp. nov.
Text-figure 3A–C

partim 1877 *Cyrtoceras pupus* Barr., Barrande, pl. 464, figs 8–10.
partim 1877 *Cyrtoceras pupus* Barr., Barrande, pp. 41–42.
2001 *Uloceras* sp. nov.; Manda, p. 270.
2009 *Parauloceras* sp. nov.; Manda and Turek, p. 134.

Derivation of name. From the Latin adjective *regulare* (regular).

Types. Holotype is NM L 34506 (Text-fig. 3A–C); paratype is an unregistered body chamber with two phragmocone chambers in Barrande's Collection (National Museum, Prague).

Type locality and horizon. Prague-Holyně (Prague Basin, Bohemia); Třebotov Limestone (Daleje-Třebotov Formation), late Emsian.

Material. Only the types are known to date.

Diagnosis. Parauloceras with relatively high phragmocone chambers, four raised growth ridges on the body chamber (in fully-grown specimens), moderately depressed cross section and thin siphuncle.

Description. The holotype is an internal mould of a slightly curved, exogastric and longiconic shell. Maximum shell length, height and width are 63 mm, 14 mm and 17 mm, respectively. The angle of expansion is *c.* 15 degrees. In cross section, the shell is depressed (height/width ratio 0.8). The septa are moderately concave, the suture straight and oblique. The height of the phragmocone chambers increases from 2 to 5 mm. The siphuncle is thin, with a maximum diameter of 2 mm; it is in contact with the shell wall and the connecting rings are very moderately vaulted. Four straight growth ridges with ventral lobes are visible on the body chamber whose length is 26 mm. The aperture is open. The hyponomic sinus is shallow and broad. A second available specimen (see Barrande 1877, pl. 464, figs 8–10) is a body chamber with two phragmocone chambers; it exhibits the same morphological features as the holotype.

Discussion. Manda (2001) and Manda and Turek (2009*a*) suggested that the specimen which Barrande (1877, pl. 464, figs 8–10) illustrated as *Cyrtoceras pupus* Barrande, 1877 was a new species of *Uloceras* Zhuravleva, 1974 or of *Parauloceras*, respectively. This species from Prague-Hlubočepy (G-g3) is here formally named.

Occurrence. Early Devonian, late Emsian. Bohemia: Praha-Holyně and Praha-Hlubočepy (upper part of Třebotov Limestone, Daleje-Třebotov Formation).

Family HERCOCERATIDAE Hyatt, 1884

Genus OTOMAROCERAS Manda and Turek, 2009

Type species. Trochoceras flexum Barrande, 1865*b*, designeted by Manda and Turek (2009*a*), Early Devonian (Pragian), Prague Basin.

Species included. Otomaroceras flexum (Barrande, 1865*b*) and *O. tardum* (Barrande, 1865*b*), both from
Pragian strata of the Prague Basin, as well as *O.* sp. nov. described below.

Otomaroceras sp. nov.

Text-figure 3D

Type/Material. A single specimen, CGS SM 339.

Type locality and horizon. Prague-Hlubočepy (Prague Basin, Bohemia); Třebotov Limestone (Daleje-Třebotov Formation), late Emsian.

Description. CGS SM 339 is an internal mould of a near-complete shell, lacking the apical part. The shell is a planispirally tightly coiled, exogastric shell. In cross section, it is depressed (height/width ratio 0.8). The length of the phragmocone chambers varies between 2 and 3 mm (measured on the lateral side). The suture is straight with broad ventral lobes. The body chamber is expanded and less coiled than the phragmocone. The shell is preserved only on the body chamber; fine growth lines are intercalated with recurrent growth ridges, the distance between them being *c.* 5 mm; growth structures are straight, oblique with shallow, narrow ventrolateral lobes and a broad ventral lobe. The body chamber is 56 mm in length. The aperture is open and oblique with a lateral sinus. The maximum shell diameter, height and width are 60, 21 and 27 mm, respectively.

Discussion. Otomaroceras sp. nov. resembles *O. tardum* from Pragian strata, but differs in having more densely packed and more oblique recurrent growth ridges with minute ventrolateral lobes and a less coiled body chamber than phragmocone in the fully-grown shell. *Otomaroceras* sp. nov. represents the first record of this genus from strata of Emsian age.

Genus ANOMALOCERAS Hyatt, 1884

Type, and sole, species. *Nautilus anomalus* Barrande, 1865*b*, designated by Hyatt (1884), Early Devonian (Emsian), Prague Basin.

Diagnosis (emended). The shell is coiled, evolute, with a broad, shallow impressed zone, the whorl section being reniform and strongly depressed. The thin empty siphuncle is slightly expanded within the phragmocone chambers; it is moderately shifted dextrally from the sagittal plane. The shell has prominent growth lines, with accentuated ridges forming a ventrolateral sinus indicating the presence of ventrolateral outgrowths adaperturally.

Discussion. Hyatt (1884) established the present genus based on Barrande's *Nautilus anomalus* in the family Hercoceratidae; no comments were added to the generic diagnosis. Later, Hyatt (1894) supported his previous statement and suggested that *Anomaloceras* was remarkable in the eccentric position of its siphuncle, but in its shell form and sculpture resembled *Hercoceras*. Zhuravleva (1974) transferred *Anomaloceras* to the Late Palaeozoic family Aipoceratidae Hyatt, 1883 (Nautilida). Dzik (1984, pp. 86, 91), albeit with a query, synonymized *Anomaloceras anomalum* with *Nothoceras bohemicum* (Barrande, 1856). *Nothoceras*, however, differs from *Anomaloceras* in having a thicker siphuncle with actinosiphonate deposits and a suture with deep ventral saddles. Nevertheless, in the same paper Dzik (1984, p. 156) also synonymized *Anomaloceras* with *Hercocoeras*. Manda and Turek (2009*a*) did not find any substantial rutoceratoid diagnostic feature in *Anomaloceras*. During the latest revision of Barrande's collection a specimen with preserved growth structures, including lateral recurrent growth lines with lateral lobes, was examined (see Pl. 1, fig. 8). This feature clearly demonstrates that *Anomaloceras* belongs to the Hercoceratidae. With respect to the reniform cross sectionl, widely open aperture, narrower dextrally shifted siphuncle and appearance of ventrolateral outgrowths in the late growth stage, it differs markedly from *Hercoceras.*

The wide evolute shell of *Anomaloceras* is rather exceptional among Early Palaeozoic nautiloids and resembles that of some Late Palaeozoic nautilids (see Zhuravleva 1974). A planispirally coiled shell usually exhibits a siphuncle positioned in the median plane; however, all *A. anomalus* shells available for study exhibit an eccentric siphuncle shifted to the right. The function of an eccentrically situated siphuncle is questionable. It may represent a non-adaptive feature, inherited from an ancestor having a slightly torticonic shell. Asymmetry in the position of the siphuncle has also been ascertained in some specimens of *Ptenoceras alatum*, *P. nudum*, *Hercoceras mirum* and *H.*? *transiens*; in *Anomaloceras*, however, this feature is the most striking.

Anomaloceras anomalum (Barrande, 1865)
Plate 1, figures 1, 6–9, 13

1865 *Nautilus anomalus* Barr., Barrande, pl. 34, figs 3–6.
1884 *Anomaloceras anomalus* Barr; Hyatt, p. 283.
1889 *Anomaloceras anomalum*; Hyatt, pp. 494, 599, pl. 8, figs 16–20.
non 1895 *Nautilus anomalus* Barr.; Katzer, pp 7, 8, pl. 2, figs 8–10.

1926 *Anomaloceras anomalum* (Barrande, 1865); Foerste, p. 382.
1962 *Anomaloceras anomalum* (Barrande, 1865); Ruzhencev *et al.*, p. 382.
1964 *Anomaloceras anomalum* (Barrande, 1865); Kummel, p. 416.
1974 *Anomaloceras anomalum* (Barrande, 1865); Zhuravleva, pp. 137, 138.
partim 1984 *Nothoceras bohemicum*; Dzik, pp. 86, 91.

Lectotype. NM L 8057, illustrated by Barrande (1865, pl. 34, figs 3–5), designated herein (see Pl. 1, figs 1, 7, 9); paralectotype is NM L 8066 (illustrated by Barrande 1865*b*, pl. 34, fig. 6).

Type locality and horizon. Prague-Hlubočepy (Prague Basin, Bohemia); Třebotov Limestone (Daleje-Třebotov Formation), late Emsian.

Material. In addition to the types, eight additional specimens, all in the Barrande Collection. A specimen figured by Hyatt (1889) and deposited in the Schary Collections at the Museum of Comparative Zoology could not be traced during our recent visit.

Description. An exogastric shell, evolute with a maximum of two and a quarter whorls; the adapertural part of the shell in fully-grown specimens may be enrolled, with the aperture widely opened. The imprint zone is broad and shallow. The angle of expansion in a lateral view is *c.* 12 degrees, whereas in ventral view it is 21 degrees. In cross section, the shell is reniform and strongly depressed (height/width ratio 0.5). The siphuncle is ventral, not in close contact with the outer shell wall, empty and thin; the segments are fusiform with short septal necks, being orthochaanitit to subortochoanitic. Septa very shallow. The suture is very slightly undulating, with a broad, shallow ventral lobe, narrow, lateral and dorsal saddles are faintly visible. The phragmocone chambers are of low height, 15 per adapertural half of the whorl in the paralectotype, 12 in the lectotype. There is some indication of recurrent ventrolateral nodes in later growth stages. Growth lines, oblique to the axis laterally, but ventrolaterally may form a small deep sinus indicating the presence of two pairs of ventrolateral outgrowths in fully-grown specimens; ventrally they form a shallow, broad hyponomic sinus. The length of the body chamber is about half a whorl. Maximum diameter, width and height of the shell are 100, 79 and 38 mm, respectively.

Remarks. All specimens available for study are internal moulds. In one specimen only (Pl. 1, fig. 8), a trace of shell sculpture is preserved ventrolaterally in the adapertural part of the phragmocone. It documents the primary presence of ventrolateral outgrowths in this part of the shell, morphologically similar to or identical with outgrowths appearing in *Hercoceras* and an important feature for classifying *Anomaloceras* amongst rutoceratoids. The specimen belongs to the unfigured original type series on which the genus was established. This is confirmed by Barrande's inscription on the specimen ('Hlubočep An 5'), which means '5th anomalum specimen', as well as by the original label attached to the specimen.

A specimen from the Koněprusy Limestone, which was identified by Katzer (1895) as *Nautilus anomalus*, in fact most probably belongs to *Ptenoceras alatum.*

Occurrence. Prague-Hlubočepy and Prague-Holyně (single shell).

Family RUTOCERATIDAE Hyatt, 1884

Genus ROUSSANOFFOCERAS Foerste, 1925*a*

Type species. Roussanoffoceras depressum Foerste, 1925*a*, designated by Foerste (1925*a*), Early Devonian (early Emsian), Novaya Zemlya, Russia.

Diagnosis. See Zhuravleva (1996, p. 19).

Discussion. Recurrent raised growth walls (megastriae) in *Roussanoffoceras* resemble those of *Goldringia* Flower, 1945 from which genus it probably is derived. However, the present genus differs in having a greater angle of shell expansion (laterally as well as ventrally). In cross section, it is compressed and ventrally flattened, the cross section in *Goldringia* being subcircular or only slightly compressed. The new species constitutes the first record of the genus outside Novaya Zemlya.

Species included. Roussanoffoceras depressum Foerste, 1925*a* (including *R. costatum* Foerste, 1925*a*; see discussion in Zhuravleva 1996) and the new species from Bohemia, named below.

Roussanoffoceras chlupaci sp. nov.

Text-figure 3E, G–H

Derivation of name. After Ivo Chlupáč (1931–2002) for his contributions to stratigraphy and palaeontology of the Early Palaeozoic.

Types. Holotype is NM L 40788 (see Text-fig. 3E, G); paratypes are NM L 13489, NM L 27420 and NM L 27421.

Type locality and horizon. Prague-Hlubočepy (Prague Basin, Bohemia); Třebotov Limestone (Daleje-Třebotov Formation), late Emsian.

Diagnosis. *Roussanoffoceras* with larger shell, closely spaced transverse ribs and a slightly to moderately depressed cross section.

Description. A gyroceraconic exogastric shell with two whorls. The angle of expansion is *c.* 15 degrees in lateral view and 20 degrees in ventral view. In cross section, the shell is depressed and dorsally flattened (height/width ratio 0.7) or subcircular and only very slightly depressed. The siphuncle is marginal, without contact with the shell wall, empty and thin; the connecting rings are weakly developed and the septal necks are short. The septa are very shallow. The suture is straight, oblique with a shallow dorsal lobe. The length of the phragmocone chambers increases from 3 mm (height 18 mm) to 7 mm (height 45 mm). Recurrent ribs are intercalated with gentle growth lines. The course of the ribs is straight and oblique to the axis of the shell; on the ventral side, shallow ventral saddles may be seen. The distance between individual ribs increases from 9 mm (height 22 mm) to 21 mm (height 55 mm). The body chamber is 48 mm in length, with a shell height of 37 mm. The aperture open. Maximum shell length, height and width are 140, 55 and 49 mm, respectively.

Discussion. All available specimens are similar in general shell shape, but differ in cross section, two specimens being slightly depressed (Text-fig. 3H) and two others markedly depressed (Text-fig. 3E, G). Intraspecific variability in cross section within the Rutoceratoidea is considerable, usually being relatively high. In four of the available shells of *R. chlupaci* sp. nov. it is not possible to examine the variability in more detail. Variation in cross section (wider *vs* narrower shell) may also reflect sexual dimorphism (for summaries see Teichert 1964; Ward 1987).

Remarks. Two specimens deposited in the National Museum were labelled as *Gyroceras nude* Novák, ‘Gyroceren böhmens’. However, O. P. Novák (1851–1892) never published any paper with this classification.

Occurrence. Early Devonian (late Emsian); Třebotov Limestone (Daleje-Třebotov Formation) of the Prague Basin, Bohemia (localities Praha-Hlubočepy and Praha-Holyně).

Genus GOLDRINGIA Flower, 1945

Type species. *Gyroceras cyclops* Hall, 1861, designated by Flower (1945), Middle Devonian (Eifelian), New York State, USA.

Discussion. Goldringia is a common rutoceratoid in the Middle Devonian of New York State and adjacent areas in the Eastern American Realm (Flower 1945, 1957; Baird and Brett 2008). The Early Devonian record of *Goldringia* is poorly documented. *Goldringia gondola* Manda, 2001, the oldest known species of the genus, occurs in Pragian and early Emsian strata of the Prague Basin (Manda 2001; Turek 2007; Manda and Turek 2009*a*). Slightly younger is *G. valnevensis* Zhuravleva, 1996 from the late Pragian of Novaya Zemlya (Russia) and *Goldringia* sp. from the early Emsian of the Robert Mountains, Nevada (unpublished specimen, CGS SM 343). All other species known to date are of Middle Devonian age (Flower 1945; Zhuravleva 1974). Consequently, *Goldringia* sp. nov. (and perhaps *G.*? *devonicans*, see above) from the late Emsian of the Prague Basin fills a gap.

Goldringia sp. nov.

Text-figure 3F

Type/Material. CGS SM 342.

Type locality and horizon. Prague-Hlubočepy (Prague Basin, Bohemia); Třebotov Limestone (Daleje-Třebotov Formation), late Emsian.

Description. The single shell available is part of a whorl with a partially preserved sculptured body chamber; on the right side, the shell is deeply corroded. The shell was probably loosely planispirally, exogastrically coiled, and slightly expanding, its maximum length and diameter being 54 and 18 mm, respectively. In cross section, it is subcircular. The siphuncle is thin and ventral. The phragmocone chambers are low in height (observed on the right-hand corroded side). Septa are very slightly convex. The suture is straight and on the lateral side. The maximum preserved length of the body chamber is 27 mm. Sculpture consists of very fine growth lines and recurrent raised growth walls, their distance increases from 2 mm (in diameter 10 mm) to 5 mm (in diameter 18 mm); growth structures are straight with a shallow, narrow ventral lobe.

Discussion. Goldringia sp. nov. differs from all congeners in having relatively low recurrent growth ridges and undulated growth lines. Transverse ridges have not been observed.¨

THE DALEJE-TŘEBOTOV FORMATION: GEOLOGICAL SETTING AND PRESERVATION CONDITIONS

In the Prague Basin, the latest Emsian Daleje-Třebotov Formation is represented by three principal facies, the Daleje Shale, Třebotov Limestone and Suchomasty Limestone. For a summary reference is made to Chlupáč (1998). The Daleje Shale (Barrande's 'etage G-g2') comprises green, grey and reddish shale and is found in the northeastern part of the Prague Synform, passing laterally into the Třebotov Limestone. Chlupáč (1959) suggested that this unit alternated with Třebotov Limestone in areas with a high siliciclastic influx. So far, no nautiloid has been described from this facies, but flattened shells of ammonoids and orthoceratoids are quite common (Barrande 1865*b*–1877; Chlupáč 1959; Chlupáč and Turek 1983).

The lower part of the Třebotov Limestone (thickness *c.* 16 m) is developed as platy red-coloured limestones intercalated with shales (*Polygnatus serotinus* and *Nowakia richteri* zones) in the Prague-Hlubočepy area. Only a few rutoceratoids housed in old collections originate from these beds. The upper part of the Třebotov Limestone (thickness *c.* 18 m) is developed as light grey, coarsely bedded biomicritic limestones (latest *P. serotinus*–early *P. costatus partitus* and *N. richteri–N. holynensis* zones; see Chlupáč 1959, 1993, Chlupáč *et al.* 1977, 1979, 1980). The vast majority of cephalopods assigned to 'Hlubočep Gg3' originate from these beds. The early Eifelian Choteč Limestone at Prague-Hlubočepy (thickness *c.* 6 m) is represented by well-bedded limestone, differing from the underlying Třebotov Limestone by subordinate, darker grey, fine-grained bioclastic intercalations and a slightly darker colour of biomicrites (Chlupáč 1959, 1993; Berkyová 2009). Consequently, the stratigraphic provenance of specimens in old collections may be evaluated upon rock character.

Cephalopods are usually preserved as more or less corroded internal moulds. However, the shells and their internal moulds are usually complete with preserved septa, only the apex is frequently missing (e.g., Pl. 1, figs 2–8). Large shells are commonly affected by limestone dissolution on their surface (e.g., Pl. 1, fig. 1). In addition, some larger shells are moderately deformed (e.g., Pl. 1, figs 12–14). Betterpreserved specimens were collected in particular from strongly weathered limestones, 'white beds', from which fossils were extracted by washing (e.g., Pl. 2, figs 2, 3) at Prague-Holyně, 'George' (Bouček 1931; Kříž 1999) and an unknown site at Prague-Hlubočepy (Text-fig. 1). Miners collected the vast majority of available cephalopods in the late nineteenth and early twentieth centuries (see Hanuš 1923; Kříž 1999) from large active quarries in the vicinity of the village of Hlubočepy (i.e., locality Hlubočep G-g3 in Barrande) and less frequently at the village of Holyně (i.e., locality Holín G-g3 in Barrande). Detailed descriptions of these quarries were provided by Barrande (1865*a*), Wahner (1916), Storm (1935) and especially by Chlupáč (1959) and Chlupáč *et al.* (1979, 1980). The assumed stratigraphic distribution of rutoceratoids based on lithological characteristics is shown in Text-fig. 2. Interestingly, the Třebotov Limestone outside the areas of Hlubočepy and Holyně yielded only few nautiloids (Chlupáč 1959). This limited distribution of rutoceratoids in the Daleje-Třebotov Limestone suggests that most late Emsian rutoceratoids (similar to others nautiloids) inhabited a relatively narrow facies (depth) zone even within the depositional area of the Třebotov Limestone (Text-fig. 5).

A relatively small-sized benthic fauna, comprising gastropods, trilobites, hyolitids and rare brachiopods, co-occurs with nautiloids in the Třebotov Limestone; it indicates a well-oxygenated, firm muddy bottom, but below wave base. Some better-preserved shells (*Hercoceras*) contain common crinoid holdfasts and in one case also *Microconchus* tubes. Nevertheless, the large crinoid reefs observed on some bedding planes of nodular limestones suggest the occasional presence of hardgrounds. Common nowakiids and stylolinids, juvenile orthoceratoids and bactritids are indicative of open marine conditions, while common, relatively complete cephalopod shells with preserved inner structures reflect a low-energy environment. Straight orthocerid shells are weakly orientated (Petránek and Komárková 1953). Consequently, it is assumed that rather weak, yet stable, bottom currents ventilated the lower level.

The Suchomasty Limestone (middle part of 'etage F-f2' of Barrande) is developed in the Koněprusy area, southwest of the Prague Synform (Rohlich 2007). This facies consists of thin-bedded, reddish crinoidal limestones (wacke-grainstone) with common trilobites, brachiopods and stromatactis cavities (Chlupáč 1998; Hladil *et al.* 2006, 2007). Orthoceratoids and ammonoids are locally common (Chlupáč 1959; Chlupáč and Turek 1983). Nautiloids are represented by relatively rare, but wellpreserved, specimens of *Ptenoceras proximum* (see Chlupáč 1955, 1996; Chlupáč and Vaněk 1957; Chlupáč *et al.* 1979). The Suchomasty Limestone overlies a karst surface; it was deposited in a shallow, well-agitated aquatic environment above wave base (Chlupáč 1998).

APERTURAL MODIFICATIONS IN RUTOCERATOIDS

Contraction of the aperture is a reliable feature indicative of a fully-grown shell (e.g., Flower and Teichert 1957; Stridsberg 1981, 1985, 1988; Manda 2008), which enables assessment of variability in shell size in cephalopod populations. In some cases, apertural modifications supposedly accompanied changes in the mode of life of nautiloids (Prell 1921; Flower 1957; Stridsberg 1981, 1985; Manda 2008). Configuration of the aperture depends totally on the accretion mode of shell material by the mantle and any disturbance of the mantle's outer edge would have produced variations in the normal apertural pattern of the species (Stridsberg 1981, 1985). The apertural shape is a feature that has been widely used for taxonomic purposes in nautiloids. However, as pointed out by Stridsberg (1985), the minor differences in morphology have occasionally been overestimated.

A contracted aperture is commonly developed in Early Palaeozoic nautiloids with straight or slightly curved breviconic shells (i.e., with a more or less downward-oriented aperture), but is exceptional in coiled nautiloids (in which the aperture was usually oriented anteriorly in life). It indicates a protective function of the contracted aperture, previously suggested by Teichert (1964). *Hercoceras mirum* and *Adelphoceras bohemicum* (Pl. 1, figs 11, 12, 14) are the only known Devonian rutoceratoids with a markedly contracted aperture. The shape of the fully-grown aperture in the latter species is poorly known, because it is not completely preserved in the specimen available (Pl. 1, fig. 14). An apertural contraction of the aperture in *Hercoceras* was originally described and illustrated by Barrande (1865*b*, 1867) and recently mentioned by Turek (2007). Its character strongly resembles apertural modifications in the Ordovician coiled tarphyceratid *Moreauoceras* Cullison, 1944, and this feature has also been reported from the Ordovician coiled tarphyceratid *Pilotoceras* Cullison, 1944 and the trocholitid *Graftonoceras* Foerste, 1925*b*. It may also be fairly common in other tarphyceratids and in the family Trocholitidae Chapman, 1857 (see Furnish and Glenister 1964), but this assumption has not yet been fully tested.

During a revision of *Hercoceras mirum*, sixty-eight specimens with a constricted aperture were found. Other specimens available for study (mainly from the Barrande Collection) were either incomplete or did not represent the fully-grown stages of the shell. The diameter of fully-grown shells ranges between 68 and 125 mm (Turek 2007). Shell material near the aperture is usually missing; consequently, the character of the aperture has to be derived from the morphology of usually incomplete internal moulds (Text-figs 4, 5). If there is shell material preserved, it is markedly thickened near the constricted aperture (as in Silurian oncocerids and discosorids; compare Stridsberg 1985; Manda 2008).

The constriction is the result of differential growth of the aperture. While the accretion of shellmaterial on the ventral margin had almost ceased, it continued dorsally but in a markedly different direction. In lateral view, the resulting aperture looks like a partially laterally-closed visor (Text-fig. 5A–C) or, more commonly, the dorsal side is bent under a right angle (Text-fig. 5D). Ocular sinuses, if present, are only vaguely indicated. The result of this process is a markedly restricted apertural opening. In frontal view, almost two-thirds of the aperture may be closed. The dorsal side in this case is vaulted, sometimes with a faint, wide median groove or it is simply flat. The apertural margin forms a very shallow dorsal sinus. The boundary between the dorsal side of the shell adjacent to the previous whorl and the free part adjoining the aperture is usually rounded. In a few cases, when shell growth continued at right angles, this boundary is sharp. Owing to retarded growth of the shell on the ventral side and presence of a wide, shallow hyponomic sinus, the apertural opening remains fairly large. Exceptionally, the aperture in fully-grown specimens is widely opened with only a slightly modified shape on the dorsal side (Text-figs 4E, 5E, F). From a deep, narrow sinus in the aperture, lateral spines originated, which morphologically (Text-fig. 4B–D) strongly resemble the spines of the Jurassic ammonite *Aspidoceras* (Checa and Martin-Ramos 1989).

The shape of the aperture in nautiloids reflects the morphology of the soft body close the aperture. Accordingly, in the fully-grown adult stage of *H. mirum* the majority of tentacles could not point directly forwards but faced obliquely downwards. In this growth stage, the animal's tentacles were in closer contact with the sea floor. A similar effect was achieved in nautiloids with an uncoiled body chamber (e.g., some tarphyceratids; see Flower 1955). Eyes were located at about one-third of the dorsoventral diameter of the whorl from the ventral side, i.e. far lower than in the Recent *Nautilus* and Triassic *Germanonautilus* Mojsisovics, 1902 (see Klug and Lehmkuhl 2004 and further references therein). The shape of the aperture, in addition to the general morphology of the shell, supports the assumed nektobenthic mode of life (Turek 2007). The advantage of a partially closed, downward-oriented aperture in the fully-grown stage may be enhanced protection of the soft parts against predators close to the bottom.

In addition to the type, *Hercoceras* also includes some other Emsian-Eifelian species (Dzik 1984; Manda and Turek 2009*a*). However, a contracted aperture has been demonstrated only in *H. mirum*. This is interesting, because the contracted aperture is usually shared by all species of a genus or even family in the Nautiloidea, for instance in the Silurian families Hemiphragmoceratidae Foerste, 1926, Mandaloceratidae Flower, *in* Flower and Teichert, 1957 and Trimeroceratidae Hyatt, 1900. Similar to sculpture strengthening, the contracted aperture is considered to be an adaptive protective feature (see Teichert 1964). Consequently, a constricted aperture should be a progressively evolving feature if the Devonian radiation of durophagous predators is taken into account (see Signor and Brett

1984). However, the limited occurrence of a contracted aperture in rutoceratoids suggests that the adaptive pressure to retain this feature was relatively low.

COMPARISON OF PRAGIAN AND LATE EMSIAN RUTOCERATOID FAUNAS IN THE PRAGUE BASIN

Comparison of Pragian and late Emsian rutoceratoid faunas is interesting with respect to possible evolutionary trends in the Early Devonian (see Signor and Brett 1984; Brett 2003; Kröger 2005; Klug 2007; Klug *et al.* 2008). Therefore, we comment here briefly on distribution patterns, abundance, shellm morphology (mode of coiling, sculpture) and range of shell size in both faunas. Pragian rutoceratoids (similar to other nautiloids) inhabited various environments, ranging from reefs to deeper-water settings on carbonate slopes below storm base; maximum diversity, however, is found in deeper-water settings just below storm wave base (see Manda and Turek 2009*a*). In comparison with Pragian faunas, Emsian nautiloid assemblages were restricted to a narrow facies belt in a deeper-water environment. It is remarkable that, despite the facies restriction, the total diversity of rutoceratoids (as in other nautiloids) increased during the latest Emsian, when compared to Pragian strata (see Text-fig. 6).

Nautiloids are, as a rule, relatively rare in both Pragian and Emsian strata in the Prague Basin. Among them, rutoceratoids are the commonest (Text-fig. 7). Both faunas exhibit a similar pattern of abundance: one or two common species (exclusively members of *Ptenoceras* and *Hercoceras*; see Dzik and Korn 1992; Manda 2001; Turek 2007) are accompanied by several markedly rare taxa. A marked predominance of one cephalopod species is a typical feature of both faunas. *Ptenoceras alatum* is the dominant species in Pragian faunas, while in late Emsian assemblages it is *H. mirum*. Calculated coefficients of dominance have relatively high values for both faunas. However, the latter value for late Emsian fauna (0.80) is significantly higher than that of the Pragian fauna (0.53). Dzik (1984, p. 187) concluded in a summary of his analysis of cephalopod phylogeny that, ‘ relatively variable compositions of the Devonian nautiloid faunas’ reflected the early radiation of ammonoids that, ‘occupied many niches utilised previously by the nautiloids’. Nevertheless, the unchanged abundance pattern between the Pragian and late Emsian rutoceratoid faunas, i.e. prior to and subsequent of ammonoid radiation (e.g., Chlupáč and Turek 1983; Klug *et al.* 2008) suggests that the appearance and radiation of ammonoids did not affect the structure of nautiloid assemblages (see also Kröger 2008), i.e., the two cephalopod clades did not occupy the same niches. In addition, the very low abundance of rutoceratoids should be taken into account in palaeobiogeographic analyses, simply because there is a strong sampling effect between traditional and poorly known terrains.

Another interesting evolutionary feature is the development of shell size (for a summary see Jablonski 1996). Text-figure 8 shows the maximum dimensions of Pragian and late Emsian rutoceratoids in the Prague Basin. The latter exhibit a wider variation in shell size and the average shell size increased in the late Emsian. A comparison of shell dimensions of nautiloids in Wenlock–early Lochkovian cephalopod assemblages from the Prague Basin (Manda and Turek 2009*b*; plus unpublished data) is interesting as it shows relative stability of shell size throughout that time period.

Rutoceratoids represent a single monophyletic Devonian clade of nautiloids with highly elaborate sculpture and shell outgrowths. Signor and Brett (1984) suggested that highly elaborate shell sculpture in nautiloids functioned as protection against predators and they also pointed out that increased diversity of well-sculptured nautiloids during the Devonian represented an adaptive reaction to the radiation of durophagous predators. In fact, the majority of Pragian and late Emsian rutoceratoids exhibit almost identical growth sculptures. The *Ptenoceras-Hercoceras* line represents a single exception; in the late Emsian, lateral outgrowths in *Ptenoceras* were reduced, contrary to the situation in the derived species, *Hercoceras mirum* in which the number of outgrowths significantly increased. Consequently, no consistent evolutionary trend is visible in the development of sculpture.

Kröger (2005) examined the diversity of tightly coiled forms and suggested an adaptive control of shell coiling. He correlated increased diversity of nautiloids with a nautiliconic shell with the radiation of durophagous predators. In addition, the diversity of rutoceratoids with a tightly coiled shell increased in the Early Devonian of the Prague Basin. Four Pragian rutoceratoids have an openly coiled shell; in the late Emsian, four species have an openly coiled shell while the shell of seven others is tightly coiled. The trend from an openly to tightly coiled shell is recorded especially in the *Ptenoceras-Hercoceras* line.

Highly dynamic changes in distribution pattern and morphology in Devonian nautiloids in the Prague Basin may reflect changes in marine communities on a global as well as a regional scale. Comparison of Pragian and late Emsian rutoceratoid faunas in the Prague Basin clearly suggests that rutoceratoids were restricted to a narrow facies zone just below storm wave base, that diversity increased (Text-fig. 9), that there were identical abundance patterns in which one or two species is (are) common while others are very rare, that amongst rutoceratoids an increased in shell size is noted, that sculpture patterns remained relatively stable, and that there was an increase in diversity of tightly coiled forms.

VARIABILITY OF SCULPTURE IN *PTENOCERAS* AND PALAEOECOLOGICAL IMPLICATIONS

Ptenoceras proximum is the sole late Emsian rutoceratoid known which has been found in both the shallow-water Suchomasty Limestone and the deeper-water Třebotov Limestone. The speces first occurred in the lowermost portion of the former unit (middle Emsian, latest Zlichovian, *N. elegans* Zone), in infill of submarine fissures (Neptunian dykes) at the Koněprusy-Voskop Quarry and in the Mramorová stěna Section (Chlupáč 1996). Shells have also been found in the pink- and red-coloured crinoidal limestone which characterizes the Suchomasty Limestone, i.e., in old material designated ‘Koněprusy’, but with exact localities unknown (see Chlupáč 1983*a*) and that from the locality Koněprusy-U transformátoru(Chlupáč and Vaněk 1957). *Ptenoceras proximum* is much commoner in biomicritic limestones such as Třebotov Limestone, at the localities Hlubočepy and Holyně (see Text-fig. 4); the species appeared in the Třebotov Limestone slightly later than in the Suchomasty Limestone, but both populations were primarily coeval.

We have compared shell morphology in assemblages from both units. The mode of coiling, cross section and direction of growth structures are almost identical. A distinct feature in which the two assemblages differ is sculpture. All seven shells available from the Suchomasty Limestone show strengthening of growth ridges in a narrow zone between the ventral and dorsal side; the growth ridges here are more pronounced and form small nodes. The vast majority of shells from the Třebotov Limestone are poorly preserved. However, shells with fine, or even very fine, growth lines may be distinguished. Shells exhibiting lateral strengthening of growth lines are also present. In addition, the strengthening in sculpture appears later in ontogeny in shells from the Třebotov Limestone than in those from the Suchomasty Limestone (Pl. 2). In summary, shells with fine growth lines predominate.

A smooth shell, or gentle growth lines, are developed in embryonic shells of *Ptenoceras proximum* from the Třebotov Limestone (Pl. 2, figs 1–4). Embryonic shells of this species from Suchomasty, however, exhibit a more elaborate sculpture. Fine irregular growth lines are developed on the apex; approximately at the position of the first phragmocone chamber, regular densely packed growth lines appear. With age, the distance between growth lines increases and a ventral lobe may also be seen (Pl. 2, fig. 9). This change in sculpture probably corresponds with hatching time.

Although the shell morphology of adult specimens and size of embryonic shells is very similar (i.e., suggesting conspecificity), the tightness of coiling varies greatly in early shells of *P. proximum*. A similarly wide range of intraspecific variation in umbilical perforation has been reported for the Pragian rutoceratoid *Ptenoceras* (Turek 2007). Specimens from the Suchomasty Limestone show a very small, drop-like umbilical perforation (width 0.5–1 mm; see Pl. 2, figs 9, 11), while shells from the Třebotov Limestone usually have a much larger umbilical perforation (maximum width 2.9 mm; Pl. 2, fig. 4), but specimens with a small and mid-range umbilical perforation can also be found (Pl. 2, figs 3, 4).

The small hatching size in *Ptenoceras* (just before the shell reached one-quarter whorl) resembles that of the Silurian *Phragmoceras* and *Boionautilus* Turek, 2008 (Manda 2008; Turek 2008); that of Mesozoic nautilids and extant *Nautilus* (Chirat and Rioult 1989, and further references therein) is much longer. Consequently, hatching size may be useful for higher-taxa grouping within the Nautiloidea, but more data are needed.

Strengthening of growth sculpture in a shallow-water environment is not surprising. Metabolic precipitation of calcium carbonate is more effective in warm and highly oxygenated water, i.e. a shallow-water setting. Many modern tropical gastropod molluscs exhibit strengthening of sculpture in a shallow-water environment (see Graus 1974; Vermej 1987). A similar pattern has been reported for Palaeozoic nautiloids by Hewitt and Watkins (1980), but, for example, a comparison of populations of Silurian nautiloids *Ophioceras* Barrande, 1865*b* and *Phragmoceras* from Gotland (a tropical carbonate platform) and the Prague Basin (a temperate zone) did not reveal any differences in shell sculpture (see Stridsberg and Turek 1997; Manda 2007*b*, 2008).

Distinct sculpture differences in occurrences of *P. proximum* in shallow- and deeper-water environments suggests that there was no significant migration between the two populations. Occasional migration from a shallow- to a deep-water setting cannot be excluded, as a single shell of *P. proximum* from the Třebotov Limestone (see Pl. 2, fig. 1) shows; this exhibits a near-identical sculpture to shells from the Suchomasty Limestone. Consequently, *Ptenoceras* should be regarded as a more or less territorial animal, which, in general, did not migrate during its lifetime between different environmental settings. Finds of early post-hatching specimens in the shallow-water Suchomasty Limestone as well as in the deeper-water Třebotov Limestone document the presence of specific hatching places in both environmental settings.

We have also compared the palaeogeographic differences in sculpture pattern in Early Devonian nautiloids and their sister clade, the pseudorthocerids, which have straight shells as in orthocerids, but a cup-like embryonic chamber with a cicatrix as in nautiloids. However, the vast majority of taxa are restricted to a certain facies or their abundance strongly changes in different facies and thus sufficient comparative material was not available. The two Pragian species selected for consideration were *Ptenoceras alatum* (Barrande, 1865*b*), which is the precursor of *P. proximum* (Manda 2001; Turek 2007) and the pseudorthocerid *Suloceras pulchrum* (Barrande, 1868).

Ptenoceras alatum exhibits a gyroceracone shell with growth lines and recurrent growth ridges, transforming during ontogeny into megastriae; two pairs of lateral outgrowths (wings) appear in fully-grown shells (for details, see Turek 2007; Manda and Turek 2009*a*). All specimens examined exhibited growth structures of identical shape. Specimens from the Koněprusy and Slivenec limestones have a larger shell size, with a maximum diameter of 60 mm (compared to 53 mm in a specimen from the Dvorce-Prokop Limestone). Specimens from the Koněprusy and Slivenec limestones also show highly elaborate sculpture and lateral outgrowths (contrary to only two specimens from Dvorce-Prokop Limestone which exhibit lateral outgrowths). In summary, specimens from shallow-water limestones exhibit a more elaborate sculpture, i.e. thicker growth lines (see specimens illustrated by Turek 2007). This corresponds with the observation in populations of *P. proximum*.

The Pragian *Suloceras pulchrum* is a relatively common species in the shallow-water Koněprusy and Slivenec limestones (at the Branžovy, Císařský, Homolák and Houbův quarries; see Manda 2001), but occurs rather sporadically in the muddy Dvorce-Prokop Limestone (at the Braník, Černá Gorge and Konvářka sections). It has a straight annulated shell, the annulation being well developed in shells with a diameter up to 15 mm, but in more mature growth stages the annulae become less pronounced. The sculpture on early shells (up to a diameter of *c.* 7 mm) consists of a regular reticulate ornament, i.e. combinations of longitudinal ribs and straight growth ridges. Adult specimens from shallow-water limestones exhibit a differentiation of longitudinal ribs into 2 or 3 orders, and an annulation is always developed (Text-fig. 10C). Specimens from biomicritic deeper-water limestone, however, in general show weaker growth sculptures, while longitudinal ribs are differentiated into two orders (Text-fig. 10A), or even reticulate ornament resembling the early shells may be developed. The annulation is weaker in or even absent from larger shells (Text-fig. 10C–E). In summary, *S. pulchrum* exhibits strengthening of growth sculptures in a shallow-water environment as revealed by both species of *Ptenoceras* examined. Interestingly, there is a reduction or even lack of annulation in some adult specimens from muddy limestones.

Intraspecific variability in Devonian nautiloids and pseudorthocerids was probably greater than previously assumed. Some differences exist in shell coiling and shell size (as noted by Dzik 1984; Turek 2007; Manda and Turek 2009*a*), but as shown above, differences also exists in sculpture and annulation, both commonly used as species-diagnostic features, and therefore need careful consideration. 'Facies dependence' of some closely related 'species', which differ in sculpture or presence of weak annulation, could be an artificial effect of splitting. Hewitt and Watkins (1984) and Evans (1994) suggested that cephalopod taxa in shallow-water settings developed a better-developed sculpture. It may be more correct to note, however, that shallow-water populations, not necessarily species, have a more elaborate sculpture.The presence of distinct nautiloid and pseudorthocerid morphotypes (phenotypes) in different environmental settings may be indicative of animal territoriality, i.e. document the limited migration of adult animals between facies/depth zones and thus the presence of local populations.

EFFECT OF THE CHOTEČ EVENT ON RUTOCERATOIDS

The Choteč Event was studied in detail by Walliser (1984, 1985), House (1985), Chlupáč and Kukal (1986, 1988) and others. Walliser (1996, p. 230) concluded that, 'Extinctions during the Choteč Event occurred in nearly all fossil groups of both neritic and pelagic facies'. However, House (2002, p. 14) suggested a rather weak extinction, but did note that the Choteč Event, 'has the first clear characters of many later Devonian events'. In the Prague Basin, the type area of the Choteč Event, light-grey muddy skeletal limestones were replaced by dark-grey coloured crinoidal pack-grainstone within lighter mudstones during the Choteč Event (Chlupáč and Kukal 1986, 1988). Changes in facies are usually explained by deepening, coupled with anoxic conditions close to the bottom (for a summary see Walliser 1996).

Data from the Prague Basin show pronounced changes in ammonoid faunas, accompanied by extinctions (Chlupáč and Turek 1983). Becker and House (1994) and Klug (2002) documented a similar overturn in ammonoid faunas in Morocco, while recently, Frýda *et al.* (2008) have assessed the effect of the Choteč Event on gastropod faunas. However, published data suggest that the Choteč Event probably also affected brachiopods, trilobites, hyoliths and ostracods (e.g., Chlupáč 1983*b*; Havlíček and Kukal 1991; Šlechta 1996; Mergl 2008; Valent and Malinky 2008; Mergl and Ferrová 2009).

Taken as a whole, with the exception of *Bolloceras*, all nautiloid genera known from the Třebotov Limestone (late Emsian) are absent in the overlying Choteč Limestone (Eifelian). The rutoceratoids *Adelphoceras*, *Anomaloceras*, *Homoadelphoceras*, *Parauloceras*, *Roussanoffoceras* and *Otomaroceras* became extinct worldwide. *Hercoceras*, *Ptenoceras* (the most abundant Early Devonian rutoceratoids), *Goldringia* and *Pseudorutoceras* ranged up into the Middle Devonian (Text-fig. 9). A high rate of extinctions amongst rutoceratoids (and other nautiloids) probably reflects their specialization in addition to their restriction to a narrow facies zone in a deeper-water setting, just below storm wave base, in the Emsian. This muddy limestone biofacies, which nearly exclusively hosted rutoceratoids, was the only facies strongly affected by dysoxic conditions which accompanied the Choteč Event (Text-fig. 6).

Recovery of nautiloid faunas took place in the late Eifelian; thus, much slower than ammonoid and benthic faunal recovery. A nautiloid fauna of low diversity, including *Aphyctoceras* sp. (Text-fig. 11B), appeared in the upper *Acanthopyge* Limestone (late Eifelian) in the shallow-water Koněprusy elevation area (Chlupáč 1959). Various species of *Bolloceras* are known from the uppermost Choteč Limestone (late Eifelian) in an old quarry in the Hluboké Valley at Karlštejn (Chlupáč 1959). The rutoceratoid *Kophinoceras* (Text-fig. 11A), which is a common element in Givetian faunas of the Old World Realm, appeared later in the latest Eifelian Kačák Shale (Srbsko Formation), i.e. just after the Kačák Event (Chlupáč 1960).

It may therefore be concluded, that the Choteč Event led to a restructuralization of nautiloid faunas and prominent extinctions. It represents the first significant extinction event affecting cephalopods in Devonian time, following previous extinctions at the Silurian/Devonian boundary (see Manda 2001, 2007*a*; Kröger 2008). The Lochkovian/Emsian time interval may be considered as a time of nautiloid radiation following the Silurian-Devonian extinction events (see also Zhuravleva 1972, 1974; Kröger 2008; Manda and Turek 2009). The rutoceratoids represent a well-documented example of this phenomenon.

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TEXT-FIG. 1. Distribution of Devonian and Dalejan rocks in the Koněprusy (D) and Hlubočepy areas (E) and the location of sections discussed in the text. For the position of the Koněprusy and Hlubočepy areas and the distribution of Early Palaeozoic rocks with the Prague Basin (central Bohemia, Czech Republic) see Text-fig. 1B, A respectively.

TEXT-FIG. 2. Stratigraphic distribution of rutoceratoids in the Třebotov Limestone (Daleje-Třebotov Formation) in the Hlubočepy area, as based on the mode of preservation of specimens in the National Museum collections (broken lines) and the range of selected zonal fossils. Reference section is the Nad tratí Quarry (after Chlupáč 1959; Chlupáč *et al.* 1979, 1980). Abbreviations: A – Daleje Shales, light green and grey-green calcareous shales in upper part with nodules of red and green-grey mudstone. B – Red nodular, thin-bedded wackestone with shale intercalations. C – Well-bedded grey and grey-green nodular wackestones with abundant intercalations of grey shales. D – Light grey, coarsely bedded nodular wackestone. E – Platy, dark grey crinoidal grainstone intercalated with mudstone. F − Thin-bedded, dark grey mud-wackestone with silicites.

TEXT-FIG. 3. All specimens illustrated are from the late Emsian Třebotov Limestone at Prague-Hlubočepy (A−G) and Prague-Holyně (H). A−C, *Paraulloceras regulare* sp. nov., NM L 34506 (holotype), in lateral (dextral), ventral and lateral (sinistral) views, respectively, x 1. D, *Otomaroceras* sp. nov., CGS SM 339, lateral view, x 0.9. E, G, H, *Roussanoffoceras chlupaci* sp. nov., E, G, NM L 40788 (holotype) in ventral (x 0.8) and lateral views (x 0.9). H, NM L 40789 (paratype), lateral view, x 0.8. F, *Goldringia* sp. nov., CGS SM 342, lateral view, x 0.9.

TEXT-FIG. 4. Apertural modifications and spine morphology in *Hercoceras mirum* Barrande, 1865 from the late Emsian Třebotov Limestone, Prague Basin. A, NM L 39074, Prague-Hlubočepy, lateral view, x 1.3. B, fragment of shell with spine, CGS SM 371, posterior view, x 2. C, fragment of shell with broken spine, CGS SM 372, anterior view, x 2. D, weathered surface of limestone with naturally prepared spine, anterior view, CGS p 276, x 1. E, NM L 395, Prague-Hlubočepy, lateral view, x 1.1.

TEXT-FIG. 5. Different shape of aperture in *Hercoceras mirum* Barrande, 1865. A–C, Dorsal side in form of a visor; frontal, lateral and ventral views. Lateral view shows a narrow slit in the location where hollow spines were formed (NM L 395). D, Dorsal side is bent under a right angle; frontal view (lectotype, NM L 242). E–F, Fully-grown stage with unusually long uncoiled part of the shell with widely opened aperture (NM L 39074).

TEXT-FIG. 6. Distribution of Early and early Middle Devonian rutoceratoids from the Prague Basin in relation to facies (depth) zones (for data see Manda and Turek 2009*a*). Main facies adopted from Chlupáč (1995, 1959, 1998) and Havlíček and Kukal (1990).

TEXT-FIG. 7. Comparison of abundance (i.e., number of available specimens) of rutoceratoids in the Pragian (for data see Manda and Turek 2009*a*) and late Emsian of the Prague Basin.

TEXT-FIG. 8. Maximum observed shell size in Pragian (circle) and Emsian (square) rutoceratoids from the Prague Basin. Abbreviations: *P. minusculum* (1), *P. pupus* (2), *Goldringia* sp. nov. (3), *P. regulare* (4), *A. annulatum* (5), *P. proximum* (6), *Otomaroceras* sp. nov. (7), *P. alatum* (8), *H.*? *transiens* (9), *P. alienum* (10), *P. nudum* (11), *H. mirum* (12), *O. tardum* (13), *O. flexum* (14), *G. gondola* (15), *H. devonicans* (16), *P. bolli* (17), *A. bohemicum* (18) and *A. anomalum* (19).

TEXT-FIG. 9. Diagrams illustrating the total (i.e., global) generic diversity of the superfamily Rutoceratoidea Hyatt, 1884 and their turnover rates (i.e., relative origination and extinction rates). Total diversity is defined as the total number of genera recorded from the time unit; normalized diversity is defined as the number of genera ranging through the time unit plus half the number of genera confined to the unit or ranging beyond the time unit, but originating or ending within it. Relative turnover rates (origination or extinction) are defined as the total number of generic level taxa originating or becoming extinct within the time unit, divided by the total generic diversity (for data see Manda and Turek 2009*a*, appendix, p. 148).

TEXT-FIG. 10. Variability of sculpture and annulations in *Suloceras pulchrum* (Barrande, 1868) from Pragian strata of the Prague Basin. A, MCZ 160444, 'Bílá skála', i.e. Braník Rock, Dvorce-Prokop Limestone, lateral view, x 0.7. B, MCZ 338, Lochkov, Dvorce-Prokop Limestone, lateral view, x 0.9. C, MCZ 61336, Kosoř, Dvorce-Prokop Limestone, lateral view, x 0.7. D, CGS SM 344, Homolák Quarry at Měňany, Koněprusy Limestone, lateral view, x 0.8. E, MCZ 61336, Černá rokle Gorge at Kosoř, Dvorce-Prokop Limestone, lateral view, CGS SM 345, x 0.7.

TEXT-FIG. 11. Middle Devonian rutoceratoids from the Prague Basin. A. *Kophinoceras* sp. (*Kophinoceras* ex gr. *acuticostatum* in Chlupáč 1960, p. 152), CGS p1989, Karlštejn, Wolf George, earliest Givetian, Kačák Member (Srbsko Formation), ventrolateral view, x 1.2. B. *Aphyctoceras* sp., one of specimens identified by Chlupáč (1959, pp. 478, 492) as *Kophinoceras eifelense* (Sandberger and Sandberger, 1852), CGS SM 340 (original documentation material collected by I. Chlupáč in 1952), Koněprusy, north slope of Zadní Kobyla Hill, late Eifelian, upper part of *Acanthopyge* Limestone (Choteč Formation), ventral view, x 1.4.

EXPLANATION OF PLATE 1

All specimens illustrated are from the late Emsian Třebotov Limestone at Prague-Hlubořepy.
Fig. 1. *Goldringia*? *devonicans* (Barrande, 1866), NM L 15414 (holotype), lateral view, x 0.7.
Fig. 2. *Ptenoceras minusculum* (Barrande, 1865), NM L 8060 (holotype), lateral view, x 0.8.
Figs 3–4. *Hercoceras*? *transiens* (Barrande, 1865), NM L 8061 (holotype). 3, lateral view, x 0.8. 4, ventral view, x 1.
Figs 5, 10. *Homoadelphoceras devonicans* (Barrande, 1866), NM L 10320 (holotype). 5, ventral view, x 0.6. 10, lateral view, x 0.6.
Figs 6–9, 13. *Anomaloceras anomalum* (Barrande, 1865). 6, 8, 13, NM L XXX. 6, apertural view, x 1.8, detail of growth structures, x 1.8. 8, detail of siphonal tube, x 1.7. 9, NM L 8057 (lectotype). 7, lateral view, x 0.8. 9, ventral view, x 1.2.
Figs 11–12, 14. *Adelphoceras bohemicum* Barrande, 1870, NM L 21496 (holotype). 11, dorsal view, x 0.5. 12, lateral view, x 0.7. 14, detail of aperture, x 0.5.

EXPLANATION OF PLATE 2

Variability of sculpture and umbilical perforation in the late Emsian *Ptenoceras proximum* (Barrande, 1865) from the Prague Basin.
Fig. 1. NM L 40790, Prague-Hlubočepy, upper part of Třebotov Limestone, lateral view, x 1.7.
Figs 2–3. CGS SM 346, Prague-Holyně, 'white beds', uppermost Třebotov Limestone. 2, lateral view, x 2. 3, ventral view, x 2.
Fig. 4. CGS SM 347, Prague-Hlubočepy, Třebotov Limestone, lateral view, x 1.8.
Figs 5–6. MCZ 136829, Koněprusy, Suchomasty Limestone. 5, lateral view, x 2. 6, ventral view, x 1.9.
Fig. 7. *Ptenoceras* cf. *proximum* (Barrande, 1865*b*), CGS SM 341, Koněprusy, Císařský Quarry ('Marble wall'), lower Suchomasty Formation, lateral view, x 1.4.
Fig. 8. NM L 40791, Prague-Hlubočepy, upper part of Třebotov Limestone, lateral view, x 1.2.
Figs 9, 12. CGS SM 370, Koněprusy, Voskop Quarry-northern wall, Suchomasty Limestone. 9, detail of embryonic chamber, x 3.8. 7, lateral view, x 1.5.
Fig. 10. MCZ 136830, Koněprusy, Suchomasty Limestone, lateral view, x 1.7.
Fig. 11. NM L 40792, Koněprusy, U transformátoru locality, Suchomasty Limestone, lateral view, x 2.5.
Figs 13–14. NM L 40793, Prague-Hlubočepy, lower part of Třebotov Limestone. 13, lateral view, x 1.4. 14, apertural view, x 1.4.

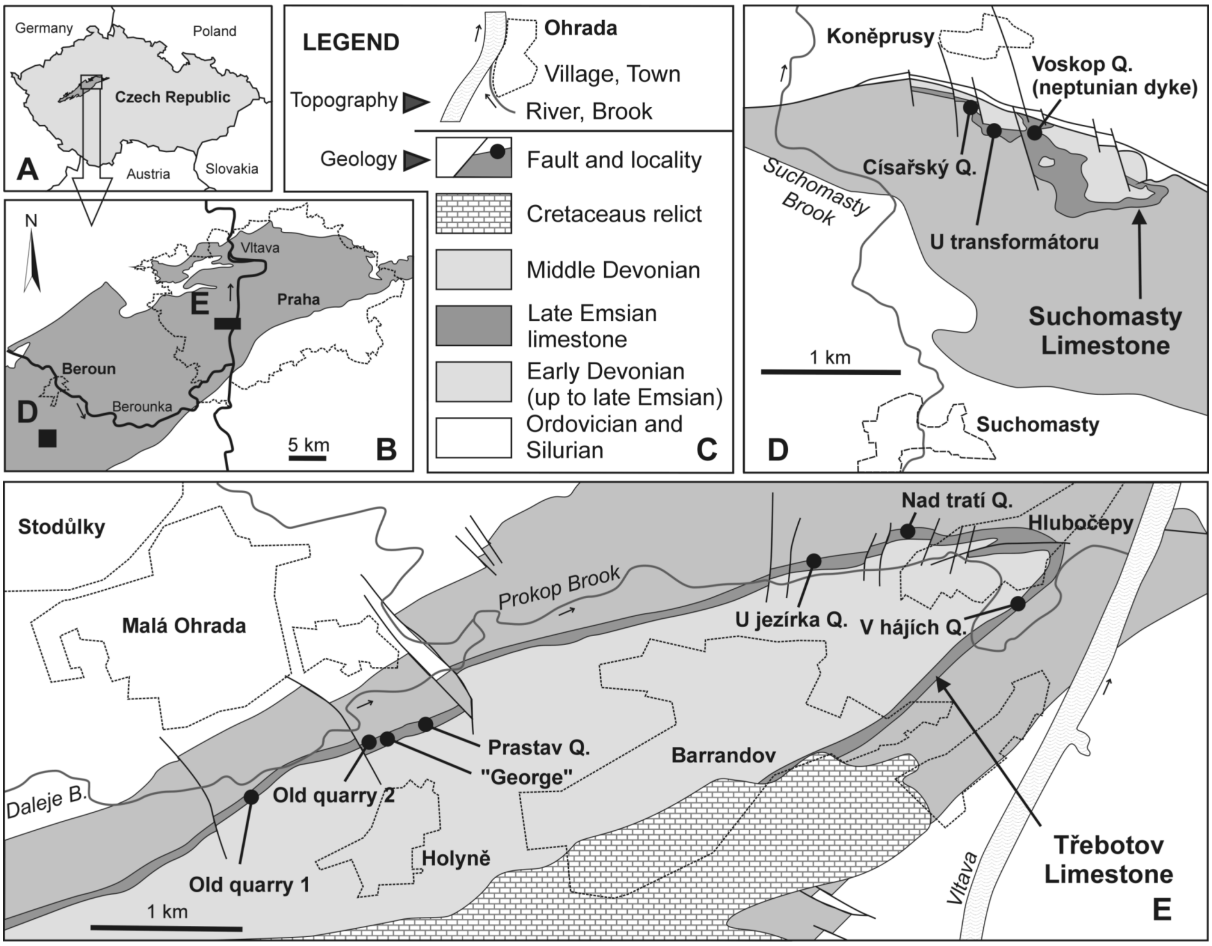
Germany
Poland
Czech Republic
Austria
Slovakia
A
LEGEND
Topography
Geology
Ohrada
Village, Town
River, Brook
Fault and locality
Cretaceaus relict
Middle Devonian
Late Emsian limestone
Early Devonian (up to late Emsian)
Ordovician and Silurian
C
N
Vltava
Praha
E
Beroun
Berounka
D
5 km
B
Koněprusy
Voskop Q. (neptunian dyke)
Císařský Q.
Suchomasty Brook
U transformátoru
Suchomasty Limestone
1 km
Suchomasty
D
Stodůlky
Malá Ohrada
Prokop Brook
Nad tratí Q.
Hlubočepy
U jezírka Q.
V hájích Q.
Barrandov
Prastav Q.
"George"
Old quarry 2
Daleje B.
Old quarry 1
Holyně
1 km
Vltava
Třebotov Limestone
E

Fig. 1

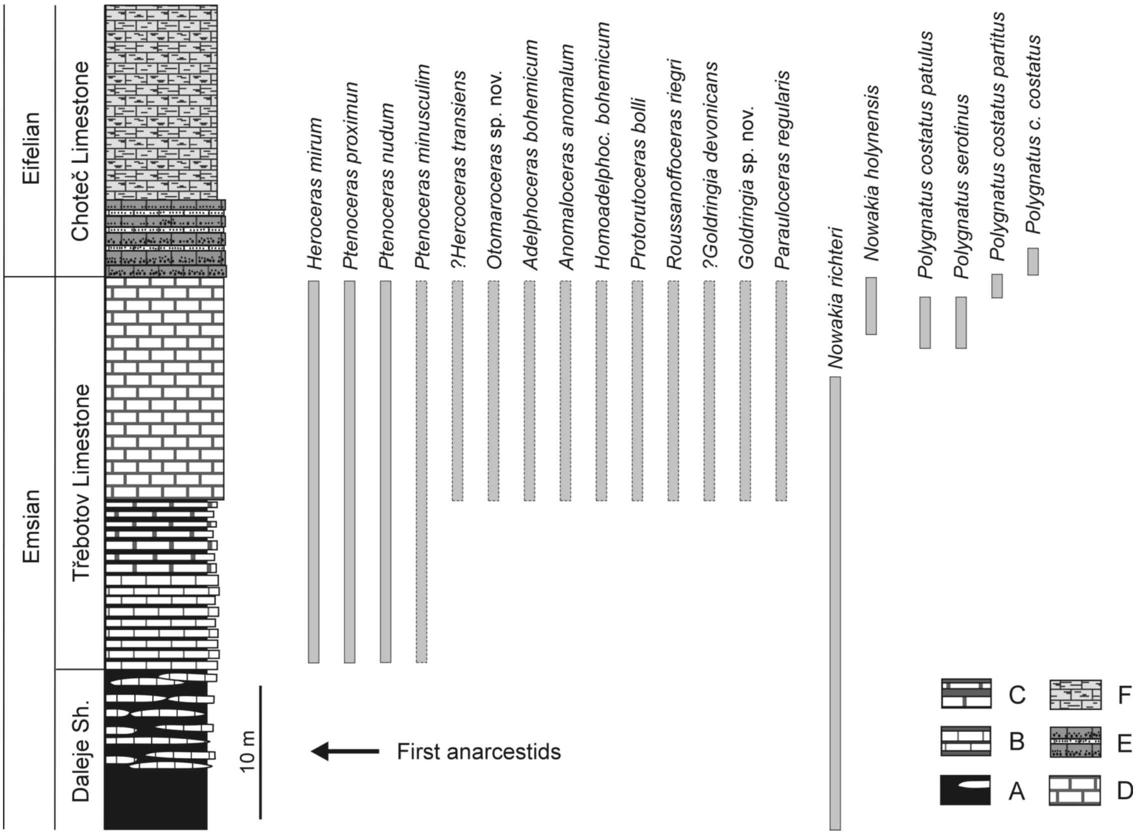
Eifelian
Emsian
Choteč Limestone
Třebotov Limestone
Daleje Sh.
10 m
First anarcestids
Heroceras mirum
Ptenoceras proximun
Ptenoceras nudum
Ptenoceras minusculim
?Hercoceras transiens
Otomaroceras sp. nov.
Adelphoceras bohemicum
Anomaloceras anomalum
Homoadelphoc. bohemicum
Protorutoceras bolli
Roussanoffoceras riegri
?Goldringia devonicans
Goldringia sp. nov.
Parauloceras regularis
Nowakia richteri
Nowakia holynensis
Polygnatus costatus patulus
Polygnatus serotinus
Polygnatus costatus partitus
Polygnatus c. costatus
C
B
A
F
E
D

Fig. 2

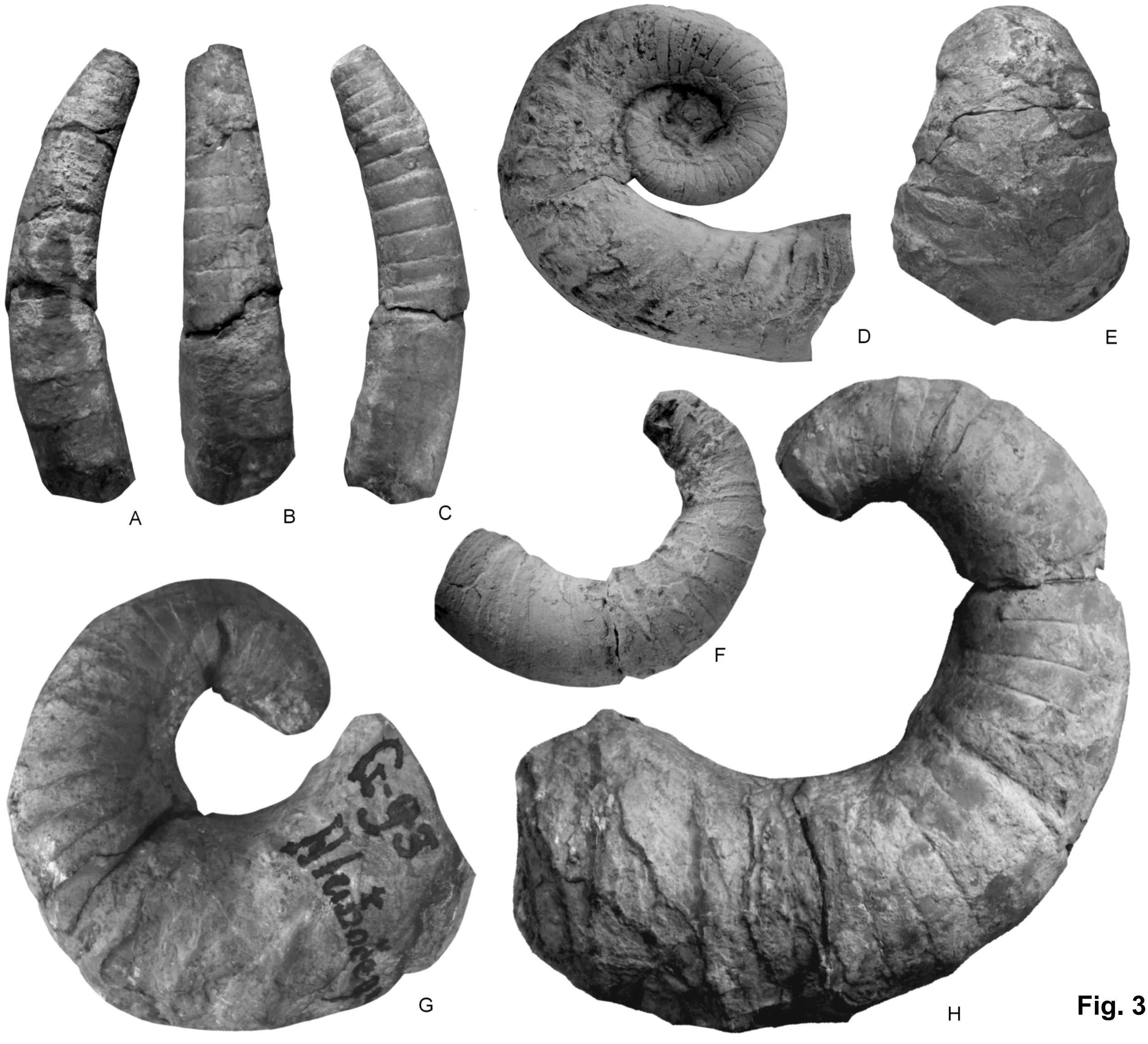

Fig. 3

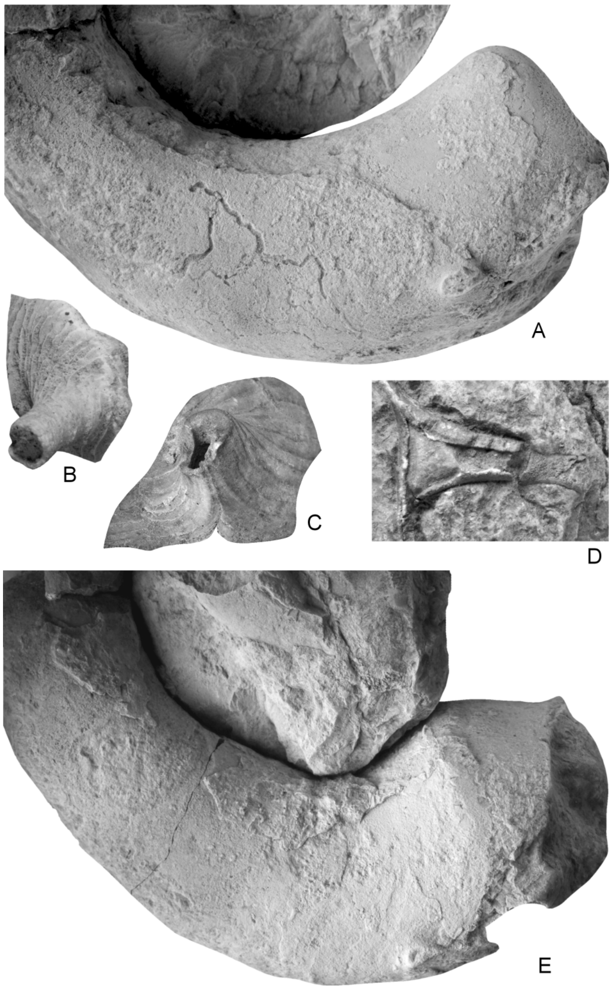

Fig. 4

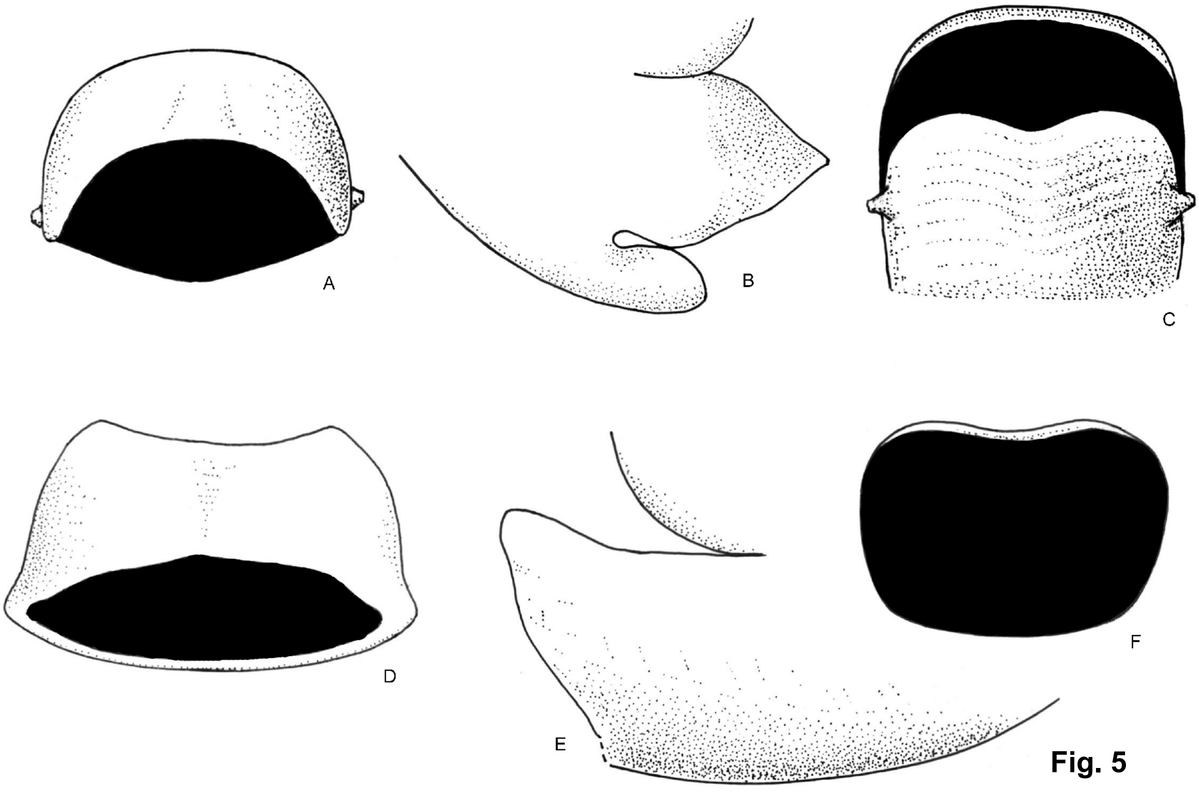

Fig. 5

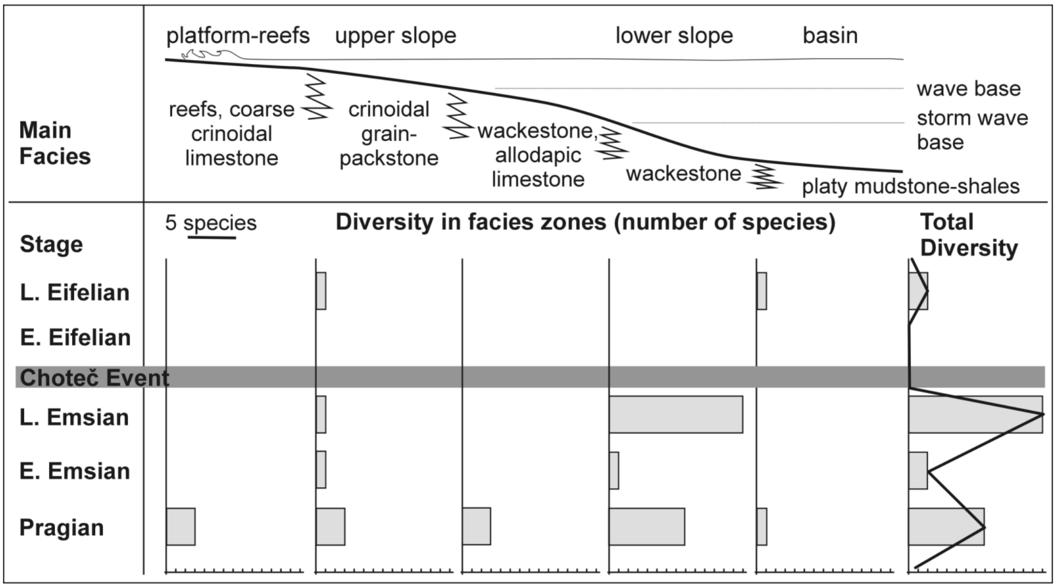

Fig. 6

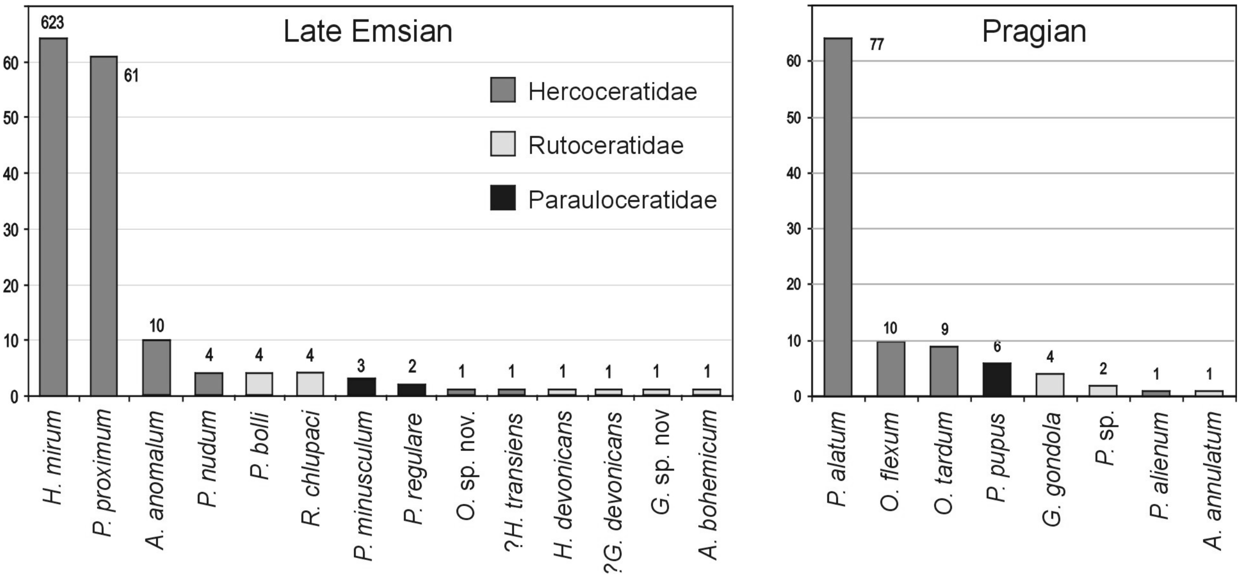

Fig. 7

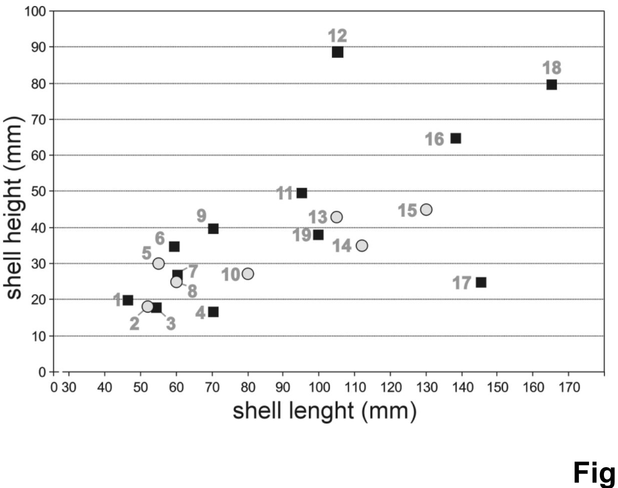

Fig. 8

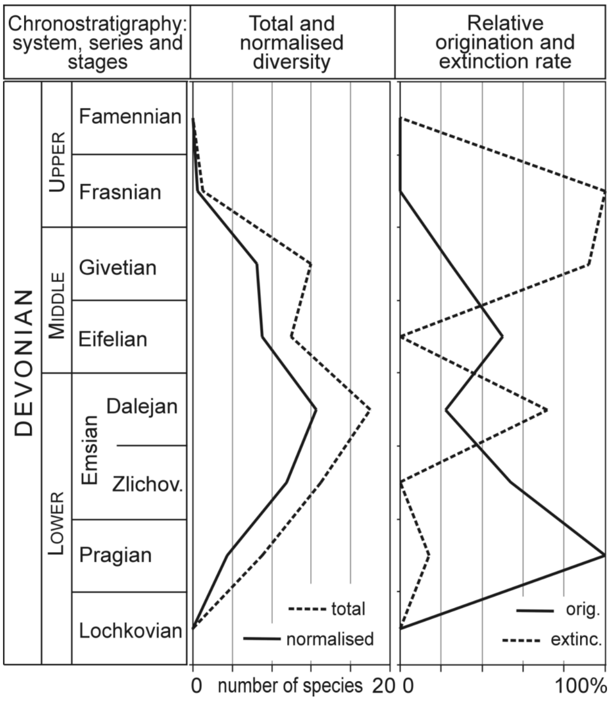

Fig. 9

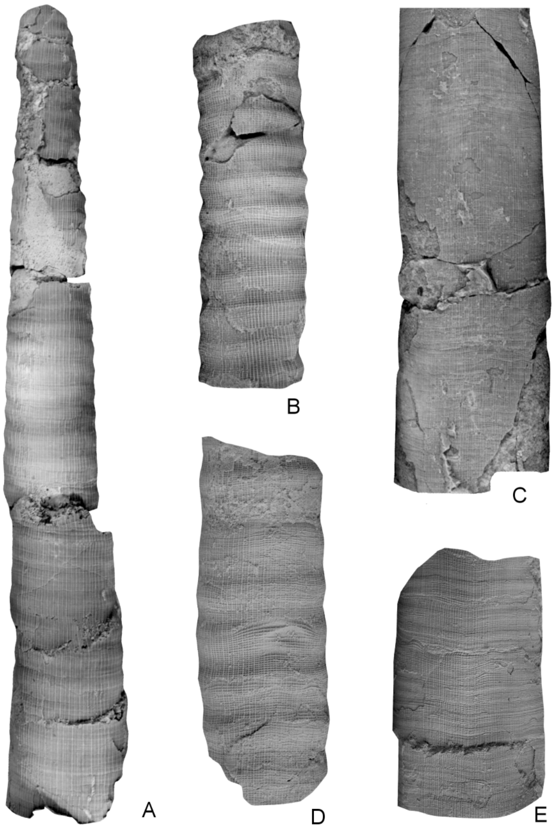

Fig. 10

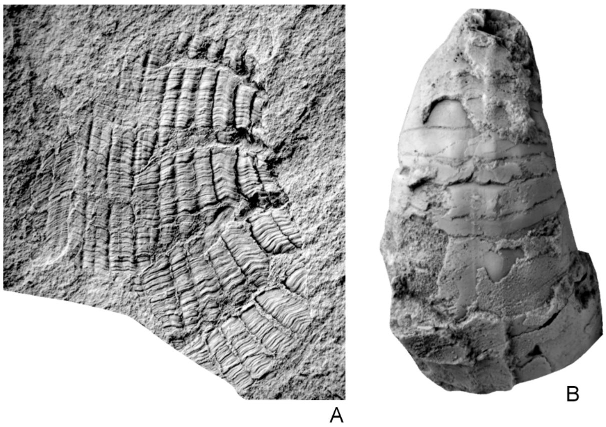

Fig. 11


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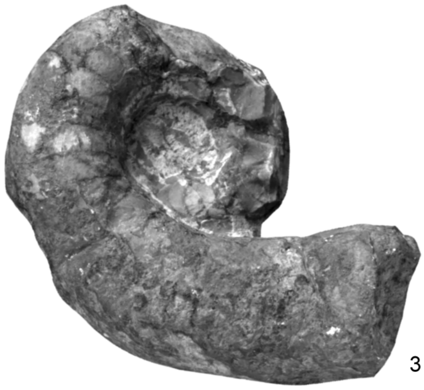
2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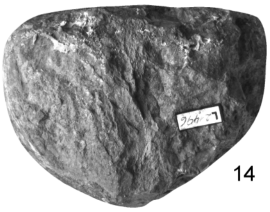
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Plate 1


1


2


3


4


5


6


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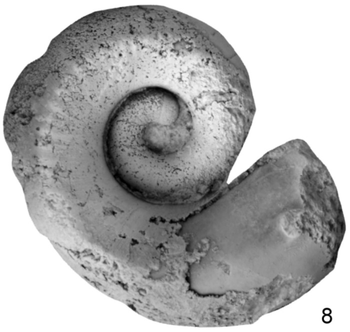
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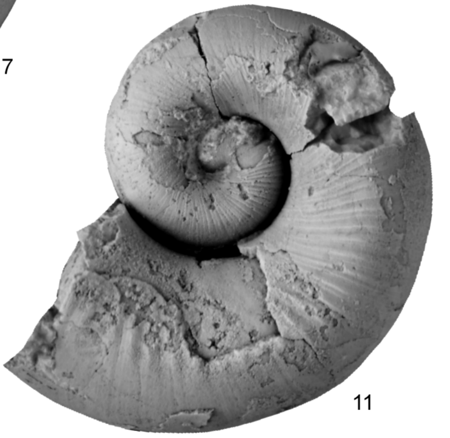
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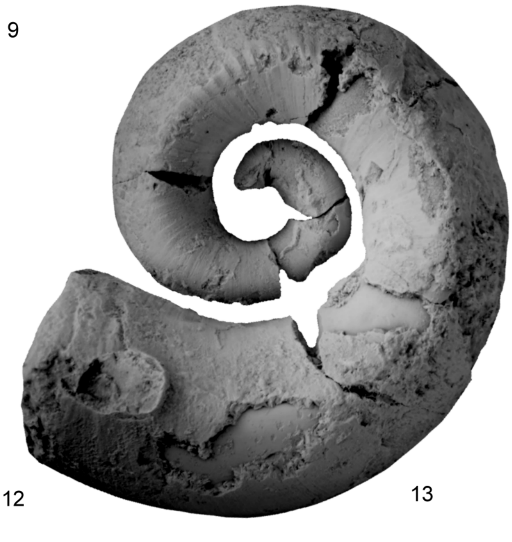
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14

Plate 2

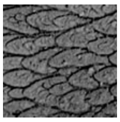
PŘÍLOHA 14

Publikovaná práce

Budil, P., Collette, J., Manda, Š. 2010. An unusual occurrence of the Laurentian phyllocarid crustacean Ceratiocaris papilio Salter in the lower Ludfordian (Silurian) of Bohemia (peri-Gondwana). Bulletin of Geosciences 85, 551–564.

An unusual occurrence of the Laurentian phyllocarid crustacean *Ceratiocaris papilio* Salter in the lower Ludfordian (Silurian) of Bohemia (peri-Gondwana)

PETR BUDIL, JOSEPH COLLETTE & ŠTĚPÁN MANDA



A rich assemblage (n = 223) of well-preserved phyllocarid crustacean remains is described from offshore calcareous shales of the Kopanina Formation (Silurian, Ludlow, early Ludfordian, *Saetograptus linearis* Biozone) exposed near the village of Všeradice, SE of Beroun. Specimens examined fall within the intraspecific variability of *Ceratiocaris papilio* Salter *in* Murchison, 1859, which is widely distributed in the Llandovery and Wenlock of Laurentia. Consequently, the Bohemian specimens represent the first occurrence of *C. papilio* outside of Laurentia. Additionally, the phyllocarid assemblage from Bohemia is younger than that of Laurentia. In Bohemia, *Ceratiocaris papilio* occurs in finely laminated calcareous shales. Its abundance varies distinctly from bed to bed, and phyllocarids are the dominant faunal component in only a few beds. Phyllocarids are associated with common graptolites and pelagic orthocerids while other benthic organisms are severely limited. Isolated or articulated furcae and telsons, and isolated mandibles are the most common components of this association, but articulated abdominal segments with caudal appendages (but without carapaces) also occur. An exceptional, slightly disarticulated specimen has articulated abdominal and partial thoracic segments, with mandibles preserved *in situ*. Additional possible occurrences of *C. papilio* and related species in Bohemia are also discussed. •
Key words: Phyllocarida, crustaceans, palaeocology, biostratigraphy, Silurian, Prague Basin, Czech Republic.

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Phyllocarid crustaceans are common in offshore facies in Přídolí and Lochkovian strata of Bohemia (Chlupáč 1994). In contrast, phyllocarids from Llandovery, Wenlock and Ludlow sedimentary succession are rare and remain poorly known. A few specimens were described by Barrande (1872) and by Novák in his unpublished manuscript (Novák 1887) and briefly commented on by Chlupáč (1994). Many authors (*e.g.*, Bouček 1937, Horný 1955 and Kříž 1992) have reported phyllocarid remains from various localities and biozones. However, these specimens are typically too poorly preserved to allow identification to the species level, and most have thus been assigned to *Ceratiocaris* sp. These occurrences nevertheless suggest that phyllocarids may be a common component of assemblages present in shale facies since the early Ludlow in the Prague Basin.

In 2009, Petr Štorch and Štěpán Manda conducted a detailed examination of the shale-dominated late Gorstian–early Přídolí sequence of the Kopanina Formation exposed in a temporary trench located NW from the village of Všeradice (Fig. 1). A sequence more than 60 m thick was sampled for graptolites. Surprisingly, numerous well-preserved phyllocarid remains were found in shales of early Ludfordian age. Mandibles, articulated furcae, and partially articulated abdomens are most common, but more complete remains of other exoskeletal parts were also found.

Occurrence of *Ceratiocaris papilio*

The Všeradice section is situated on the SW flank of the Prague Synform, NE from the village of Všeradice (Fig. 1). In palaeogeographic and tectonic models of the Prague Basin, the Všeradice section is situated in the so-called western segment of the basin, which is characterized by deeper water hemi-pelagic sedimentation and intensive subsidence (Kříž 1991, 1992, 1998). The Všeradice section was briefly described by Horný (1960), and investigated in detail by Kříž (1992), Kříž *et al.* (1993), Kozlowska *et al.*

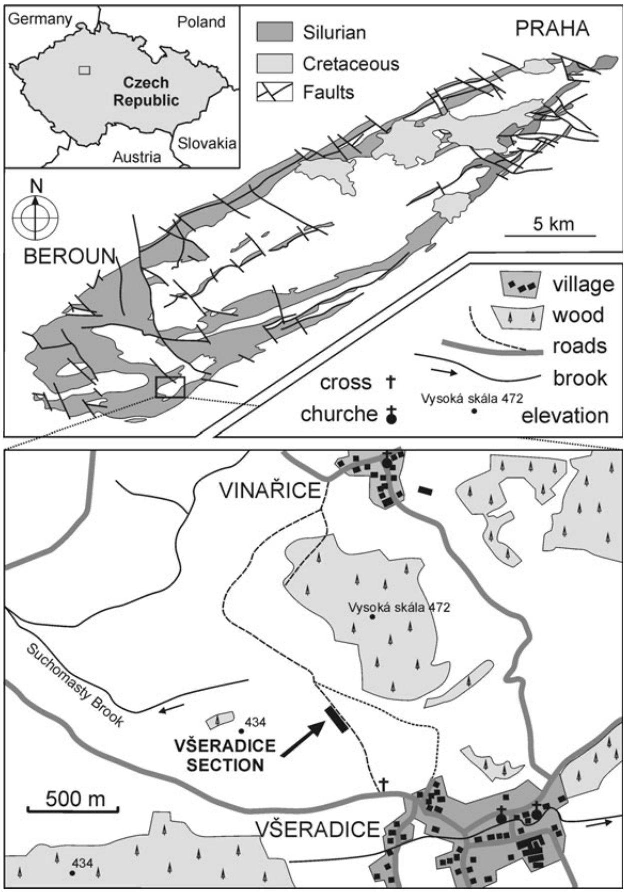


Figure 1. Distribution of the Silurian rocks in the Prague Basin and the location of the Všeradice VŠ-2 pit.

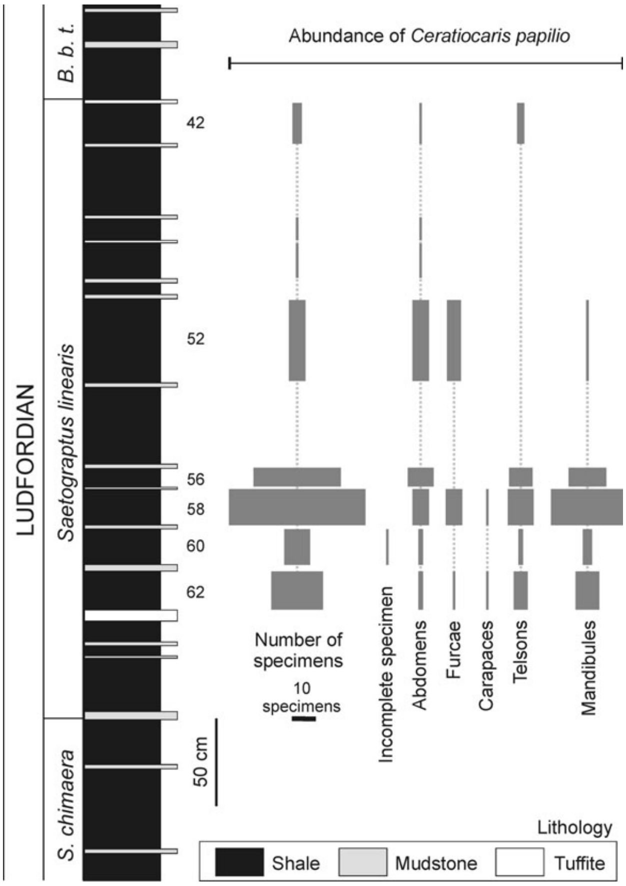


Figure 2. Abundance of *Ceratiocaris papilio* at the Všeradice VŠ-2 pit section. For exact number of phyllocarid remains, see Appendix.

(2001) and Manda & Kříž (2006). The base of the shale-dominated Všeradice section is middle Wenlock and continues up to the early Přídolí. Limestones (mostly argillitic mudstones) and tuffites form thin beds in shales locally. Shales contain abundant graptolites and ostracods (*Entomis* and *Bolbozoe*), while straight cephalopods (*e.g. Parakionoceras originale*) and bivalves (*e.g. Cardiola*) are less common. Rare dendroid graptolites, inarticulate brachiopods, trilobites, crinoids, monoplacophorans and microconchids occur in a few isolated beds only. The Všeradice sections thus represent a deeper water offshore setting, while a lack of benthos suggests prevailing anoxic bottom conditions.

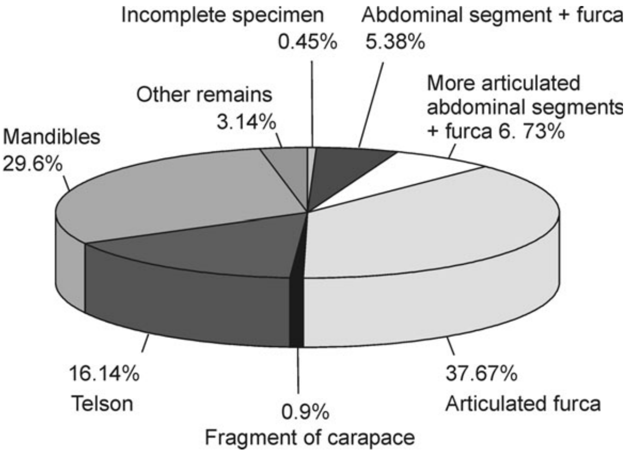


Figure 3. Ratio of phyllocarid remains in entire association in the Všeradice VŠ-2 pit section.

Phyllocarids occur only in part of the section (beds 42–62; note that low section numbers represent younger beds, while higher numbers represent older beds). Phyllocarid remains are most abundant in beds 56–62, and are rather rare in other beds in which they also occur (Fig. 2). Based on graptolite biostratigraphy, phyllocarids appear 50 cm above the base of *Saetograptus linearis* Zone and disappear at the base of *Bohemograptus tenuis* Zone (Petr Štorch, personal communication), and are absent from both the underlying and overlying beds. Because of the uniform lithology of the shales, and the similar taphonomic conditions throughout phyllocarid-bearing beds, it is unlikely that phyllocarid occurrences restricted exclusively to the shales of the *Saetograptus linearis* Zone represent a preservational bias. In coeval shallow water

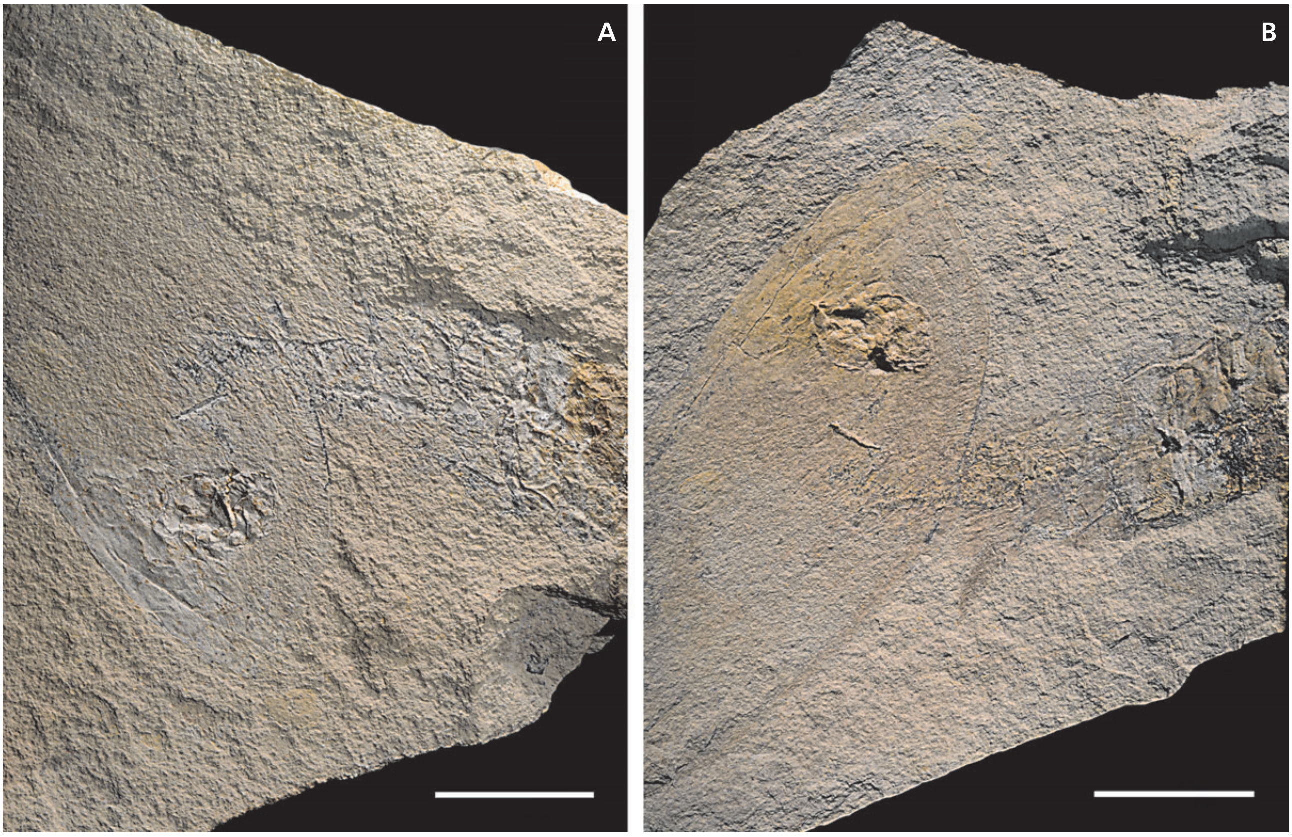


Figure 4. *Ceratiocaris papilio* Salter *in* Murchison, 1859. Lower Ludfordian, Silurian, Kopanina Formation, Všeradice, VŠ-2 pit. • A, B – left valve of the carapace with displaced but articulated thoracic and abdominal somites. A – positive part, CGS PB 505b; B – the same specimen, a negative counterpart. Scale bars = 1 cm.

setting, the *Saetograptus linearis* Zone corresponds with prominent shallowing (limestones banks with *Metacalymene baylei*, *e.g.*, Kosov and Mušlovka quarries) and basinward extension of carbonate facies (see Horný 1955, Kříž 1992, Manda & Kříž 2006). This extension is consistent with assumed global low-stand in the *S. leintwardinensis* Zone (replacing the Bohemian *Saetograptus linearis* Zone on the global scale) suggested by Johnson *et al.* (1998) and others. Additionally, small-scale slumps in shales and a tuffite (bed No. 43) contain benthic remains of shallow water provenance in the *Saetograptus linearis* Zone of the Všeradice section; such remains are also consistent with shallowing in this part of the basin. Consequently, the phyllocarid population in Všeradice is restricted to low stand. *Ceratiocaris papilio* disappears in bed No. 42; this level corresponds with a graptolite extinction known as the Leintwardinensis Event (for summary see Melchin *et al.* 1998, Manda & Kříž 2006).

Phyllocarid remains from the Všeradice section are flattened but otherwise well-preserved; only mandibles are preserved in relief. Sculpture is commonly clearly visible. Presence of specimens with significant articulation or their parts (*e.g.* furcae) are indicative of a low energy environment with no significant transport. Even disarticulated exoskeletal elements are well-preserved (*e.g.* long, narrow telson spines are often preserved intact). An interesting exception to this lack of transport appears to be local accumulations of mandibles on some bedding planes. Abundance and type of phyllocarid remains are given in Figs 2 and 3.

Depository. – All specimens from the Všeradice section are stored in the collection of Petr Budil (prefix PB) in the Czech Geological Survey, Praha, Czech Republic. Comparative material and Barrande's types are deposited in National Museum, Praha (prefix L).

Systematic palaeontology

Class Malacostraca Latreille, 1806
Subclass Phyllocarida Packard, 1879
Order Achaeostraca Claus, 1888
Family Ceratiocarididae Salter, 1863

Genus *Ceratiocaris* M'Coy, 1849

Type species. – *Ceratiocaris solenoides* M'Coy, 1849. Silurian, Ludlow, Westmoreland.

Diagnosis. – See Collette & Rudkin (2010), p. 119.

Bohemian species assigned. – *C*. sp. ex gr. *papilio* Salter *in* Murchison, 1859, Silurian, Llandovery–Wenlock, Motol Formation; *C*. cf. *scharyi* Barrande, 1872, Silurian, Wenlock, Motol Formation; *C. inaquealis* Barrande, 1872, Wenlock, Motol Formation; *C. docens* Barrande 1872, Ludlow, Kopanina Formation; *C. scharyi* Barrande, 1872, Silurian, Ludlow, Kopanina Formation; *C. papilio* Salter *in* Murchison, 1859, Silurian, Ludlow, Kopanina Formation; *C. bohemica* Barrande, 1872, Silurian, Přídolí, Požáry Formation.

Ceratiocaris papilio Salter _in_ Murchison 1859
Figures 4A, B, 5A–F

1859 *Ceratiocaris papilio* n. sp.; Salter *in* Murchison, p. 262, text-figure 1.
1860 *Ceratiocaris papilio* Salter *in* Murchison. – Salter, pp. 155, 156, text-figure 1.
1860 *Ceratiocaris stygius* (Salter *in* Murchison). – Salter, p. 156, text-figs 2, 3.
1865 *Ceratiocaris papilio* Salter *in* Murchison. – Woodward, pp. 401–403, pl. 11, figs 1, 2.
1885 *Ceratiocaris stygia* (Salter *in* Murchison). – Jones & Woodward, pp. 394–397, pl. 10, fig. 2.
1888 *Ceratiocaris stygia* (Salter *in* Murchison). – Jones & Woodward, fig. 7; pl. 11, figs 3, 7.
1896 *Ceratiocaris monroei* (Salter *in* Murchison). – Whitfield, pp. 301–302, pl. 13, figs 1–5; pl. 14, figs 3–8.
2010 *Ceratiocaris monroei* (Salter *in* Murchison). – Watkins, Meyer & Coorough, pp. 9, 10, figs 15.4–15.5, 16.1–16.4, 17.1–17.6, 18.1–18.5, 19.1–19.8.
See Collette & Rudkin (2010) and Collette & Hagadorn (2010) for additional synonymy.

Material from Bohemia. – Twenty-seven well-preserved specimens including abdominal segments with furca, articulated furcae, isolated mandibles, one slightly disarticulated incomplete specimen, and three fragments of isolated carapace valves. In addition, 196 less well-preserved, fragmentary specimens from the same locality share morphological characteristics, and are likely conspecific. All specimens included herein are from the Všeradice section.

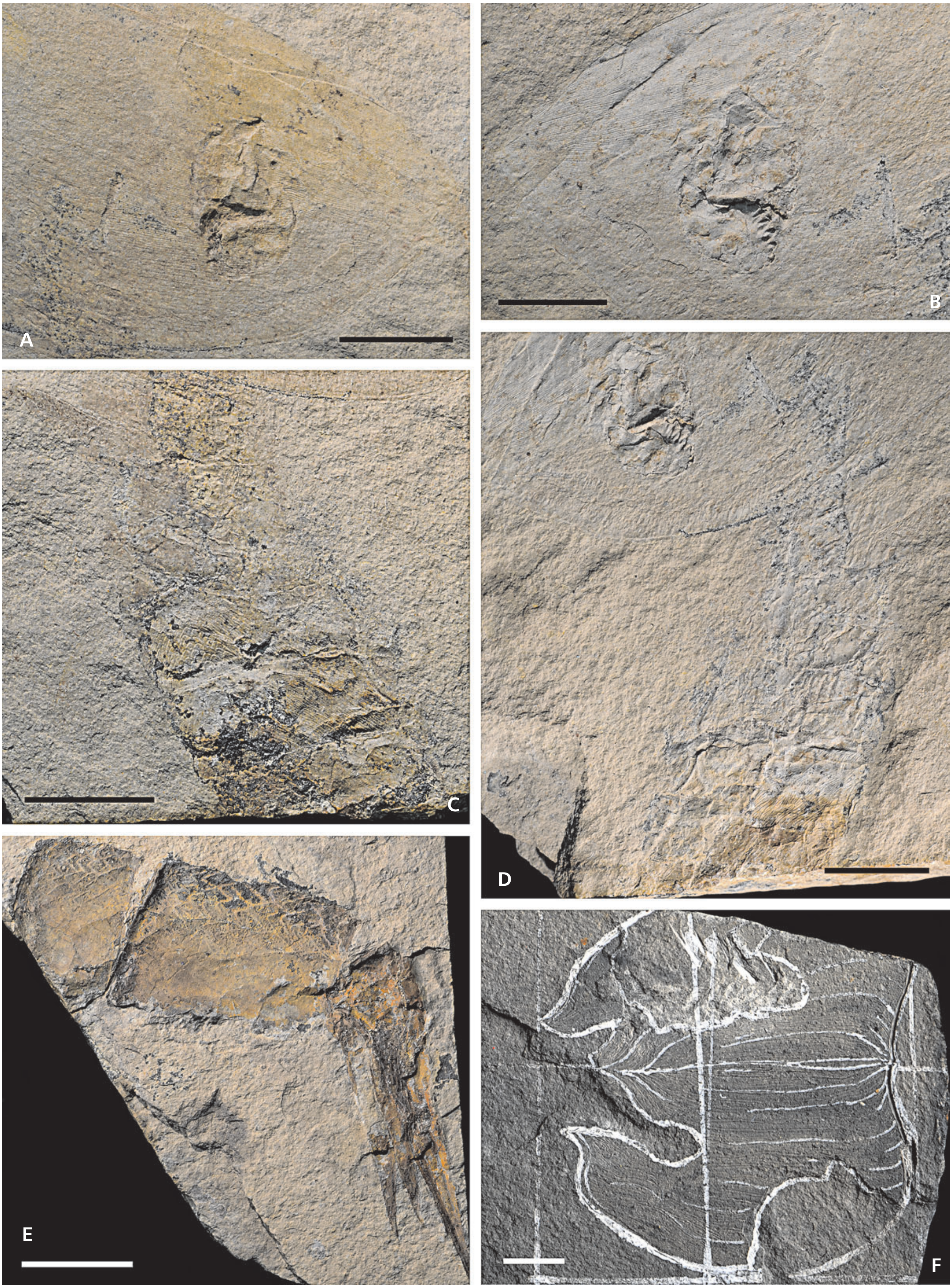
Diagnosis. – See Collette & Rudkin (2010), p. 119.

Description of Bohemian material. – Carapace: Incompletely known. Carapace valves subquadrate to subovate, 19.34 mm wide, >45.41 mm long (posterior part broken, CGS PB 505a, b, see Fig. 4), estimated length to height ratio approximately 2.5 (deformed by tectonism). Cuticle very thin (see Figs 5A–D, 6B). Dorsal hinge line straight; anterodorsally produced into a slightly concave rostral notch forming the dorsal side of the carapace horn. Anterior carapace horn acuminate with blunt anterior terminus. Ventral margin broadly rounded, posterior margin unknown. A narrow thickened border is developed along the free margins of the valves; border thickest ventrally, thins slightly anteriorly and posteriorly; doublure present. Posterior margin and hinge nodes unknown. Surface of valves covered by fine longitudinal raised striae approximately parallel with carapace margins; striae regularly parallel, rarely anatomizing. Density of striae diminishes slightly from dorsal to ventral carapace margins. In specimen CGS PB 505, *in situ* mandibles are preserved beneath the cuticle of the carapace valves in approximately the first fifth of the carapace length. Mandibles have 7–8 teeth, and a relatively narrow base.

Thorax: Incompletely preserved. Thoracic segments of very low relief; at least six thoracic somites preserved. Segments shorter antero-posteriorly than abdominal segments, smooth (Fig. 5C, D).

Abdomen: Abdomen of seven segments, which increase in length posteriorly in unequal proportions. Segments thickened at articulating margins where articulating grooves are indicated (Fig. 7F). Anterior segments A1 and A2 short; ornamented with faint striations oriented approximately 45° from the trunk axis; fine chevron-like ornament is locally present dorsally (Figs 5C, D, 6A). Posterior segments A6 and A7 most completely known; nearly entire surface of A6 and A7 covered with chevron-like ornament forming a leaf- or scale-like pattern (posterior ends of “scales” are commonly in contact). Fine striations are also present, predominantly on anterior and ventral parts of A7 and A6. This fine striation covers nearly entire surface of abdominal segments A5 anteriorly (see Fig. 5C). Finer-scale ornament described by Rolfe (1961, 1962) and Collette & Rudkin (2010) has not been observed. Ratio of abdominal segment A7 to A6 is 1.74–1.98 (mean 1.88, n = 8).

Figure 5. A–E – *Ceratiocaris papilio* Salter *in* Murchison, 1859. Lower Ludfordian, Silurian, Kopanina Formation, Všeradice, VŠ-2 pit. • A, B – detail of the articulated mandibles, CGS PB 505. A – negative counterpart CGS PB 505b. B – the positive part of the same specimen, CGS PB 505a. • C – CGS PB 505b, a detail of last abdominal and the first thoracic somites, negative counterpart CGS PB 505b. • D – the positive part of the same specimen, CGS PB 505a. • E – the negative counterpart of abdominal somites A6 and A7 with articulated telson, CGS PB 506. • F – *Ceratiocaris*? sp. An unpublished holotype of *Holocaris univalvis* Novák MS, mentioned by Chlupáč (1994) as *Ceratiocaris* sp. ex gr. *papilio* Salter *in* Murchison, 1860. Llandovery, Telychian, Litohlavy Formation, section near Litohlavy water reservoir, NM L 27965. Scale bars = 5 mm.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Telson and furcal rami: Telson elongate, styliform; produced into a narrow spine. Telson head robust, strongly broadened; two lateral nodes and two ventro-lateral ridges (damaged by deformation) are present in the best-preserved material. Telson with more than four prominent postero-ventrally directed furrows. Rows of round to subround pits are present on each lateral side of telson; spacing of pits approximately uniform, but decreases posteriorly (see Fig. 5G). Furcal rami broad and flattened, styliform; taper evenly to sharp terminus. Dorsal surface smooth or with very indistinct striations, commonly with thickened margins. Distal termini of furcal rami often slightly upturned dorsally (Fig. 7A, C). Telson to furca ratio 1.55–1.97 (mean 1.79, n = 10).

Discussion. – Prior to the discovery of the present material, *Ceratiocaris papilio* Salter *in* Murchison, 1859 was known only from the late Llandovery to Wenlock of Laurentia, *e.g.* present-day Scotland, USA and Canada (Collette & Rudkin 2010). The new material presented herein extends the range of *C. papilio* to the Ludlow (early Ludfordian, *Saetograptus linearis* Biozone). This is a remarkably long range for a biological species.

Morphometric ratios of Bohemian specimens agree well with ratios of Scottish material. For example, the ratio of abdominal segments A7 to A6 is 1.74–1.98 (mean = 1.88) in Czech specimens, while in Scottish specimens of *C. papilio*, this same ratio is 1.43–2.38 (mean = 1.89 ± 0.171). The telson to furca ratio of Bohemian specimens is 1.55–1.97 (mean = 1.79); this ratio for Scottish *C. papilio* specimens is 1.36–2.39 (mean = 1.873 ± 0.2278). Additional morphological details that ally Czech material with other occurrences of *C. papilio* include pits for the insertion of spinules on the lateral telson surfaces, the trigonal ornament of abdominal segments, and the fine parallel rarely anastomosing striae of the carapace valves.

The observation of *in situ* mandibles in Czech specimens corresponds well with the estimated location of the anterior or "optic" node in specimens from other localities. This observation generally supports the interpretations of Collette & Rudkin (2010), Rolfe (1962), and Salter *in* Murchison (1859) that this 'node' is probably an artifact of the very thin carapace cuticle 'draping' over the mandible. Such a consistent position of the mandible in *C. papilio* indicates the likely location of the mouth. It should be noted, however, that structures with possible sensory function occupy a similar anterolateral position in other archaeostracans taxa (see Crasquin *et al.* 2009 for discussion). Morphologically similar isolated mandibles occur throughout the phyllocarid-bearing parts of the studied section; these are probably conspecific with *C. papilio*.

Minor differences in morphology exist between geographic occurrences of *C. papilio*. For example, Czech specimens do not preserve the three hingeline nodes of the carapace present in some Scottish specimens, nor do they have the finer-scale trigonal micro-ornament 'overprinting' of the abdominal 'scales' preserved in specimens from the Eramosa Lagerstätte. The absence of the fine-scale ornament described by Collette & Rudkin (2010), however, could be due to post-mortem, pre-lithification processes – such as abrasion, or dissolution while the exoskeleton was exposed on the surface of the sea floor during early diagenesis (see also Chlupáč 1977), and/or by modern weathering of the silty shales. One of us (J. Collette) observed specimens of *C. papilio* from the type locality (Lenarkshire, Scotland) and also from the Eramosa Formation (Ontario) with similarly effaced areas between patches of preserved scale ornamentation that were interpreted as being caused by modern weathering. The smooth furcal rami usually present in Bohemian specimens are more atypical of Scottish and Canadian examples of *C. papilio*, which often display fine, parallel longitudinal striae. However, the holotype of *C. papilio* (GSM 7479, British Geological Survey, Keyworth, England) also possesses similarly smooth furcal rami (see Fig. 8).

We do not consider the minor morphological differences discussed above to be a significant departure from the range of intra-specific morphology known in *C. papilio*; thus, the new Bohemian specimens are placed within *Ceratiocaris papilio*. It is probable that some of these minor differences may be explained by differing local taphonomic conditions (*e.g.* – dissolution of fine ornamentation of the exoskeleton, flattening, tectonic deformation). The most morphologically similar ceratiocaridid "species" to the new Czech material is the invalid species *Ceratiocaris stygia* Salter *in* Murchison, 1859, considered by Rolfe & Burnaby (1961) to be a junior synonym of *C. papilio* (similarities include: the carapace outline, robust and short 6th and 7th abdominal somites with characteristic ornamentation, robust telson and relatively broad furcal rami *etc.* – see Jones & Woodward 1888, pl. 11, fig. 3). In the newly studied Bohemian association, there are no specimens larger than 8 cm in length for complete animals.

Notes on Landovery–Ludlow phyllocarids in Bohemia and the occurrence of "*Ceratiocaris papilio* group"

A stratigraphically oldest occurrence of *Ceratiocaris* sp. ex gr. *papilio* Salter *in* Murchison, 1859 in Bohemia (Litohlavy Formation, likely *Spirograptus turriculatus* Zone, Telychian) was briefly mentioned by Chlupáč (1994) in a discussion of the unpublished species "*Holocaris univalvis* Novák MS". This unique specimen, figured herein as Fig. 5F is too poorly preserved to be determinable. However, the supposed outline of the carapace differs from that of *C. papilio*. Without any data on abdominal and telson

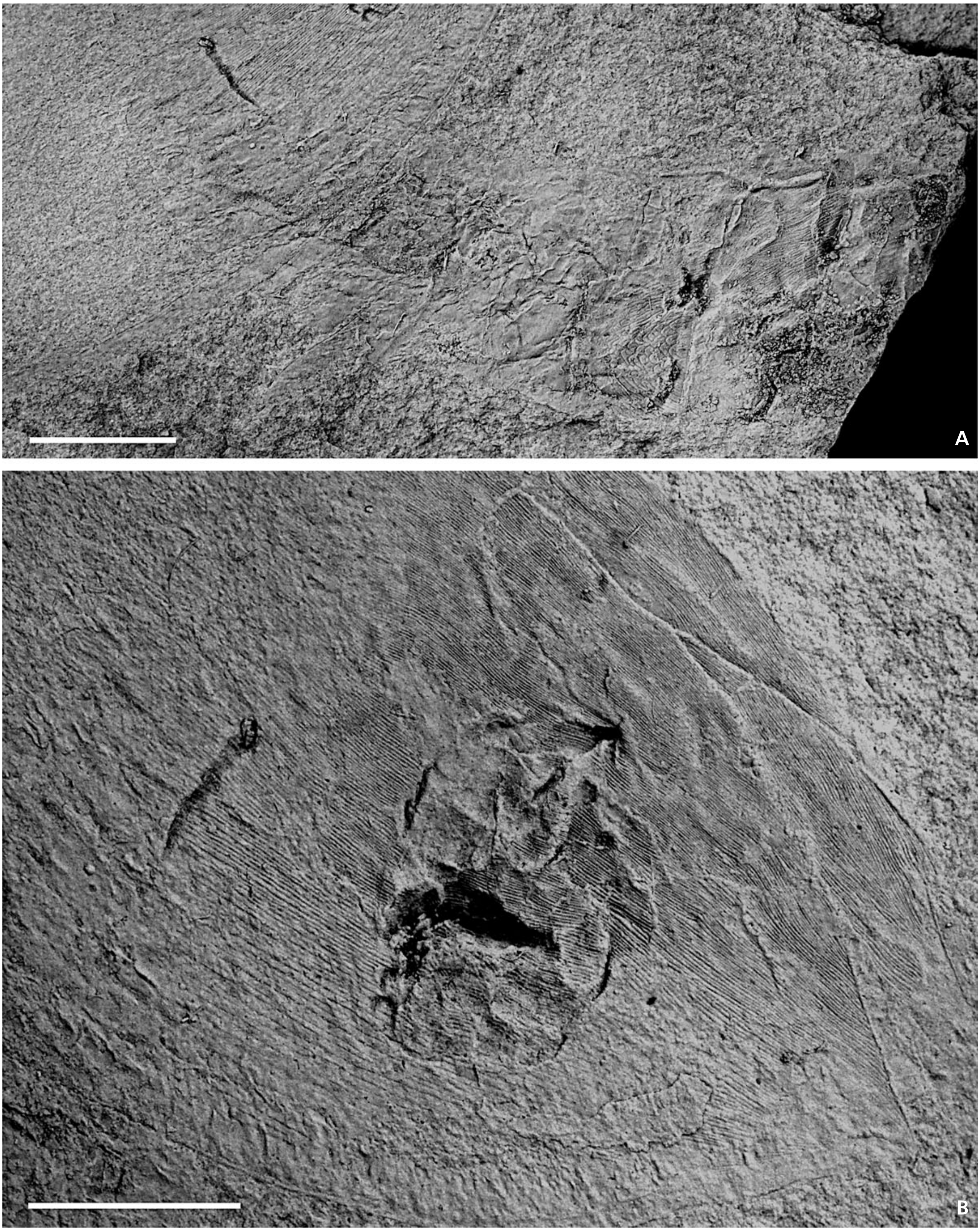


Figure 6. *Ceratiocaris papilio* Salter *in* Murchison, 1859. Lower Ludfordian, Silurian, Kopanina Formation, Všeradice, VŠ-2 pit. Left valve of the carapace with displaced but articulated thoracic and abdominal somites, CGS PB 505a. • A – detail of the thoracic and abdominal somites with fine ornamentation. • B – detail of the carapace ornamentation. The specimen was coated by ammonium chloride. Scale bars = 5 mm.

morphology, affiliation of this specimen with the genus *Ceratiocaris* may be considered as questionable. Chlupáč (1994, Table 1) lists the occurrence of *Ceratiocaris* (*C.*) sp. in the Llandovery and Wenlock strata of the Bohemia; however, it is questionable whether within this indeterminable material (mostly isolated telsons without prominent longitudinal ridges) representatives of *C. papilio* could be present.

Ceratiocaris scharyi Barrande, 1872 (Ludlow, Kopanina Formation) resembles *C. papilio* in overall shape of abdominal segments, and especially in having similar sculpture (see also Jones & Woodward 1888, p. 42). *Ceratiocaris papilio* and *C. scharyi* are closely related, but *C. scharyi* is distinguished from the former on the basis of its rounded leaf-like rather than chevron-like abdominal ornamentation (see Fig. 9A, B). *Ceratiocaris scharyi* is thus far known only from the holotype, which occurs in earlier Ludfordian limestones. Consequently *C. scharyi* is coeval with *C. papilio* in Bohemia, but it possibly inhabited a rather shallow water environment. Note that several fragments of ceratiocaridid telsons were found in the type locality and horizon of *C. scharyi* indicating that ceratiocaridids were relatively abundant there. Unfortunately, the mode of preservation and fragmentary material precludes precise determination.

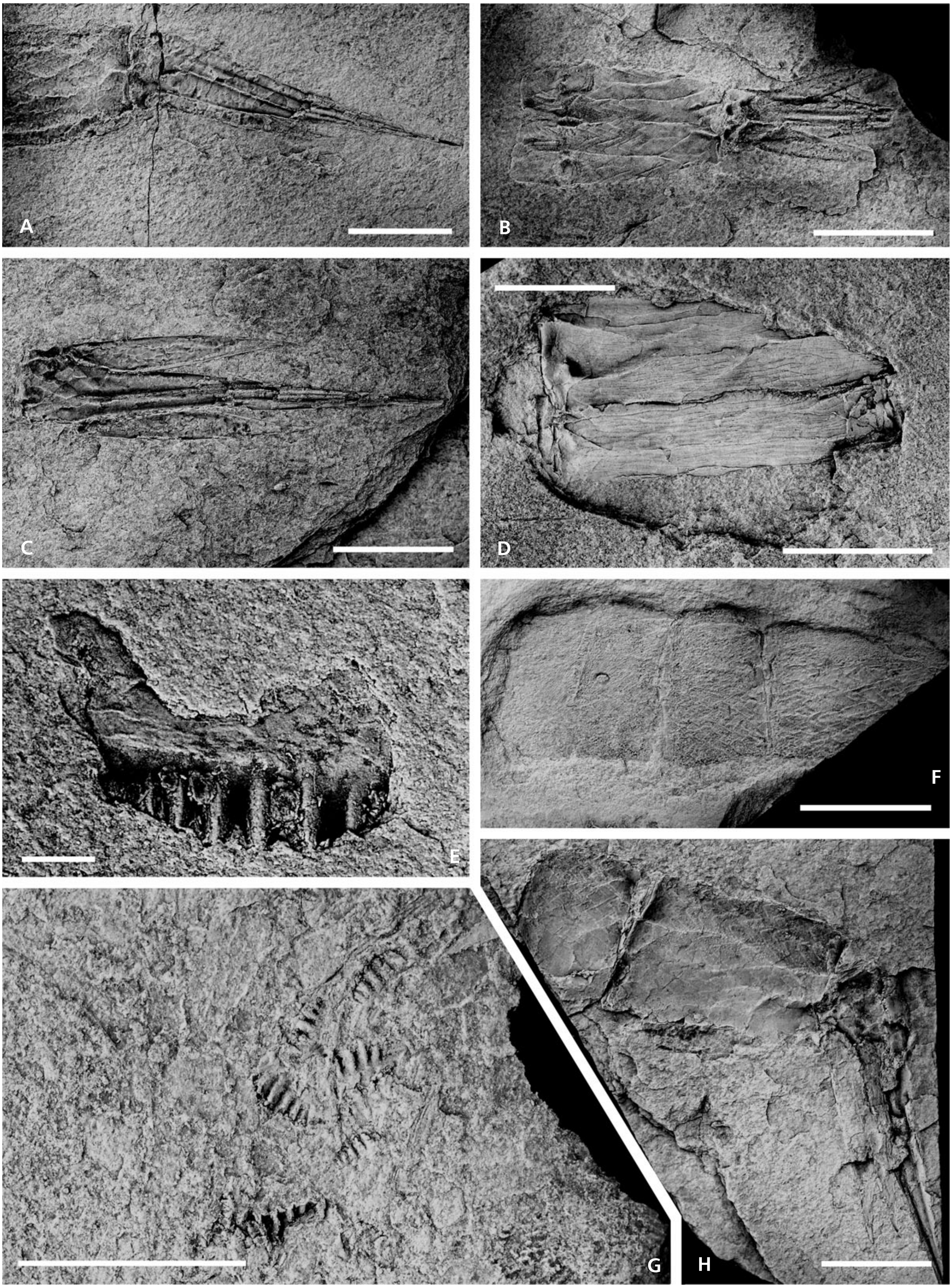
Chlupáč (1994) also mentions an occurrence of *C.* cf. *scharyi* in the tuffaceous shale of the *Monograptus belophorus* Zone in the Černidla section near Loděnice (see Kříž 1992 for locality description). He described a single specimen, smaller than typical *C. papilio* and *C. scharyi*, and also reported similar specimens from late Wenlock strata from Lejškov and Koněprusy localities (Chlupáč 1994), indicating that his *C.* cf. *scharyi* (rather *C.* aff. *scharyi*) is older than *C. scharyi*. Unfortunately, no specimen assigned to *C.* cf. *scharyi* was found in any collection in the Prague National Museum, Charles University, or the Czech Geological Survey. Consequently, a verification of Chlupáč's conclusion is impossible. The studied specimen of *C. scharyi* somewhat resembles the younger *Warneticaris grata* (Chlupáč, 1984) (Požáry Formation, Přídolí), but this species markedly differs from *C. scharyi* in possessing a much longer A7, ventrally coarser striation of the carapace valves, and by imperceptible pits posterior to minute lateral spines on the telson (see Chlupáč 1994).

Ceratiocaris inaequalis Barrande, 1872, which occurs in calcareous shales of middle and late Wenlock age, Motol Formation (*Cyrtograptus rigidus* to *C. lundgreni* zones), was referred by Chlupáč (1994) to his invalid subgenus *Ceratiocaris* (*Bohemicaris*). This species also somewhat resembles *C. papilio* in the general morphology of its abdominal segments but differs in having very prominent longitudinal ridges on the telson and especially by distinct longitudinal anastomose striation of A6 and A7 (see Barrande 1872, pl. 19, figs 14, 15). This type of striation is shared with *C. bohemica* Barrande, 1872, to which it was referred by Racheboeuf (1994), a view also supported by Collette & Hagadorn (2010).

Ceratiocaris docens Barrande, 1872 occurs in Kopanina Formation (Ludlow), *Ananaspis fecunda* to *Prionopeltis archiaci* 'horizons', *i.e. N. latilobus* and *M. fragmentalis* zones) is another species considered to be of doubtful validity by Chlupáč (1994). Subsequent examination and phylogenetic analysis has confirmed this suspicion, and this species has been referred back to *Ceratiocaris bohemica* Barrande, 1872, which occurs in overlaying Požáry Formation of Přídolí age (see table 1 in Collette & Hagadorn 2010 for synonymy). It was on the basis of *C. bohemica* that Chlupáč established the subgenus *Ceratiocaris* (*Bohemicaris)* to contain this and other ceratiocaridids with a short carapace lacking striations, an elongate and slender seventh abdominal segment, elongate telson and furcal rami (both with longitudinal ridges or striae) and abdominal and telson head sculpture (Chlupáč 1994). Collette & Hagadorn (2010) subsequently located a partially complete specimen of *C. bohemica* in the collections of the Czech National Museum (L 21193) that confirms the presence of typical ceratiocaridid carapace valve ornamentation. All other characters on which this subgenus was based occur in other ceratiocaridid taxa, and this subgenus was considered by Collette & Hagadorn (2010) as insufficiently differing from *Ceratiocaris sensu stricto* to be separated from this subgenus.

A thorough search of collections of the Prague National Museum, Charles University collections and the collections of the Czech Geological Survey have failed to locate other specimens previously attributable to *C. papilio*. Thus, the new material from the Všeradice section described herein represents the only occurrence of *Ceratiocaris papilio* currently known from Bohemia. The reconstruction of phyletic lines in Bohemian phyllocarids is difficult, and is complicated by variations in preservational style and a paucity of some species. Previously described specimens mentioned by O.P. Novák (MS) and I. Chlupáč (1994) to be

Figure 7. A, B, E–G – *Ceratiocaris papilio* Salter *in* Murchison, 1859. Lower Ludfordian, Silurian, Kopanina Formation, Všeradice, VŠ-2 pit. • A – articulated segment A7 and furca, CGS PB 507. • B – articulated segment A7 and furca, CGS PB 511. • C – articulated furca, showing smooth furcal rami and a telson with row of fine impressions, which match with attachment places of lateral spines, dorsal view, CGS PB 510. • D – *Ceratiocaris* sp. Lower Ludfordian, Silurian, Kopanina Formation, Všeradice, VŠ-2 pit. Isolated abdominal segment (A3–4?) with ornamentation consisting exclusively of fine striation, CGS PB 509. • E – isolated mandible, detail, CGS PB 512. • F – articulated segments A4–A7 with typical ornamentation, CGS PB 508. • G – clustered mandibles, CGS PB 513. • H– articulated segments A6+A7 with furca, CGS PB 506, showing typical ornamentation. Scale bars A–D, F–H = 1 cm; E = 1 mm.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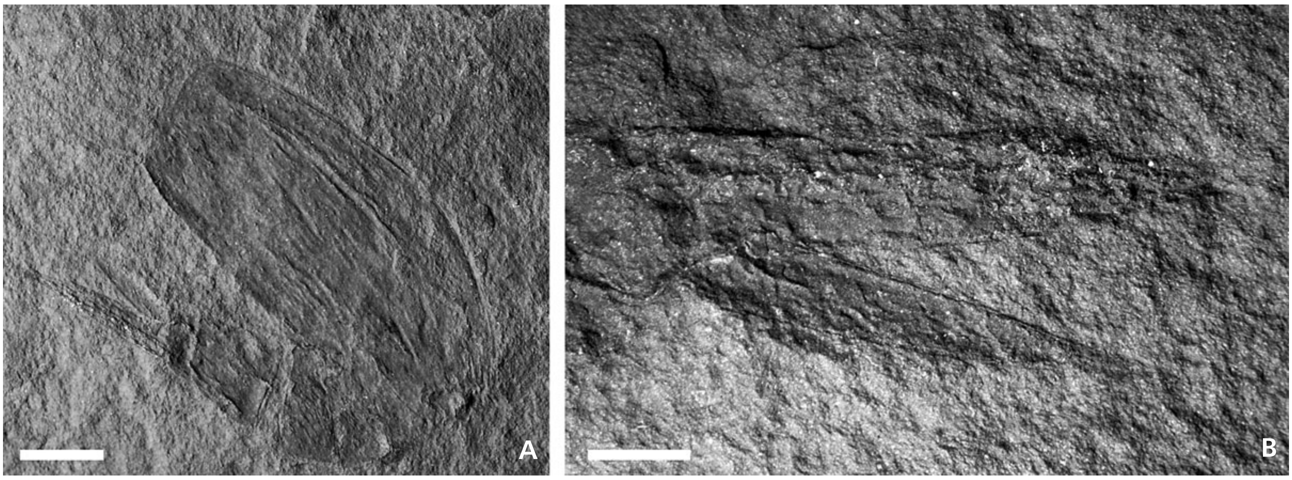


Figure 8. Scottish type specimen of *C. papilio* Salter *in* Murchison, 1859 (GSM 7479, neotype) photographed by P. Shepherd. • A – *C. papilio* neotype, entire specimen. • B – detail of neotype illustrating the smooth furcal rami without longitudinal striae. Scale bars A = 1 cm; B = 2 mm.

attributed to *C. papilio* have not been found in any collection. Among species occurring in Bohemia, *Ceratiocaris papilio* appears most closely related to the coeval *C. scharyi. Warneticaris grata*, which is common in Silurian-Devonian boundary strata also somewhat resembles *Ceratiocaris papilio* (Chlupáč 1984). It may be noted that *Ceratiocaris papilio* and allied forms inhabited rather more offshore environments, while *Ceratiocaris bohemica* and closely related taxa occur in shallower water environment.

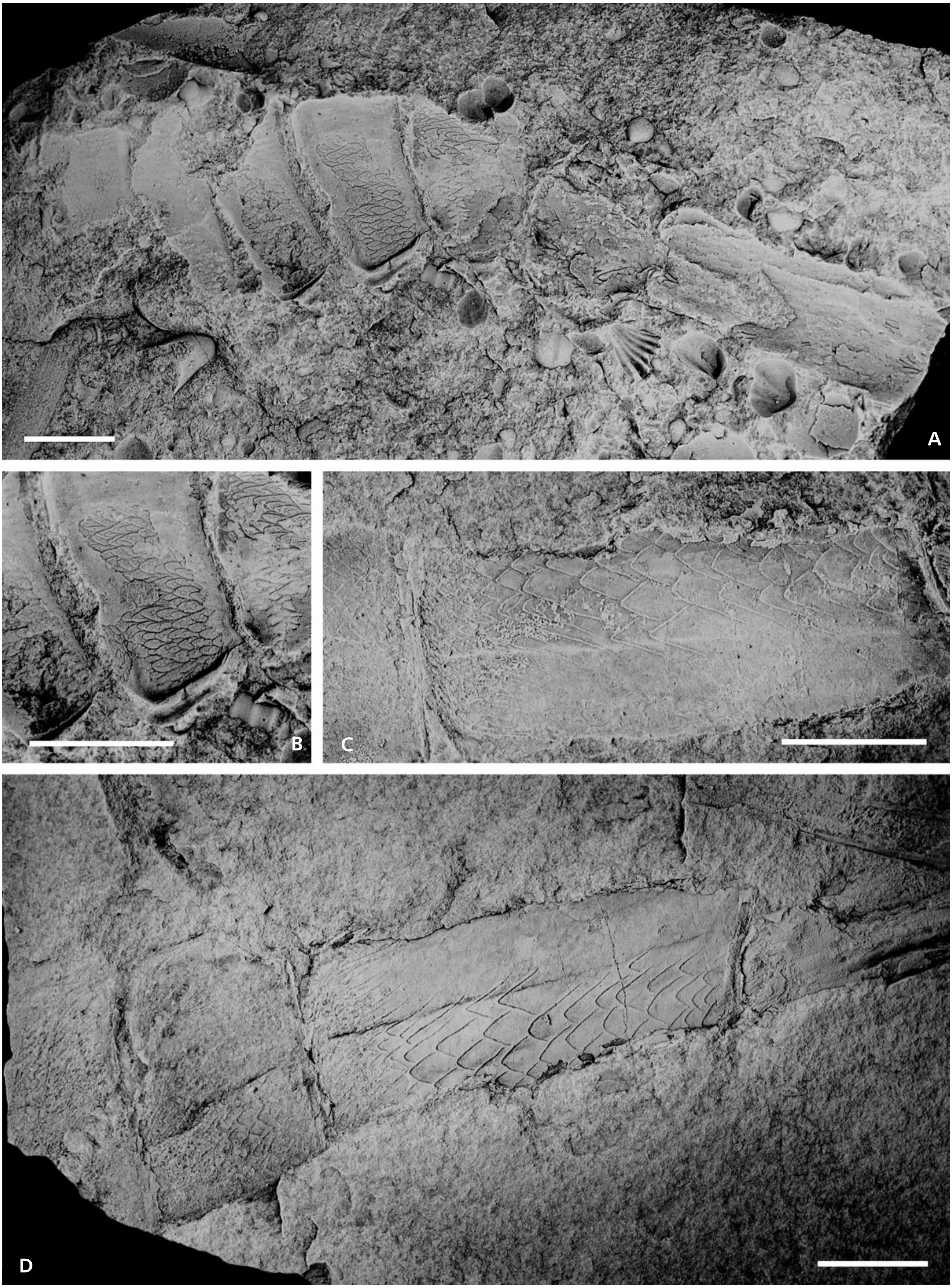
Conclusions and palaeogeographical consequences

Silurian phyllocarids are considered to be deeper-water mud dwellers and nektonic predator-scavengers (Vannier *et al*. 1997, 2003; for an analogy with modern leptostracans see Mauchline 1984 and Lee & Morton 2005). The palaeobiogeographic distribution of Silurian phyllocarids is still poorly known, but published data show rather high provinciality (Chlupáč 1994). This is remarkable because planktic and nektic marine animals generally show low provinciality in Silurian times; this is true in graptolites as well as cephalopods (*e.g*. Cocks & Torsvik 2002, 2006). The occurrence of *Ceratiocaris papilio* in the Ludfordian of Bohemia is quite unexpected. Prior to the discovery of Bohemian material, this species was known only from the Llandovery and Wenlock of Laurentia (Collette & Rudkin 2010). The presence of species related to *C. papilio* in the Llandovery to Ludlow of Bohemia was suggested by Chlupáč (1984, 1994); however, at present, we cannot confirm these results with certainty.

The early Palaeozoic succession preserved in the Prague Synform of central Bohemia is a relict of a former rift-like structure called the Prague Basin (for summary see Kříž *in* Chlupáč *et al.* 1998). Based on palaeomagnetic data, the basin was situated in the southern hemisphere during the early Ludlow. Various authors have calculated the paleogeographic position of the basin to be approximately 28–25° S (Krs *et al*. 2001, Kříž *et al*. 2003), or alternatively, slightly to the north (Cocks & Torsvik 2002, 2006), or to the south (Fatka & Mergl 2009). The latitudinal position is generally accepted to be within this range. The longitudinal position of the basin, however, and relation to other terrains is still quite controversial. The Prague Basin was located on a separate micro-plate called Perunica by Havlíček *et al.* (1994) and Fatka & Mergl (2009); alternatively, the Prague Basin may represent part of a Saxothuringian Assemblage Terrain (see Stampfli *et al*. 2002). Despite the general faunal similarity between Bohemia and peri-Gondwanan terrains, faunas from Bohemia contain many warm-water elements (see Manda 2008, Fatka & Mergl 2009). The differences between Bohemia and other peri-Gondwanan terrains in faunal composition suggest higher water temperature than in other peri-Gondwanan basins.

Ceratiocaris papilio is a well-known and easily distinguished species. It is currently known from the late Llandovery and Wenlock of Scotland, Iowa, Wisconsin

Figure 9. A, B – *Ceratiocaris scharyi* Barrande, 1872. • A – articulated abdominal segments A1 to A7, negative counterpart, NM L 18823, holotype by monotypy, figured by Barrande (1872) on pl. 32, figs 24–29, loc. "Wohrada" = Praha-Řeporyje, Ludfordian, Silurian, Kopanina Formation, bioclastic limestone. • B – the same specimen, a detail of ornamentation. • C, D –*Warneticaris grata* (Chlupáč, 1984). • C – detail of the ornamentation, holotype NM L 21191, figured by Chlupáč (1984) on pl. 1, figs 1–4, Požáry Formation, Velká Chuchle. • D – articulated abdominal segments A6+A7 plus furca, the same specimen. Scale bars = 1 cm.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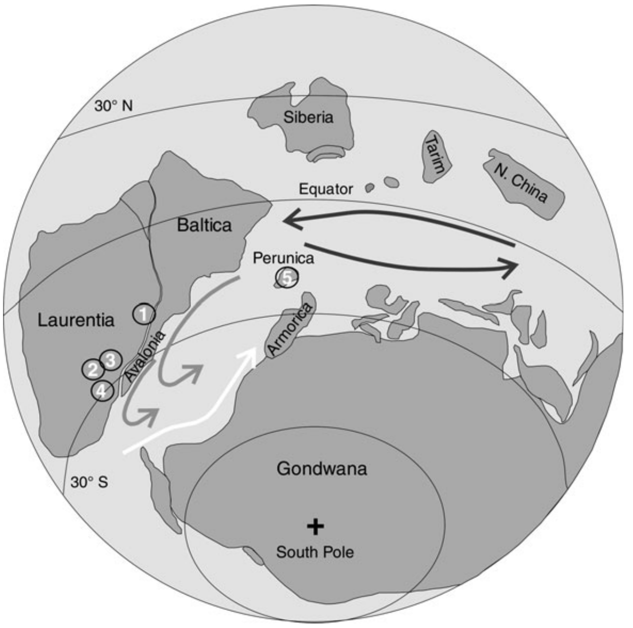

Figure 10. Hypothesized palaeogeographic map of the world in the early Ludlow (modified from Cocks & Torsvik 2002, 2006, supplemented by data of Scotese & McKerrow 1990, Wilde *et al.* 1991, Krs *et al.* 2001, Stampfli *et al.* 2002, Kříž *et al.* 2003 and Manda 2008). Hypothesized palaeogeographic position of the microcontinent Perunica slightly modified after Fatka & Mergl (2010). Dark-colored circles with Nos 1–4 show supposed position of currently known occurrences of *Ceratiocaris papilio* after Collette & Rudkin (2010): 1 – Lamarkshire, Scotland, UK (upper Llandovery to Wenlock); 2 – Waukesha, Wisconsin, USA (upper Llandovery); 3 – Wiarton, Ontario, Canada (Wenlock); 4 – Quincy, Iowa, USA (Wenlock). Number 5 represents supposed position of the new association from the Prague Basin (Ludlow, Ludfordian). Abbreviations: EQ – Equatorial Current; ST – South Tropical Current; SSP – South Subpolar Current. See discussion in the text.

and Ontario. Consequently, *C. papilio* represents an unequivocal Laurentian faunal element in the Prague Basin. No occurrence of *Ceratiocaris papilio* is currently known from northern Gondwana or peri-Gondwana. *Ceratiocaris bohemica* and *Warneticaris cornwalensis*, both common in Bohemia, are also known from Sardinia (Gnoli *et al.* 2009) and Armorica (Racheboeuf 1994). The Bohemian population of *Ceratiocaris papilio* is approximately 2 Ma younger than those of Laurentia. The distribution pattern of *C. papilio* implies an open seaway between Laurentia and Bohemia.

However, there is still the problem of possible migration routes between Laurentia and peri-Gondwanan terrain. These should be severely limited by the paleogeographic position of Avalonia, which lay close to the eastern Laurentia margin in Silurian time (see Fig. 7). Such a location for a unified Avalonian terrane (*e.g.* not subdivided into the West and East Avalonia sub-terranes, since the Ordovician-Silurian transition fused with Baltica, *sensu* Cocks & Fortey 2009) would be expected to cause at least a partial geographic barrier at that time, especially for a deeper-water fauna. Deeper water faunas might be expected to migrate across, or preferentially rather, along slopes. The same authors (Cocks & Fortey 2009) suggest 425 Ma (late Wenlock, mid-Homerian) as the probable timing of the closure of the Iapetus Ocean and the origin of Laurussia. A questionable occurrence of *Ceratiocaris papilio*, respective *C. stygia*? in Avalonia [*e.g.*, at the Welsh Borderland (see Anderson 2007 and Jones & Woodward 1888)], could not be confirmed here with certainty. Therefore, a possible scenario is presented in Fig. 10, in which the *Ceratiocaris papilio* population in the latest Wenlock appears to be using a migration route along the southern margin of Avalonia (after the closure of the Iapetus Ocean when deeper-water fauna should have migrated out of this area). In this scenario, it is possible that part of the *C. papilio* main population could have become entrained in the Southern Rheic Ocean Gyre Current and/or by the South Tropical Current *sensu* Wilde *et al.* (1991) and Manda (2008).

Even though material presented herein represents a fairly isolated and late occurrence of *C. papilio*, there are surprisingly few morphological differences when this population is compared with those known from Laurentia: *e.g.* smooth furcae in Czech specimens which also do not preserve the three hingeline nodes of the carapace, nor do they have the finer-scale trigonal micro-ornament 'overprinting' of the abdominal 'scales' preserved in Eramosa specimens. These differences might be explained by differing taphonomic conditions, or alternatively by small 'genetic drift'-like differences within populations or variability in a time-geographically constrained population. These minor morphological differences, however, in our opinion, do not exceed the limits of intra-specific variability already known in *C. papilio*. *Ceratiocaris papilio* appears to be a relatively long ranging taxon, with a range of perhaps 8.7 million years from the late Llandovery (430 ± 1.5 Ma) to the early Ludfordian (421.3 ± 2.6 Ma). Patchy or mosaic distribution patterns between populations suggests that *Ceratiocaris papilio* may have formed local populations with high abundance and ability to migrate over relatively long distances.

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Appendix

Abundance of *Ceratiocaris papilio* at Všeradice VŠ 2 section. A means abdominal segment.

No. of bed	42	46	48	52	56	58	60	62	Rock debris	Summa
"Incomplete specimen"							1			1
A4567								1	1	2
A567					2	2	1			5
A67					5	1	1		1	8
A7		1	1		4	4		2		12
Furca				6	19	20	5	14	20	84
Fragment of carapace						1				1
Telson	3				10	11	2	6	5	37
Mandibles				1	16	31	4	10	4	66
Other remains						1	2	2	2	7
Summa	3	1	1	7	56	71	16	35	33	223