Univerzita Karlova

Přírodovědecká fakulta

Studijní program: Geologie

Studijní obor: Geologie

Mgr. Martina Aubrechtová

Vybraní hlavonožci (Cephalopoda) ordoviku pražské pánve a Baltiky (Estonsko a Švédsko): taxonomie, paleobiogeografie a paleoekologie

Disertační práce

Školitel: doc. RNDr. Martin Košťák, Ph.D.

Konzultant: RNDr. Vojtěch Turek, CSc.

Praha, 2018

Charles University

Faculty of Science

Study programme: Geology

Study branch: Geology

Mgr. Martina Aubrechtová

Selected cephalopods from the Ordovician of the Prague Basin (Bohemia) and Baltica (Estonia and Sweden): taxonomy, paleobiogeography and paleoecology

Doctoral thesis

Supervisor: doc. RNDr. Martin Košťák, Ph.D.
Consulting supervisor: RNDr. Vojtěch Turek, CSc.

Prague, 2018

Prohlašuji, že jsem tuto dizertační práci zpracovala samostatně a že jsem použila pouze zde citované informační zdroje uvedené v seznamu literatury. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

V .... dne .... podpis autora

I declare that I prepared this dissertation thesis independently under the guidance of my supervisor and consultant, and that I used only the sources I quote and include in the list of references. This thesis, or a substantial part of it, has not been submitted to obtain another or the same academic title.

In .... date .... signature of the author

Abstrakt

Předkládaná dizertační práce shrnuje pět článků publikovaných v recenzovaných, impaktovaných odborných časopisech. Články jsou taxonomickými revizemi dříve neznámých nebo málo známých kolekcí fosilních hlavonožců ze spodního paleozoika Čech, Estonska a Švédska. Práce shrnují a zpřesňují paleogeografické a stratigrafické rozšíření jednotlivých taxonů a srovnávají jej s rozšířením podobně starých hlavonožcových tafocenóz známých z jiných oblastí. Tafocenózy jsou následně analyzovány a paleoekologicky interpretovány.

Dizertační práce se sestává ze tří hlavních částí. První část je zaměřena na morfologii hlavonožců a uvádí základní diagnostické znaky, které se při popisu hlavonožců používají. Shrnuje také dosavadní názory na systematiku hlavonožců a stručně představuje hlavní skupiny významné pro období ordoviku. Druhá část práce charakterizuje geologické podmínky a vývoj oblastí, ze kterých studovaní hlavonožci pocházejí. Třetí a poslední část pak shrnuje výsledky publikovaných studií.

Ze středního ordoviku pražské pánve byli studováni rod *Bactroceras* a dále zástupci řádu Lituitida. Rod *Bactroceras* Holm, 1898 je stratigraficky nejstarším známým zástupcem řádu Orthocerida. Ortoceridi byli prvními hlavonožci, kteří osídlili hlubokovodní, pelagická prostředí. Paleogeografické a stratigrafické rozšíření rodu *Bactroceras* ukazuje, že se ortoceridi poprvé objevili ve spodním ordoviku ve vysokých zeměpisných šířkách peri-Gondwany a později, během středního a svrchního ordoviku, se šířili do oblastí v nízkých zeměpisných šířkách. Nakonec se ortoceridi stali jednou z nejpočetnějších a nejdiverzifikovanějších skupin hlavonožců v paleozoiku. Morfologicky unikátní schránky další skupiny studované v pražské pánvi, hlavonožců náležejících řádu Lituitida, byly také adaptovány na podmínky pelagických a relativně hlubokovodních prostředí. Na rozdíl od ortoceridů byli ale lituitidi charakterističtí pro oblasti nízkých a středních zeměpisných šířek a ve vysokých šířkách, např. v pražské pánvi, se objevovali jen vzácně.

Adaptace hlavonožců na život ve volném vodním sloupci a jejich rozšíření do pelagických prostředí je jednou z nejvýznamnějších událostí ordovické biodiverzifikace (Global Ordovician Biodiversification Event, GOBE). Další její důležitou fází je globální rozšíření bioherm, které jsou dominantně budovány mnohobuněčnými organismy s pevnou kostrou. Tyto typy bioherm výrazněji vznikaly od svrchního středního ordoviku. Na tato útesová prostředí byla vázána bohatá a diverzifikovaná hlavonožcová fauna a jejich rozšíření bylo tudíž milníkem ve vývoji diverzity globálního ekosystému. V předkládané práci byly studovány dvě tafocenózy hlavonožců z prostředí bioherm svrchního ordoviku Baltiky: ze souvrství Vasalemma (Estonsko) a Kullsberg Limestone (Švédsko). Obě tafocenózy obsahují společenstva hlavonožců, která se vyvíjela přibližně ve stejném časovém úseku (svrchní stupeň sandbian) v témže sedimentačním prostoru (Baltická pánev), přesto se ale výrazně liší svým taxonomickým složením. Tyto rozdíly pravděpodobně souvisí s odlišnými podmínkami paleoprostředí obou oblastí – horniny tvořící souvrství Vasalemma jsou interpretovány jako mělkovodní, kdežto souvrství Kullsberg Limestone je interpretováno jako relativně hlubokovodnější. Společenstvo hlavonožců ze souvrství Kullsberg Limestone spíše odpovídá svým taxonomickým složením společenstvu již dříve popsanému ze souvrství Boda Limestone (Švédsko), které je stratigraficky mladší (svrchní stupeň katian–spodní stupeň hirnantian) a je také interpretováno jako hlubokovodnější. Hlavonožci ze

souvrství Vasalemma a Kullsberg Limestone jsou druhově velmi rozmanití a endemičtí, ale na taxonomických úrovních vyšších než druh vykazují afinitu ke vzdáleným oblastem, hlavně k Laurentii. V neposlední řadě byl ze svrchního siluru Estonska popsán stratigraficky nejstarší silurský zástupce řádu Ascocerida z Estonska. V siluru jsou askoceridi známí hlavně ze švédského ostrova Gotland a z pražské pánve a jejich výskyt v Estonsku je tudíž významným doplněním znalostí o paleogeografickém rozšíření skupiny a příkladem uplatnění fosilních hlavonožců pro paleogeografické interpretace i v dalších fázích paleozoika.

Abstract

This dissertation thesis is a summary of five studies published in peer-reviewed, impacted scientific journals. All of the publications are taxonomic revisions of previously unknown or little known collections of fossil cephalopods from the Early Paleozoic strata of Bohemia, Estonia and Sweden. Paleogeographical and stratigraphical distributions of the respective taxa were summarized, refined and compared with contemporary fossil assemblages known from other regions. Implications on the paleoecology of the cephalopods and original environmental conditions were made.

The text of the thesis is divided into three main parts. In the first part, the morphology of cephalopods is explained, stressing out the most important diagnostic characters used for their descriptions. The current systematics of the Cephalopoda is overviewed and the main cephalopod groups during the Ordovician are briefly introduced. The second part of the thesis describes the geological development and settings of the regions, from which the studied fossil cephalopods originate. The third and final part of the thesis provides a discussion and interpretation of the results of the published studies in the context of the previously published research.

The genus *Bactroceras* Holm, 1898 and some members of the order Lituitida were studied from the Middle Ordovician of the Prague Basin. *Bactroceras* is unique as the earliest known representative of the order Orthocerida. The orthocerids have straight, slender shells and were the first cephalopods to have inhabited deeper-water, pelagic environments. The paleogeographic and stratigraphic distribution of *Bactroceras* implies that orthocerids originated during the Early Ordovician in the high latitude regions of peri-Gondwana and later, during the Middle and Late Ordovician, expanded their habitats to low latitude regions. Subsequently, the orthocerids became one of the most abundant and diverse groups of the Cephalopoda of the whole Paleozoic. The morphologically peculiar shells of another cephalopod order studied from the Prague Basin, the Lituitida, were likewise adapted to the conditions of the pelagic and relatively deep water conditions. By contrast to the orthocerids, the lituitids were, typical for the low and mid latitude regions. In the high latitude regions, such as the Prague Basin, the lituitids appeared only occasionally.

The departure of cephalopods to the free water column and pelagic environments is one of the crucial events of the Global Ordovician Biodiversification Event (GOBE). Another important phase is the global expansion of metazoan-dominated (skeletal) reefs that more significantly progressed since the latest Middle Ordovician. Abundant and diverse cephalopod faunas inhabited these reefs. Herein, two cephalopod taphocoenoses from the late Sandbian reefal environments of Baltoscandia were studied: from the Vasalemma Formation (Estonia) and the Kullsberg Limestone Formation (Sweden). Both taphocoenoses come from roughly coeval strata that originated in the same basin (Baltic Basin) but are still taxonomically distinct. The differences in the occurrence and abundance of individual taxa probably reflect different paleoenvironmental conditions under which both cephalopod faunas lived: the reefal limestones of the Vasalemma Formation represent the more proximal and shallow water environment, while the mud-mounds of the Kullsberg Limestone Formation are interpreted as the relatively deeper-water. The Kullsberg cephalopods are in fact more similar in taxo-

nomic composition to those of the previously described, stratigraphically younger (late Katian – early Hirnantian) and also deeper-water mud-mounds of the Boda Limestone Formation (Sweden). On the species level, both the Vasalemma and Kullsberg cephalopods are uniquely diverse and highly endemic. On the genus- and higher taxonomic levels, however, they show similarities to fossil assemblages from distant regions, such as Laurentia.

Additionally, the earliest member of the order Ascocerida from the Late Silurian strata of Estonia is reported herein. During the Silurian, the ascocerids are mainly known from the Swedish island of Gotland and the Prague Basin. Their occurrence in Estonia is thus an important addition to our knowledge on the paleogeographical pattern of the group and an example of the use of fossil cephalopods for paleogeographical purposes also in later phases of the Paleozoic.

Acknowledgments
At the first place, I would like to thank my parents, Ing. Ladislav Aubrecht and Ing. Helena Aubrechtová, and my sister, Ing. Markéta Aubrechtová, without which the completion of this dissertation thesis would have not been possible. Also, I would like to thank my friends, Jakub Vodička, Martina Vokáčová, Martin Bachura and my boyfriend Mikuláš Muroň for their company, endless support and belief in my abilities.

I am very grateful to my supervisors, doc. RNDr. Martin Košťák, Ph.D. (Charles University, Faculty of Science, Prague) and RNDr. Vojtěch Turek, CSc. (National Museum, Prague), for their immense help and always constructive discussions and supervision. Vojtěch Turek and Mgr. Martin Valent, Ph.D are also acknowledged for enabling the access and help during the work in the collections of the National Museum (Prague). I additionally thank RNDr. Petr Budil, Ph.D. and RNDr. Eva Kadlecová for the access and help at the collections of the Czech Geological Survey (Prague).

Very special thanks belong to prof. Tõnu Meidla (University of Tartu) and Dr. Björn Kröger (University of Helsinki), who kindly supervised my work during my respective internships in Estonia and Finland, during which I have gained not only important professional but also great personal experiences. In relation to that, I am deeply indebted to all of the curators and colleagues, who enabled me to study the respective museum collections, always kindly helped me to find corresponding literature, helped while transporting the borrowed specimens and advised me in practical matters. I namely thank Dr. Mare Isakar (University of Tartu), Dr. Ursula Toom (Tallinn University of Technology), Dr. Karin Truuver and Dr. Sander Olo (Estonian Museum of Natural History, Tallinn), Dr. Christian Skovsted (Swedish Museum of Natural History, Stockholm), Dr. Dieter Korn and Dr. Andreas Abele (Museum für Naturkunde, Berlin). Gennadi Baranov (Tallinn University of Technology) and Lenka Váchová (National Museum, Prague) are acknowledged for a crucial help with photographing of some of the specimens.

I thank prof. doc. RNDr. Oldřich Fatka, CSc. (Charles University, Faculty of Science, Prague) and doc. RNDr. Petr Kraft, CSc. (Charles University, Faculty of Science, Prague and Museum of Dr. Bohuslav Horák, Rokycany) for many valuable discussions and advices and provision of some of the missing literature. Also acknowledged is Mgr. Jan Wagner, Ph.D. (National Museum, Prague) for the help with literature and solving nomenclatorical issues.

I would like to thank the Faculty of Science of the Charles University (Prague), the National Museum (Prague) and the Czech Geological Survey (Prague) for enabling the access to their respective collections and providing needed workspace and essential equipment.

Some of the research included in this thesis was supported by the European Social Fund's Doctoral Studies – the Internationalisation Programme DoRa, Deutsche Forschungsgemeinschaft (grant Kr 2095/7-1), and SYNTHESYS3 which is financed by the European Community – Research Infrastructure Action under the Seventh Framework Programme (FP7/2007-2013, grant agreement n°226506).

The last but not the least, I am grateful to the numerous libraries and cafeterias, that provided me with a suitable workplace and material resources to finalize this dissertation thesis.

Contents

1. Introduction

Cephalopods are evolutionary successful, highly diversified and abundant carnivorous marine mollusks with a vertebrate-like intelligence, complex behaviors (Fiorito *et al.* 1990; Nixon & Young 2003; Mather 2004, 2008; Langridge *et al.* 2007; Hanlon & Messenger 2018) and a unique buoyancy system for locomotion (Westermann 1977, 1998; Kröger 2002, 2003; Greenwald & Ward 2010; Hoffmann *et al.* 2015). Typically, they are active predators feeding on vertebrate fish, other mollusks or arthropods (Boyle & Rodhouse 2005). The cephalopods inhabit nearly all marine environments; they range from tropical to arctic latitudes, they may live associated with shallow-water coral reefs, as well as in the deep sea or be fully pelagic (Boyle & Rodhouse 2005).

By contrast to the extant representatives of the group, most fossil cephalopods had external, hard shells that were often preserved in rocks ranging in age from the Late Cambrian up to the present (Clarke & Trueman 2013). Cephalopod shells may even be so characteristic for some rocks that these have been referred to as the cephalopod facies, or terms have been used, such as the orthoceratite, Vaginatum, or Endoceras Limestone of the Ordovician of Baltoscandia (Kröger 2012), the cephalopod limestones in the Silurian of Bohemia (e.g., Manda & Kříž 2007) or the Ammonitico Rosso limestones in the Jurassic of the Alpine-Mediterranean region (e.g., Jenkyns 1975).

As early as in the Early Paleozoic, the cephalopods have been among the top predators (Westermann 1998; Brett & Walker 2002; Kröger & Zhang 2009) and thus a key component of ecosystems, sensitively reacting to the changes in trophic chains and their structure (Servais *et al.* 2008a; Kröger & Zhang 2009). Consequently, many studies have used fossil cephalopods for paleoecological but also paleogeographical and stratigraphical interpretations (e.g. Bogolepova 1995; Ferreti & Kříž 1995; Gnoli 2003; Manda & Kříž 2006, 2007; Evans 2007; Manda 2008a, b; Manda & Frýda 2010; Evans *et al.* 2013, 2015; Kröger & Lefebvre 2012; Kröger 2013a). Stable isotope data have been collected from their shells (e.g., Wierzbowski 2004; Lukeneder *et al.* 2010). The rapid diversification of cephalopods and development of their assemblages in the lower to middle Paleozoic ecosystems is one of the most important phases of the Global Ordovician Biodiversification Event (GOBE; Webby *et al.* 2004; Kröger *et al.* 2009b; Kröger & Zhang 2009; Servais *et al.* 2008a; Kröger 2013a; Servais & Harper 2018) and the Devonian Nekton Revolution (Klug *et al.* 2010). During the former Event, the Paleozoic Evolutionary Fauna of Sepkoski (1978, 1979, 1981, 1984) was established. This dissertation thesis presents studies of some selected Ordovician cephalopods from Bohemia and Baltoscandia. The majority of the studied specimens came from old, extensive but previously unpublished and/or unrevised collections of cephalopods deposited in several museum collections in the Czech Republic, Estonia and Sweden. The aim was to make modern taxonomic revisions that would add reliable and up-to-date stratigraphic and paleogeographic data to the current understanding of the changes in Ordovician environments and ecosystems. Five publications are summarized below and referenced and attached to this dissertation thesis as Appendices 1–5.

2. Class Cephalopoda Cuvier, 1795

2.1 Morphology and diagnostic characters of fossil cephalopods

As all mollusks, the cephalopods are characterized by the presence of calcite and/or aragonite shells, which provide protection to the soft body and function as a powerful device for buoyancy regulation (i.e., hydrodynamic and hydrostatic organs, see below). In the majority of extant cephalopods, the Coleoidea (vampyropods and decabranchians), the shell has been mostly internalized, significantly reduced or entirely disappeared (Kröger *et al.* 2011). The primary external shell has been fully retained only in the comparatively rare genera *Nautilus* Linnaeus, 1758 and *Allonautilus* Ward & Saunders, 1997 (Nautiloidea; Strenzel 1964, K59–K93) and has thus been crucial to the understanding of the morphology, development and function of the shells of extinct cephalopods.

Herein, the terminology of the shells of fossil cephalopods largely follows Teichert (1964a, K13–K59); the terms used to describe coiled shells follow those of Korn (2010) and terms related to sculpture and internal structures are adopted from Kröger (2008). It is important to note that the conventionally used orientation of cephalopod shells (particularly the usage of terms "dorsal" and "ventral") does not correspond to the biological orientation (see Flower 1939; Teichert 1964a, K15; Mutvei 1957, 1964; Fig. 1 herein). However, the conventional orientation is used widely throughout the published literature and is thus followed in this thesis, as well.

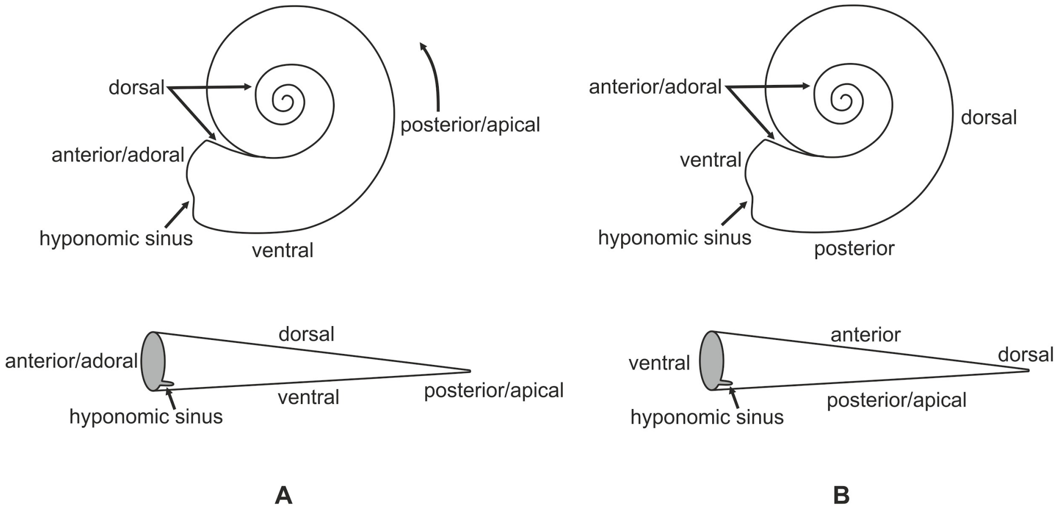

Figure 1: Comparison of "conventional" (**A**) and "biological" (**B**) orientation of orthoconic and coiled cephalopod shells. After Teichert (1964a, K20).

2.2 Internal structure of the shell

The shell (conch) consists of two parts. The posterior part is termed the phragmocone (Fig. 2); it is divided by bowl-shaped septa into phragmocone chambers (camerae). The adoral part of the shell is termed the living chamber (body chamber; Fig. 2) and this is where most of the soft tissues of the animal are located and attached to the interior side of the shell wall with muscles.

The septa have a free part, which separates individual chambers and is directed with its convex surface adapically, and their mural part, which is attached to the interior part of the shell wall. On the internal mould, the place of the attachment of septa is marked by a line called the suture. The sutures are either directly transverse to the longitudinal axis of the shell and straight in shape, or they may be oblique and sinuous in shape (with lobes and saddles). The septa are perforated by the septal foramen (septal perforation). The margins of the septal foramen are inflexed backwards (apically) and form the septal necks. Structurally modified continuations of the septal necks, that connect two successive septal necks, are called the connecting rings. Septal necks and connecting rings are collectively termed the ectosiphuncle and enclose the fleshy extension of the animal's body, the siphuncular cord. The ectosiphuncle and the siphuncular cord together form the siphuncle.

The most important characteristics of the siphuncle are as follows: its position respective to the longitudinal axis of the shell, its diameter, type of the septal necks and type of the connecting rings. The position of the siphuncle can vary between perfectly central to marginal, when the siphuncle is in direct contact with the shell wall. Variable is also the diameter of the siphuncle. There are cephalopods with very narrow, as well as very wide siphuncles, the latter can take up to 1/2 of the corresponding diameter of the shell. The different types of septal necks are distinguished based on their length and degree of deflection (Fig. 3). Terms such as achoanitic, orthochoanitic, loxochoanitic, cyrtochoanitic, holochoanitic or macrochoanitic are used. The connecting rings are distinguished based on their shape (tubular/cylindric or expanded) and thickness (thin or thickened). Orthochoanitic septal necks are often linked with tubular or nearly tubular connecting rings (Fig. 3B,C, F, G), while cyrtochoanitic septal necks are typically accompanied with expanded or very thick connecting rings (Fig. 3A, D, E, H).

Mutvei (1997; 1998; 2002a, b; 2013; 2015) studied the ultrastructure of the siphuncle in various cephalopods and identified two basic types of the connecting rings: the *Nautilus*-type and the calcified-perforate type. In the former type, the connecting rings consist of two layers, the outer spherulitic-prismatic layer (a continuation of the same layer of the septal neck), and a fibrous, glycoprotein (conchiolin) layer, the latter is an uncalcified continuation of the nacreous layer of the septal neck. By contrast, in the latter type of the connecting rings, the inner layer is not organic but calcified and perforated with pores.

Siphuncle and/or phragmocone chambers may be infilled with carbonatic matter (endosiphuncular and cameral deposits; Fig. 3B, G) that is gradually secreted by the animal during its life in order to stabilize and maintain the appropriate orientation of the shell in the water column (see also Teichert 1964a; Fischer & Teichert 1969 and Turek & Manda 2012). Cameral deposits start to be formed in apicalmost chambers (mainly on their ventral side) and their formation continues adorally. Thus, the deposits are always ontogenetically younger than the respective phragmocone chamber and never present in adoralmost portions of phragmocones and in living chambers (Flower 1955; Fischer & Teichert 1969). In some groups, the cameral deposits may grow into the siphuncle through the intact connecting ring (Mutvei 1957; Fischer in Fischer & Teichert 1969; Dzik 1984), in others the connecting ring may be ruptured or partially/fully resorbed (Flower 1939, 1941, 1955, 1964; Teichert 1964a; Holland 1965; Teichert in Fischer & Teichert 1969; Histon 1993; Kolebaba 1999a, b, 2002; Turek & Manda 2012) and the deposits cover the septal necks and form the so-called epichoanitic deposits (Kröger 2008).

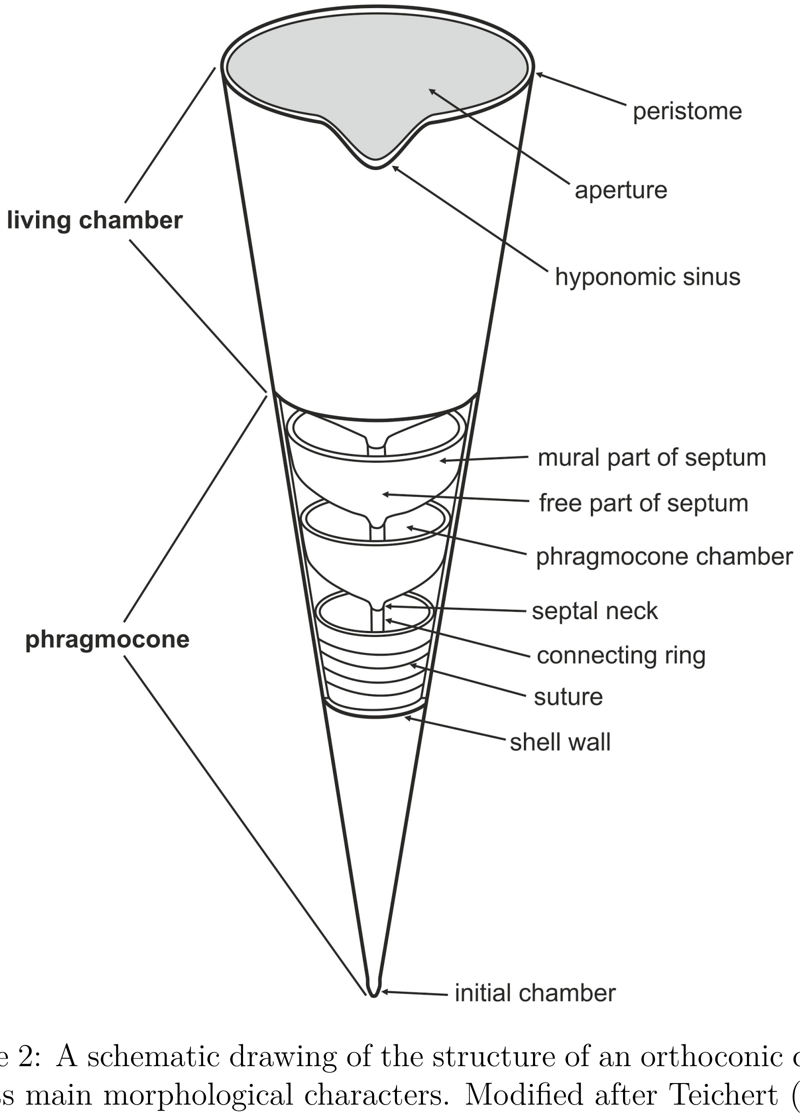

Figure 2: A schematic drawing of the structure of an orthoconic cephalopod shell and its main morphological characters. Modified after Teichert (1964a, K14).

The position of cameral deposits within chambers is described using terms like hyposeptal (located on the convex side of the septum), episeptal (concave side of the septum) and mural (on the mural part of the septum). For endosiphuncular deposits, different terms are used to describe their shape, form and location within the siphuncle. Diaphragms (transverse elements), lamellae (longitudinal elements), endocones (transversely oriented conical elements), central cylindrical tube, parietal (covering siphuncular side of connecting rings) and annulosiphonate deposits (covering siphuncular side of septal necks) are distinguished.

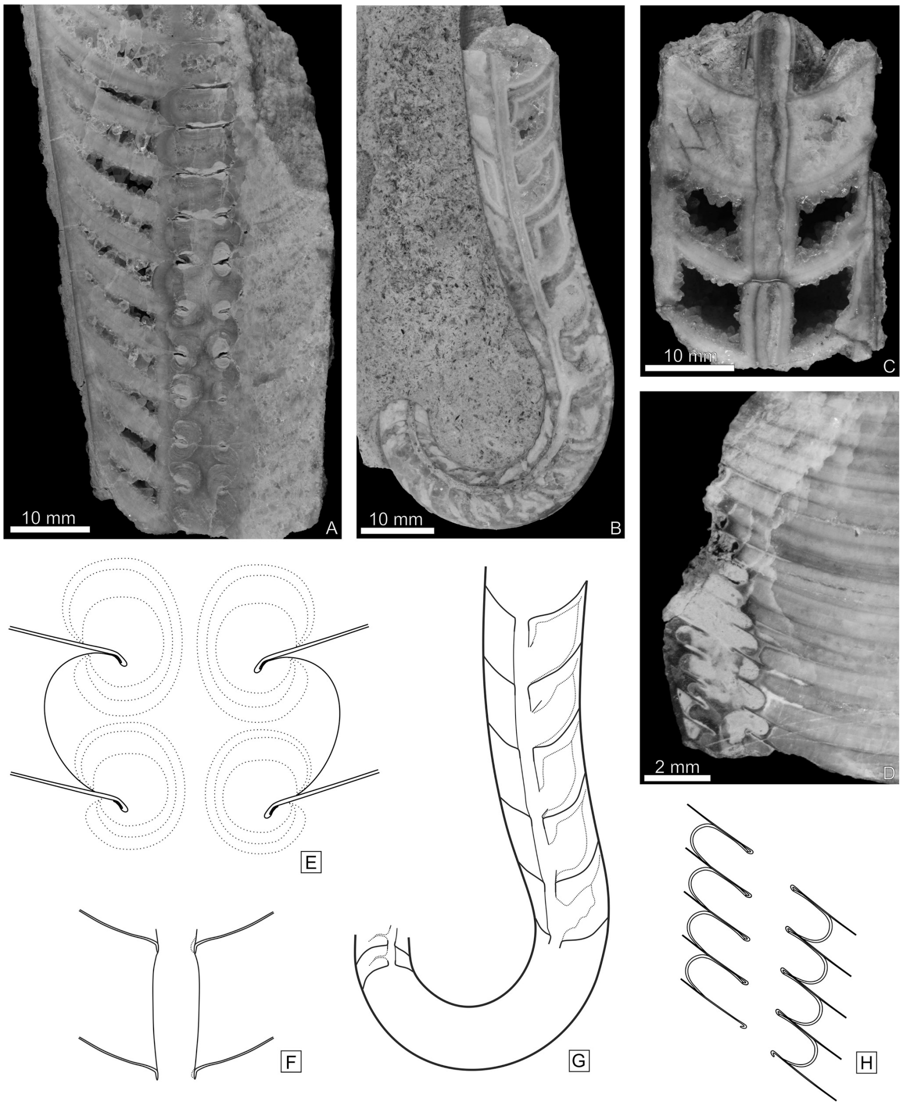

Figure 3: Photographs and drawings showing different types of internal structures in some cephalopods. **A**, **E** – the actinocerid *Orthonybyoceras* Shimizu & Obata, 1935 with cyrtochoanitic, recumbent septal necks, thin, strongly expanded connecting rings and heavy annulosiphonate deposits, TUG 1307-1; **B**, **G** – the lituitid *Lituites* Bertrand, 1763 with moderately short, orthochoanitic septal necks, tubular connecting rings and heavy cameral deposits, note the impaired connectings rings in some chambers, GIT 146-8 from the Väo Formation, Middle Ordovician, Estonia, Gennadi Baranov (Tallinn University of Technology); **C**, **F** – the orthocerid *Ordogeisonoceras* Frey, 1995 with short, slightly suborthochoanitic septal necks, slightly expanded connecting rings and small annulosiphonate deposits, TUG 939-10; **D**, **H** – the discosorid *Hemibeloitoceras* Balashov, 1962 with short, cyrtochoanitic septal necks with free brims and strongly expanded connecting rings, TUG 1612-12. **A**, **C**, **D**–**F**, **H** – specimens from the Vasalemma Formation, Upper Ordovician, Estonia (Kröger & Aubrechtová 2018 – Appendix 3).

The living chamber opens adorally with the aperture (Fig. 2 herein). The very edge of the aperture is the peristome, which is ventrally indented forming the hyponomic sinus. The peristome may be either simple or have additional indentations and other modifications, the latter case is termed modified or contracted aperture. Retractor muscles are attached to the inner side of the living chamber leaving muscle scars (impressions, imprints) that can be seen on internal moulds at the base of the living chamber. The retractor muscle scars are either dorsomyarian, ventromyarian or pleuromyarian according to their shape and position (Mutvei 1957, 2002b; Sweet 1959).

2.3 External form of the shell and ornamentation

The shell is a conical object, in which the maximum and the minimum diameter is measured and which expands under a certain angle of expansion (expansion rate, apical angle). The transverse cross section of the shell may be circular, subcircular, laterally compressed or dorsoventrally depressed in shape, depending on the ratio between the lateral and dorsoventral diameter of the shell.

Longitudinally, the shell can have many different shapes and forms (Fig. 4). Completely straight shells are called orthocones (adjective orthoconic), while more or less curved shells are cyrtocones (adjective cyrtoconic). A longicone (adjective longiconic) is a slowly expanding shell, typically with an open or only slightly modified mature aperture. By contrast, brevicones (adjective breviconic) have a swollen, rapidly expanding shell, often with a restricted, modified aperture upon maturity.

When the shell curvature reaches at least 360°(this forms a whorl), then the shell is coiled. A gyrocone is loosely coiled, i.e., individual whorls are not in touch. In tightly coiled shells, the whorls touch each other and several terms may be used to express the degree of coiling and general shape (e.g., serpenticone, tarphycone, ellipticone, sphaerocone, nautilicone, oxycone, platycone). A special case is a lituiticone, in which the last whorl diverges from the preceding one and the shell becomes straight at the end.

In coiled shells, the umbilicus is developed in the center (Fig. 4); the umbilicus may be open (perforated) or closed.

The terms endogastric and exogastric are used for curved or coiled shells to express the position of the ventral side of the shell on either the inner or the outer side of the curvature/whorl respective to its longitudinal axis.

In tightly coiled shells, where the whorls are in contact with each other, several terms are used to expressed the degree of whorl impression. Evolute shells have whorls, that are weakly impressed or not impressed at all. In convolute shells, the whorls are moderately impressed. In involute shells, the whorls are strongly impressed and the last whorl envelopes and covers preceding whorls.

In many cephalopod taxa, the shell surface is elaborately sculptured (ornamented). The sculpture (ornamentation) is either directly transverse, oblique or longitudinal with respect to the longitudinal axis of the shell. Elements of sculpture include: striae (faint, simple, parallel grooves); lirae (raised lines); ridges (local thickenings of the shell); annuli (transverse elevations); ribs (costae; pronounced transverse or obliquely running elevations); and more rarely nodes and spines. Undulations originate, when the shell wall itself is transversely sinuous (undulated); unlike annuli, undulations are visible on internal moulds. When no ornament or only the growth lines are present on the shell surface, then the shell is termed smooth. The growth lines are generally straight and directly transverse to the longitudinal axis of the shell, forming only the so-called hyponomic sinus on their ventral side.

The apicalmost part of the phragmocone, which developed earliest in the ontogeny, still in the egg, is called the embryonic shell. The first phragmocone chamber formed is the initial chamber (initial camera, first camera, apical camera; Fig. 2). The initial chamber includes the initial segment of the siphuncle called the caecum. A furrow (an elongated structure or an initial plate; Mutvei *et al.* 1993; Arnold *et al.* 2010) on the exterior of the initial chamber seen in some groups of cephalopods is called a cicatrix. The size, shape, presence or absence of constriction between the initial and second chamber and the presence or absence of cicatrix are important features used in higher-level systematics and paleoecological interpretations in cephalopods (see Kröger 2006; Kröger & Isakar 2006; Manda & Frýda 2010 and references therein).

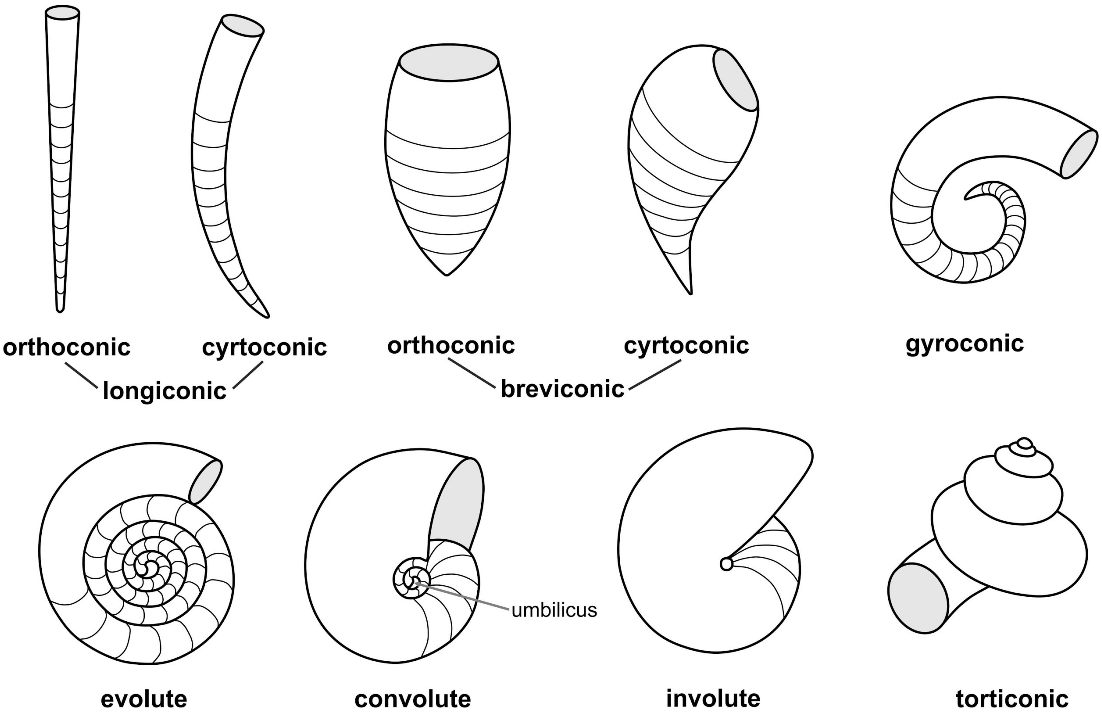

Figure 4: Distinction of cephalopod shells based on their shapes and modes of coiling. After Teichert (1964a, K21).

2.4 Morphology and mode of life

Within the aquatic environment, the cephalopod, regardless of whether it has an external, internal or reduced shell, has to cope with three main forces: the ambient (hydrostatic) pressure that is exerted by the water column; buoyancy, which has an upward direction and originates from the presence of low-density gas-filled phragmocone chambers with the shell; and gravity, which has a downward direction and is exerted through the weight of the living chamber with the soft body and cameral/endosiphuncular deposits within the phragmocone (if these are present).

The assumption is such that cephalopods, whether fossil or extant, have been able to remain neutrally buoyant (e.g., Packard 1972; Denton 1974; Nesis 1987), which means that the overall density of the animal equals that of the surrounding environment. The animal maintained at a certain depth and does not need to actively (hydrodynamically) lift itself up (Westermann 1998).

Already in the Early Paleozoic, cephalopods have developed a variety of shell designs that permitted them to inhabit many marine environments (shallow to deep) and use a wide range of life strategies. Each environment and life strategy requires a different set of characters to control buoyancy and provide a sufficient degree of strength towards hydrostatic pressure. Numerous works that studied the link between morphology and mode of life have been published, namely those of Ward (1982), Westermann (1998) and Kröger (2003). Recent studies of Kröger & Zhang (2009) and Kröger *et al.* (2009b) summarized sedimentological and other data that provide additional information on the environments and life habits of extinct cephalopods.

Westermann (1998) described and illustrated the basic morphotypes in the Cephalopoda and evaluated in each morphotype its maximum habitat depth (vs. shell implosion depth; Fig. 5), orientation of the shell during life and the degree of mobility. The morphotypes are the following:

- Orthocones
    - *Orthoconic longicones*: slender, thin shells with a simple, open aperture, circular transverse cross-section, tubular, usually central siphuncles and lacking extensive cameral and/or endosiphuncular deposits. Orientation during life vertical or slightly inclined. Planktonic, possibly vertical migrants that were able to descent into greater depths.
    - *Curved longicones*: often compressed, thin shells. Orientation during life inclined. demerzal, slow, forward swimmers.
    - *Large orthocones*: heavy cameral and/or endosiphuncular deposits, cross-section often depressed, siphuncle wide, often submarginal or marginal in position. Orientation during life horizontal, capable of forward swimming in moderately high speed. Backward swimming interpreted by the Westermann (1998) as uncontrolled and used for escape. This group included active predators some of which were restricted to shallow-water environments (order Actinocerida) but others capable of descending to greater depths and pelagic environments (order Endocerida).
    - *Cyrtocones*: strongly curved shells without cameral and/or endosiphuncular deposits.
      Orientation during life inclined. Movement slow, downwards or to the sides but not easily upward. Benthic predators.
- *Brevicones*: straight or curved shells with a modified, restricted aperture, the shell strong towards turbulences. demerzal predators limited to shallow seas.
- *Gyrocones*: slowly swimming, restricted to shallow-waters, planktonic or demerzal, able to move in all directions.

- *Torticones*: helically coiled shells without cameral/endosiphuncular deposits. Orientation during life vertical. The shell compact and strong, motion vertical, some possibly planktic.
- *Tightly coiled shells*: shells generally more compact, more stable and stronger towards hydrostatic pressure and serve as a good defence against predators.
  - The animals were good horizontal swimmers, when the apical angle was high, when the whorls were compressed and impressed and when the outer side of the shell was sharp in shape. The coiled shell was more stable, when the living chamber was shorter. The compressed shells are however more vulnerable towards ambient pressure and thus, various types of supporting structures and complex sutures are developed in many taxa.
  - In extant *Nautilus*, the aperture is oriented obliquely downwards and the animal has a "rocking motion", a similar type of motion may be assumed for extinct cephalopods with similar morphology, as well.
  - Some coiled shells are ventrally flattened. It is assumed, that such animals commonly rested on the sea floor and thus were restricted to shallow-water environments.

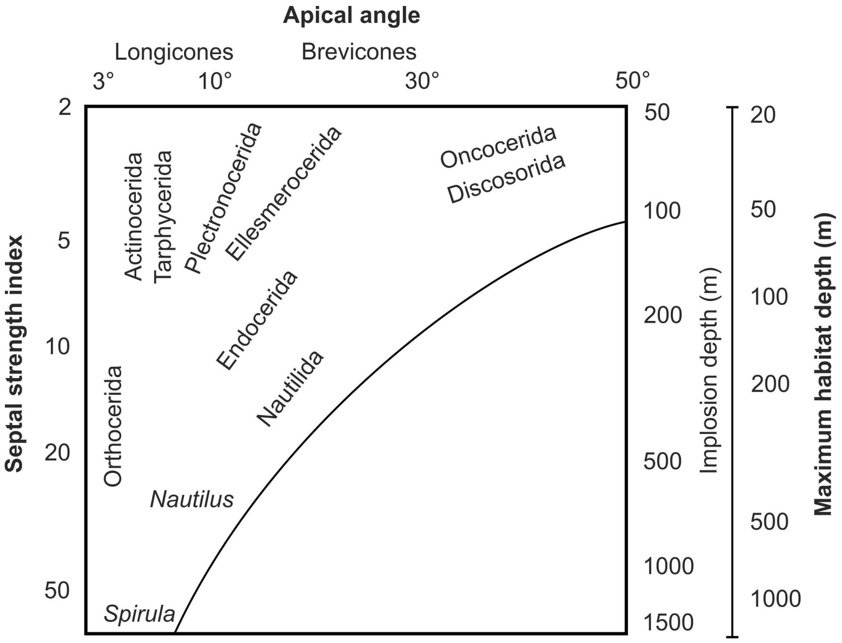

Figure 5: Maximum habitat depth and shell implosion depth estimated for the basic morphotypes of the Cephalopoda. After Westermann (1998).

2.5 Significant groups of the Cephalopoda during the Ordovician

The most important works dealing with the higher-level taxonomy of the class Cephalopoda and summarizing previous literature are those of Flower & Kummel (1950), Moore (1957, 1964) and Ruzhencev (1962).

In the *Treatise of Invertebrate Paleontology* (Moore 1957, 1964), the class Cephalopoda was divided into five subclasses: Endoceratoidea (orders Endocerida and Intejocerida), Actinoceratoidea (order Actinocerida), Nautiloidea (eight orders Ascocerida, Barrandeocerida, Discosorida, Ellesmerocerida, Nautilida, Oncocerida, Orthocerida and Tarphycerida), Bactritoidea (order Bactritida) and Ammonoidea (see Moore 1957). The above scheme has remained relatively unchanged until the present (see summary in Evans 2005 and Shevyrev 2006a, b). Mutvei (1957, 1997, 2002a, b), Doguzhaeva & Mutvei (1993) and Mutvei & Dunca (2011) studied the retractor muscle attachments and internal structure of the siphuncle across the Cephalopoda and Mutvei (2013, 2015) created several order- and higher-level taxa on that basis. In his comprehensive study, Dzik (1984) proposed some changes on the ordinal level within the subclass Nautiloidea; the author for example included the Lituitida and Actinocerida under the Orthocerida (see also Mutvei 2002a, b) and the Barrandeocerida under the Tarphycerida (see also Flower 1984). Zhuravleva (1994) created the superorder Orthoceratoidea and included into it the Orthocerida, Pseudorthocerida and the newly defined Dissidocerida. Engeser (1996) studied the position of the Ammonoidea within the Cephalopoda and distinguished two groups within the class, Nautiloidea and Angusteradulata, based on the morphology of their radula, type of early ontogeny and other characters. Evans (2005) disregarded Endoceratoidea and Actinoceratoidea but accepted the use of Orthoceratoidea and the order Dissidocerida. Evans & King (2012) suggested the polyphyly of the Endocerida and separated from it the new order Bissonocerida. Kröger & Mapes (2007) proposed that the order Actinocerida is a sister group to the Pseudorthocerida (see also below). A synopsis and discussion of other publications dealing with the above issues has been provided by Shevyrev (2006a,b).

As seen above, the high-rank taxonomy of the Cephalopoda is a complex issue, which is still far from being fully solved. There are some problematic taxa, such as orders Ascocerida, Barrandeocerida, Lituitida, Pseudorthocerida or the genera *Isorthoceras* Flower, 1962a and *Sphooceras* Flower, 1962b, in which their affinities and/or internal taxonomy has not yet been satisfactorily resolved. In this thesis, the taxonomy is generally based on the scheme of the *Treatise of Invertebrate Paleontology* (Moore 1964) and the more recent work of Evans (2005).

2.6 Order Ellesmerocerida (Subclass Nautiloidea Agassiz, 1847)

Stratigraphically earliest (Late Cambrian) cephalopods belong to four high-level taxa (orders): Ellesmerocerida Flower *in* Flower & Kummel, 1950 (emended by Kröger & Mutvei 2005), Plectronocerida Chen & Teichert 1983, Protactinocerida, Chen *et al.* 1979 and Yanhericerida Chen *et al.* 1979. Only the **Ellesmerocerida** crossed the Cambrian/Ordovician boundary. Ellesmerocerids have small, variably shaped shells with short phragmocone chambers, marginal siphuncles with connecting rings that protrude into the siphuncle, and multiple-paired muscle scars (Kröger & Mutvei 2005; Kröger *et al.* 2011). Late Cambrian ellesmerocerids were restricted to shallow carbonate platforms of low latitude regions (Kröger & Zhang 2009; Kröger 2013a) but during the Ordovician, the group expanded also to deep-water, distal environments of high-latitudes (Kröger *et al.* 2009b).

Ellesmerocerids are considered to be ancestors of all later (Ordovician) cephalopod groups (Flower 1988; Engeser 1996; Kröger 2007). Most dominant of these were the following orders: **Actinocerida** Teichert, 1933; **Endocerida** Hyatt, 1900 (emended by Evans & King 2012 but cf. Kröger 2012); **Discosorida** Flower *in* Flower & Kummel, 1950; **Lituitida** Starobogatov, 1983; **Oncocerida** Flower *in* Flower & Kummel, 1950; **Orthocerida** Kuhn, 1940 and **Tarphycerida** Flower *in* Flower & Kummel, 1950. The above orders are briefly characterized in the following paragraphs.

2.7 Order Actinocerida (Subclass Orthoceratoidea McCoy, 1844)

Actinocerids are medium-sized to large orthocones, often ventrally flattened, with wide siphuncles, cyrtochoanitic septal necks, thin but strongly expanded connecting rings (of the calcified-perforate type), heavy cameral and endosiphuncular deposits and large initial chambers (e.g., Schindewolf 1944; Zhuravleva & Balashov 1981). The actinocerid siphuncle is unique in that it consists of a system of canals (the central canal and multiple radial canals; Teichert 1933, 1964b; Flower 1957; but cf. Mutvei 1996) that permitted rapid changes in buoyancy. Actinocerids were fast, horizontally swimming demerzal predators. They were, however, limited to shallow depths because they had thin connecting rings and thin septa (Westermann 1998). This limitation is expressed also in that they largely occur in shallow platform sediments and reefal environments (Kröger 2013a).

Actinocerids originated in the Early Ordovician and persisted until the Late Carboniferous (Teichert 1988; Kröger & Mapes 2007).

2.8 Order Endocerida (Subclass Nautiloidea Agassiz, 1847)

Endocerids are orthocones or cyrtoconic brevicones that may often reach considerable sizes (Teichert & Kummel 1960; Sweet *et al.* 1964, K108; Holland 1987). They have large, marginally positioned siphuncles with heavy endosiphuncular deposits (endocones) and very long septal necks. During life, endocerids were oriented horizontally. They were fast, forward swimming predators, as noted by, e.g., Flower (1964), Frey (1989) and Westermann (1998). Early endocerids lived demerzally in shallow, tropical epeiric seas but later forms were also nectonic and able to descent into moderately deep waters (Westermann 1998; Kröger & Zhang 2009).

Endocerids have been abundant especially during the Early and Middle Ordovician (Kröger & Zhang 2009) and became extinct in the Early Silurian (Evans & Holland 1995; Evans & King 2012; Evans *et al.* 2015).

2.9 Orders Discosorida and Oncocerida (Subclass Nautiloidea Agassiz, 1847)

Discosorids and oncocerids are two cephalopod groups that superficially resemble each other, especially with regards to the shell shape, size and also the presence of characteristic muscle-scars imprints that consist of paired “pits” across the circumference (Mutvei 1964; Kröger & Mutvei 2005). Discosorids and oncocerids also shared common life-style and occupied similar environments (see below). In the following paragraphs, the main morphological features of each of the two groups are summarized. Exceptions to the morphological characteristics occur, however, making the systematic distinction of discosorids and oncocerids difficult in some cases (see references in Kröger *et al.* 2009a).

Discosorids have small, endogastrically curved shells (Kröger *et al.* 2009a) with large siphuncles, thick, expanded connecting rings and endosiphuncular deposits. Septal necks are cyrtochoanitic. The septa are thin and closely spaced. Ordovician discosorids generally had open apertures but stratigraphically younger representatives often developed highly modified, specialized apertures upon adultery (Manda 2008a). The shell orientation during life was inclined, subvertical, with downwards facing aperture, which facilitated bottom-feeding. The discosorids were sluggish horizontal and/or vertical swimmers, although some may have been more active (Westermann 1998).

Oncocerids, by contrast, were predominantly exogastric (Kröger *et al.* 2009a). They originally had cyrtoconic shells but later forms developed a wide range of other shell shapes, from orthoconic to torticonic (Westermann 1998; Kröger 2003). Connecting rings are tubular but may also be slightly and even strongly expanded; septal necks are orthochoanitic or cyrtochoanitic. Endosiphuncular and cameral deposits are lacking in many forms but may be present in others (e.g., Teichert 1964a, K40). Septal spacing is narrow, septa are moderately thin. As in discosorids, highly modified apertures developed in many, especially Silurian and Devonian, taxa (e.g., Manda & Turek 2011). The shell orientation in oncocerids was probably vertical to subvertical. They were sluggish, demerzal bottom-feeders with limited horizontal and vertical swimming (Westermann 1998).

Discosorids and oncocerids were abundant especially in the low-latitude regions in shallow depths, often associated with reef environments. They originated in the Early Ordovician (e.g., Chen 1987; Kröger *et al.* 2009a) and diversified mainly during the Middle and Late Ordovician (Kröger & Zhang 2009). Both groups persisted and are well-represented in the Silurian and Devonian rocks (e.g., Zhuravleva 1972; Manda & Turek 2011), where some representatives reach relatively large sizes (e.g., the discosorid *Phragmoceras*, see Manda 2008a). The Discosorida became extinct by the end of the Devonian, the Oncocerida persisted until the early Carboniferous (Teichert 1988).

2.10 Order Lituitida (Subclass Orthoceratoidea McCoy, 1844)

The lituitids have an initially coiled shell, which, however, rapidly uncoils early in ontogeny and the shell subsequently becomes straight (orthoconic). The shell is ornamented with sinuous annuli and/or lirae and the late ontogenetic growth stage has a modified aperture (see Furnish & Glenister 1964b). Thick episeptal and hyposeptal cameral deposits are present. Muscle scars are dorsomyarian. The siphuncle is subdorsal to central, with relatively long orthochoanitic septal necks and tubular connecting rings of the calcified-perforate type.

The lituitids were most diverse during the Middle Ordovician but were common up to the Late Ordovician (the assignment of some Silurian and Devonian taxa to the Lituitida as proposed by Dzik 1984 and Kröger 2008 are controversial, see, e.g., Turek & Manda 2012). The lituitids are interpreted as passive, vertical migrants (Mutvei 2002a; Kröger 2013a; Kröger & Zhang 2009), typically of low-latitudes and open-water environments (Kröger *et al.* 2009b). The possession of small spherical initial chambers without a cicatrix indicates a pelagic life-style of the larvae (Shimansky & Zhuravleva 1961; Kröger & Zhang 2009; Kröger *et al.* 2009b; Mutvei 2002a; Manda & Frýda 2010).

2.11 Order Orthocerida (Subclass Orthoceratoidea McCoy, 1844)

Orthocerids are slender orthocones or cyrtocones with high phragmocone chambers and narrow central or subcentral siphuncles. Septal necks are typically orthochoanitic with thin, tubular or only slightly expanded connecting rings. Cameral deposits are usually not present but in some taxa may be well-developed. Endosiphuncular deposits are absent or strongly suppressed. The orthocerids have a small to medium-sized, spherical or sub-spherical initial chamber invariably without a cicatrix. Muscle scars are small, dorsomyarian.

The orthocerids first appeared in the Early Ordovician (Kröger & Evans 2011) and expanded during the Ordovician from their original pelagic habitats in the high-latitude regions to the low latitudes and shallow-water environments. They became the most abundant cephalopod group in the Silurian, and the Early Devonian (Kröger & Zhang 2009), when the bactritids, the stem-group for coleoids and ammonoids, diverged from them (Schindewolf 1932; Erben 1964; De Baets *et al.* 2012a, b; Korn & Klug 2003; Kröger and Mapes 2007). Orthocerids were among the few ancient Paleozoic cephalopod groups that survived the Permian/Triassic crisis and extinction. Stratigraphically latest orthocerids were reported from the Lower Cretaceous strata of Caucasus (Zhuravleva 1994). A questionable orthocerid was reported also from the Early Eocene strata of Antarctica (Doguzhaeva *et al.* 2017); it is, however, recently re-interpreted to represent a parallel lineage of the Coleoidea (Paracoleoidea) or, alternatively, a representative of the order Teuthida (Coleoidea; Fuchs *et al.* 2018).

Together with the aforementioned order Lituitida, the orthocerids were the first cephalopods that colonized and utilized the pelagic, off-shore environments (see discussion and summary in Kröger & Zhang 2009, Kröger *et al.* 2009a and Kröger 2013). Just like the lituitids, the orthocerids are interpreted as vertical migrants that passively drifted with oceanic currents and that had pelagic larvae (e.g., Mutvei 2002; Kröger & Zhang 2009; Kröger *et al.* 2009a; Kröger 2013).

The order Orthocerida originally contained two families, the Orthoceratidae and the Pseudorthoceratidae (see Sweet 1964). Cephalopods included in the latter family deviated significantly in morphology from the above described characteristics, which led some authors to challenge the monophyly of the Orthocerida (Ristedt 1968; Barskov 1963, 1968, 1972; Engeser 1996). Barskov (1963) erected a separate order Pseudorthocerida (see also Flower 1964; Zhuravleva 1994; Evans 2005; Kröger 2006 and Kröger & Mapes 2007). Main arguments for extracting the pseudorthocerids included the different morphology of the embryonic shell, the presence of cameral and endosiphuncular deposits and differences in the type of connecting rings and septal necks. Kröger & Mapes (2007) considered pseudorthocerids to be a sister group to the order Actinocerida. However, the distinction of the pseudorthocerids and orthocerids is sometimes not straightforward and many taxa exist (e.g., *Isorthoceras*), that combine characters of both groups. Thus, some studies do not distinguish between the pseudorthocerids and orthocerids (e.g., Kröger & Aubrechtová 2018 – Appendix 3) and some different concepts have been offered (Dzik 1984; Mutvei 2002a, 2016).

2.12 Order Tarphycerida (Subclass Nautiloidea Agassiz, 1847)

Tarphycerids possessed coiled, planispiral shells, often elaborately ornamented, with thin septa, narrow to moderately wide siphuncles with thin to thickened organic connecting rings (*Nautilus* type) and ventrally or ventro-laterally positioned muscle scars (Mutvei & Dunca 2011 and Kröger & Mutvei 2005); the shells lack extensive cameral and endosiphuncular deposits.

The tarphycerids were active forward swimmers, probably demerzal but some of them were also nektonic and/or planktic, at least in some growth stages (see Manda & Turek 2018 and references therein). The group mostly inhabited low-latitude, shallow-water epeiric seas (Flower 1957; Westermann 1998). Tarphycerids range from the Early Ordovician up to the Late Silurian (Manda & Turek 2018).

The presence of the coiled shell has led some researchers to include the above discussed Lituitida and another Early Paleozoic order, the Barrandeocerida Flower *in* Flower & Kummel, 1950, among the tarphycerids (see Furnish, W.M. & Glenister 1964b). In lituitids, however, the shell becomes straight in ontogeny and possesses thick cameral deposits. The connecting rings structure (calcified-perforate type), type of muscle scars (dorsomyarian) (see, e.g., Mutvei 2002a) and the morphology of the initial chamber (small, without a cicatrix) are also different (Kröger 2006). The affinities of the Barrandeocerida are still not clear but some reportedly differ from tarphycerids in the structure of the connecting rings (they are of the calcified-perforate type; see Mutvei & Dunca 2011). In addition, the barrandeocerid family Lechritrochoceratidae Flower *in* Flower & Kummel, 1950 differs from the Tarphycerida in the shell ornamentation, presence of a loosely coiled, slender juvenile growth stage and in the structure of the siphuncle. Dzik & Korn (1992) thus assumed that the lechritrochoceratids have phylogenetic relationships with the barrandeocerid family Uranoceratidae rather than with the Tarphycerida.

2.13 Order Ascocerida (Subclass Nautiloidea Agassiz, 1847)

Of interest herein is the rare but morphologically unique order Ascocerida Kuhn, 1949. Early in ontogeny, ascocerids have a cyrtoconic shell with a tubular, ventrally shifted siphuncle. The juvenile shell, however, gets periodically truncated as it grows (Barrande 1855, 1877; Furnish & Glenister 1964a) and an inflated (ephebic) shell is then developed. In the ephebic shell, phragmocone chambers are separated by thin sigmoidal septa and located above the living chamber. The truncation accompanied with changes in shell shape and internal arrangement during life led to a gradual change in the orientation of the living animal from nearly vertical/inclined to horizontal (Kröger *et al.* 2011). The structure and function of the ephebic shell is often compared to the cuttlebone of the unrelated, extant genus *Sepia* (Flower 1941; Kröger 2007; Kröger *et al.* 2011).

The ascocerid fossil record ranges from the Middle Ordovician (Flower 1941) up to the Late Silurian (Barrande 1877). Ascocerids are almost exclusively known from low- or mid-latitude regions (see references in Aubrechtová & Meidla 2016 – Appendix 2), they are extremely rare in high-latitudes (Cichowolski *et al.* 201X, in press).

2.14 Development and paleoecology of cephalopod faunas during the Ordovician

The stratigraphically oldest, undoubted cephalopod is the small cyrtocone *Plectronoceras cambria* (Walcott, 1905) from the middle Late Cambrian Fenghsan Formation of North China that developed in a shallow, tropical, epicratonic sea (see Landing & Kröger 2009; Kröger 2007; Mutvei *et al.* 2007; Kröger *et al.* 2011; Kröger 2013a and Klug *et al.* 2015 and references therein).

In the latest Cambrian, the early cephalopods diversified rapidly (Teichert 1988). Their morphological disparity increased and they expanded their habitats from the original very shallow-water and reef-related environments (Flower 1957; Chen & Teichert 1983) to the sublitoral (Chen & Qi 1982; Zou 1987). The group spread widely across South China (e.g., Li 1983; Xu & Lai 1983) and appeared even as far as Laurentia (Landing & Kröger 2009) and Gondwana (West Antarctica, Webers *et al.* 1992). The Cambrian cephalopods are not known from mid-/high latitudes and from outside the neritic environments (Kröger *et al.* 2009b; Kröger 2013a).

During the Ordovician, the cephalopods experience of what is one of the most spectacular radiations of the whole Phanerozoic. The cephalopods diversified strongly, spread from their original tropical, neritic environments to the high latitudes and inhabited the pelagic habitats and the deep ocean. They reached global occurrence in almost all marine environments and paleogeographic areas. The size of their shells and bodies increased. Newly developed shell designs allowed for a better balance between buoyancy control, resilience against ambient pressure, stability and motility. The cephalopods became the largest predators of the Ordovician oceans, although some also developed microphagous and planktotrophic life-styles (Westermann 1998; Kröger *et al.* 2009b; Manda & Frýda 2010).

The diversity of cephalopods peaked three times during the Ordovician. Each peak was preceded by a diversity crisis and followed by a faunal change. Discussing the possible drivers of these cephalopod diversifications, Kröger & Zhang (2009) observed that the diversification events do not correlate with major Ordovician physical events but better correspond to the changes in benthic assemblages and development of reef ecosystems. This indicates, that the causes for the rapid cephalopod diversification were biotic, rather than abiotic. From a more general point of view, cephalopod development during the Ordovician can be seen as a part of the Great Ordovician Biodiversification Event (GOBE; see Webby *et al.* 2004; Servais *et al.* 2008a, 2010 and Servais & Harper 2018). The GOBE is a collection of many separate diversification events in individual fossil groups that in the end led to a significant increase of diversity at all taxonomic levels and a higher ecological complexity including more complex and stable trophic chains, greater tiering, expansion of plankton, origination of planktotrophy and a greater occupation of the free water column and distant, off-shore environments. The Paleozoic Evolutionary Fauna of Sepkoski (1978, 1979, 1981, 1984) was established during the time period. The GOBE is together with the Cambrian Explosion and the Devonian Nekton Revolution seen by some researchers as a single, large-scale diversification, the so-called Early Paleozoic Radiation (Servais *et al.* 2010).

During the mid-Tremadocian, the cephalopods diversified for the first time in the Ordovician. Endocerids started to dominate in many epeiric, low-latitude carbonate platforms (as documented by the so-called "cephalopod facies"; Kröger & Landing 2008) and were accompanied there by tarphycerids and some ellesmerocerids. Earliest cephalopods appear in pelagic, deep water environments of the high-latitudes, as well (Kröger 2008; Flower 1968; Cichowolski & Vaccari 2011; Evans *et al.* 2013), among them were stratigraphically earliest representatives of the Orthocerida (Kröger & Evans 2011), orthoconic ellesmerocerids and some endocerids that expanded their habitats from the tropical platforms. Cephalopods with coiled or breviconic shells and actinocerids were extremely rare or completely missing in the high-latitude pelagic regions (Kröger *et al.* 2009b).

During the Floian, the diversification of cephalopods in the tropical platforms continued and the expansion of especially orthocerids into pelagic environments progressed. The late Floian–early Dapingian was a time interval of a significant faunal change (Kröger & Zhang 2009). The diversity was reduced, especially in the Endocerida, Ellesmerocerida and Tarphycerida. By contrast, groups with a more active buoyancy regulation (Actinocerida, Discosorida) and those that were able to utilize open-water habitats (Orthocerida, Lituitida) flourished. Discosorida and Oncocerida radiated rapidly in low-latitude shallow-water and reef environments (Stridsberg 1985; Watkins 1991; Kröger 2007). Kröger *et al.* (2009b) and Kröger & Zhang (2009) interpreted discosorids and oncocerids as "ecological successors of the Ellesmerocerida". Kröger & Zhang (2009) implied that the causes behind the changes in cephalopod faunas in the late Floian – early Dapingian time interval were linked with changes in the benthic assemblages reported for trilobites, brachiopods, gastropods and the onset of the diversification of ostracods.

During the Darriwilian, extinction rates were generally low in cephalopods and this is thus a time interval of further diversification. Kröger & Zhang (2009) interpreted this as a consequence of stable food webs established in the open sea, higher competition within the benthos and an overall high complexity and resilience of ecosystems.

In distant environments and in high-latitudes, cephalopod assemblages were already well-established and widespread in the Darriwilian (e.g., Marek 1999; Evans 2005; Evans *et al.* 2013). Orthocerids, lituitids, orthoconic endocerids and cyrtocerinids (order Cyrtocerinida, e.g., genus *Bathmoceras*) dominated the cephalopod faunas. In the shallow-water environments and in low-latitudes, orthocerids and lituitids were also abundant (Kröger 2004) but the dominant groups there were actinocerids and/or endocerids (Kröger 2013b; Kröger & Rasmussen 2014; Fang *et al.* 2018) followed by tarphycerids, discosorids and oncocerids (Kröger *et al.* 2009b).

During the Late Ordovician (late Sandbian–early Katian) the cephalopod diversity reached its absolute Ordovician peak (Kröger & Zhang 2009; Kröger 2013a). Cephalopod faunas were dominated by actinocerids, pseudorthocerids, discosorids and oncocerids. Orthocerids diversified and further invaded the low-latitude and shallow-water regions. Ellesmerocerida and Lituitida experienced their final decline, Endocerida were significantly reduced. Ascocerida spread in the low-latitude Laurentia (Flower 1963) and Baltica (Kröger 2007, 2013b).

The end-Ordovician extinction, that is ranked among the five most severe extinctions in the whole Phanerozoic (Harper *et al.* 2014), affected mainly those cephalopods that had highly-specialized shells (Teichert 1988), like endocerids, actinocerids, discosorids and ascocerids. On the other hand, the straight-shelled orthocerids started to dominate the cephalopod faunas after they recovered from the Ordovician extinction.

3. Geological settings

3.1 Prague Basin (central Bohemia, Czech Republic)

The Prague Basin is a tectonically predisposed, linear sedimentary depression possessing the deepest part and the maximum thickness of infilling along its central axis (Havlíček 1981, 1982). The present denudation relict of the Basin is located between cities Brandýs nad Labem, Praha and Plzeň (Fig. 6) and reaches a maximum width of c. 25 km. According to Havlíček (1981), the sea must have flooded areas far beyond the extent of the present relict, at least in some time periods. Marginal segments of the Prague Basin are preserved only rarely (Havlíček 1998).

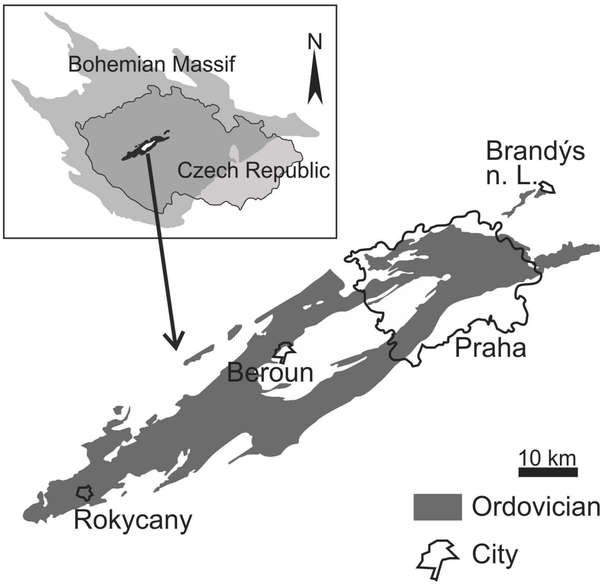

Figure 6: The position of Ordovician rocks of the Prague Basin within the Bohemian Massif. Modified after Manda (2008).

The infilling of the Prague Basin rests with an angular unconformity on either the deformed Late Proterozoic (Cadomian) or undeformed Cambrian basement (Havlíček 1998; Kachlík 2003). The succession consists of clastic and carbonate sedimentary rocks, ferrolites and volcanic rocks that developed without a significant interruption from the Early Ordovician up to the Middle Devonian. The sedimentation was terminated by the Variscan Orogeny (Chlupáč 1998).

The Prague Basin was during its existence presumably situated on the Perunica microcontinent (microplate) (Figs 7, 8). Perunica was first defined by Havlíček *et. al* (1994) on the basis of apparent differences in the composition and development of Ordovician fauna between the Prague Basin and other regions. Fatka & Mergl (2009) revised the original concept of the Perunica microcontinent, which they supported not only by paleontological but also paleomagnetic and sedimentological data (note, however, that Servais & Sintubin [2009] considered Perunica as a paleobiogeographical province only). During the Early Paleozoic, Perunica gradually drifted away from Gondwana towards Baltica, i.e., moved from high to low southern paleolatitudes (Havlíček 1998; Cocks & Torsvik 2006). The movement is well-documented in the rock succession of the Prague Basin by the transition from clastic (Ordovician) to carbonate (Silurian and Devonian) sedimentation. Correspondingly, a change in the composition of fossil faunas, including the appearance of reef-building organisms, is apparent. The Silurian and Devonian carbonate successions of the Prague Basin, that developed in the subtropical and tropical realms, are exceptionally well-preserved and globally stratigraphically important (see summary and references in Kříž 1998 and Chlupáč 1998).

Besides the Prague Basin, numerous other European and African basins originated along the active margin of Gondwana during the Early Paleozoic. These basins are collectively referred to as the peri-Gondwana (Cocks 2000; Cocks & Torsvik 2002, 2006; Torsvik & Cocks 2013, 2017) and included under what is called the Mediterranean Province (Havlíček *et al.* 1994). During the Ordovician, faunal provincialism was high and relatively abrupt changes in the distribution of continents occurred, e.g., in relation to the spreading of the Rheic Ocean (Servais *et al.* 2010). This hindered international correlation of the Ordovician strata and numerous regional scales were created (e.g., Havlíček & Marek 1973) and used until the global Ordovician chronostratigraphic scale was implemented in the 90's (see discussions and references in Havlíček & Marek 1973; Webby *et al.* 2004; Gutiérrez-Marco *et al.* 1995, 2017; Servais *et al.* 2010).

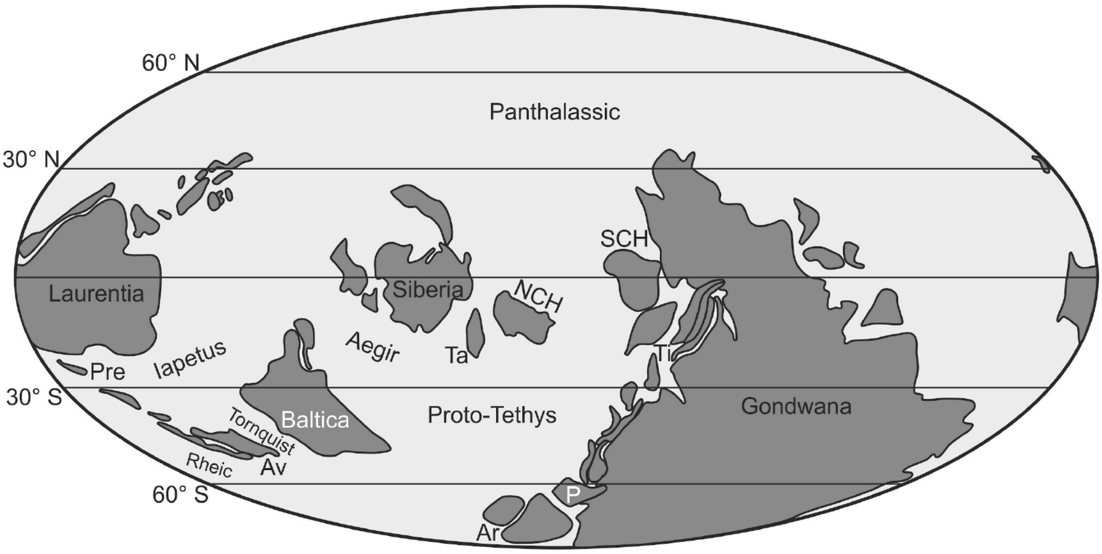

Figure 7: Paleogeographical map for the Middle Ordovician highlighting the inferred position of the Perunica microcontinent (microplate) and the Baltica paleocontinent. Modified after Torsvik & Cocks (2017). Abbreviations: Ar=Armorica; Av=Avalonia; NCH=North China; P=Perunica; SCH=South China; Pre=Argentine Precordillera; Ta=Tarim; Ti=Tibet.

3.2 Ordovician of the Prague Basin

The Ordovician strata of the Prague Basin constitute from an unmetamorphosed, richly fossiliferous, continuous succession of diverse clastic sediments accompanied with iron ores and volcanic rocks. The rich fossil fauna has been studied already in the 19th century (Barrande 1865–1877) and used since then for stratigraphical, paleogeographical and paleoecological interpretations (see, e.g., Havlíček 1981, 1982, 1989; Dzik 1983; Paris & Mergl 1984; Frýda 1988; Servais & Fatka 1997; Mergl 2004; Polechová 2013; Lajblová & Kraft 2014).

The sedimentation in the Prague Basin initiated under an extensional regime linked to the origin of the Rheic Ocean that separated Avalonia from Gondwana (Cocks & Torsvik 2006). This tectonic unrest later led to extensive volcanic activity, segmentation and subsequent facial differentiation of the Basin.

Stratigraphically earliest sediments of the Prague Basin developed during the Tremadocian (Třenice and Mílina formations) in what was a very shallow, narrow sea bay. The central, rapidly subsiding depression did not exist until the Floian and Dapingian stages (Lower to Middle Ordovician; Klabava Formation), when the initial deepening, sea-level rise and segmentation occurred in the Prague Basin (Havlíček 1998).

During the early and middle Darriwilian (Šárka Formation), the transgression and deepening of the Basin further progressed and was accompanied by extensive volcanism. The diverse facies of the preceding time interval were mostly replaced by clayey shales, locally associated with iron ores and volcanic rocks (Havlíček 1998; Servais *et al.* 2008b). The shales contain originally carbonatic, secondarily silicified (Kukal 1962) nodules with excellently preserved and abundant fossil invertebrate fauna that often shows paleogeographic affinities to mid- or low-latitude regions, namely Baltica. During the upper Darriwilian and lower Sandbian stages (Dobrotivá Formation), the pattern of sedimentation remained relatively unchanged (Havlíček *et al.* 1994) but the fauna shows much weaker relationships to Baltica and other distant regions.

During a time interval from the early Sandbian to the mid-Katian (Beroun Regional Stage; Libeň, Letná, Vinice, Zahořany and Bohdalec formations), the Prague Basin further deepened (Havlíček 1998). A thick succession of dark shales, claystones and siltstones, pyroclastics, sandstones and iron ores developed (Havlíček & Marek 1973; Havlíček 1998). Shallow-water facies are less common to missing due to later denudation of marginal parts of the Basin. Some parts of the succession contain rich and well-preserved fossil invertebrate fauna (see Havlíček & Vaněk 1966 and a summary in Havlíček 1998; later works include, e.g., Kácha & Šarič 2009; Rak *et al.* 2009; Fatka *et al.* 2013; Ernst *et al.* 2014) and ichnofossils are common (e.g., Chlupáč & Kukal 1988; Mikuláš 1990).

The Králův Dvůr Formation (upper Katian Stage) is characterized by strongly bioturbated clayey to silty shales with limonitic, originally carbonatic nodules (Štorch & Mergl 1989). Unique is the upper part of the Formation, where calcitic shales, carbonatic claystones and clayey limestones are developed (Marek 1952; Štorch & Mergl 1989) and contain fragmentary but very abundant fossil fauna (Havlíček & Vaněk 1966; Mergl 2011a). Interestingly, the deposition of the Králův Formation is roughly coeval with the globally recognized Boda Event (Fortey & Cocks 2005; Cherns & Wheeley 2007; see also Kröger *et al.* 2016a, b).

Stratigraphically youngest lithostratigraphic unit of the Ordovician of the Prague Basin is the Kosov Formation (Hirnantian Stage), which records the end-Ordovician global cooling, glaciation and associated eustatic sea level fall and extinction (Melchin *et al.* 2013). The clastic sediments of the Kosov Formation contain glacimarinne diamictites (Havlíček 1982; Štorch & Mergl 1989; Brenchley & Štorch 1989) and dropstones (Hladil 1991). Bioturbation is common and the character of fossil fauna contrasts strongly to that of the preceding formations (Havlíček & Vaněk 1966; Mergl 2011b).

3.3 The Baltica paleocontinent

Baltica was together with Gondwana, Laurentia, North China, Siberia and South China one of the prominent continents of the Early Paleozoic (Torsvik 1998; Cocks & Torsvik 2002, 2005; Bergström *et al.* 2013) (Figs 7, 8). It included what is today Scandinavia, the Baltics, Poland, eastern Europe and large areas of Russia (as far as the Tajmyr Peninsula, Novaya Zemlya, Ural mountains, the Caspian Sea and the Black Sea) (Cocks & Fortey 1998; Cocks & Torsvik 2005). The independent history of Baltica started in the Late Proterozoic, when the Iapetus Ocean separated it from Laurentia (Hartz & Torsvik 2002). However, the core of Baltica is formed by much older, Archean and Proterozoic, metamorphosed rocks of the East European Craton (Cocks & Torsvik 2005).

During the Early Paleozoic, Baltica gradually drifted from high to low latitudes (Jaanusson 1973; Fedorov 2003; Cocks & Torsvik 2002, 2005; Bergström *et al.* 2013), which is reflected by the changing patterns of facies and composition of fossil associations (Cocks & Torsvik 2005). At about the Ordovician/Silurian boundary, Baltica collided with Avalonia, and later, in the Silurian, with Laurentia in the course of the Caledonian Orogeny (Cocks & Torsvik 2002, 2011; Roberts 2003; Torsvik & Cocks 2005; Bergström *et al.* 2013). This origin of the continent Laurussia marks the end of Baltica's independent development. During the Variscan Orogeny in the Devonian and Late Paleozoic, Laurussia further merged with Gondwana and became part of the supercontinent Pangea (Ziegler 1989, 1990; Cocks & Torsvik 2011).

On Baltica, the Early Paleozoic (especially Ordovician and Silurian) strata are widely distributed, well-preserved, generally undeformed and often contain rich fossil faunas that have been studied for a long time (e.g., Angelin & Lindström 1880; Isberg 1934). Some regions on the former Baltica, like south and central Sweden, the Island of Gotland, the Island of Öland and northwest Estonia are among the most intensively studied in the world (Webby 1984; Nestor 1995). In the course of the herein presented research, fossil cephalopods from localities in Estonia and Sweden were revised and thus, main aspects of the geology and stratigraphy of both regions are briefly overviewed below.

3.4 The geological development of Estonia

The modern-day Estonia is situated on the southern slope of the Fennoscandian (Baltic) Shield of the East European Craton. The penepled surface of the metamorphosed Precambrian crystalline basement is covered with late Ediacaran–Devonian sedimentary succession (Puura *et al.* 1997; Meidla *et al.* 2014). The thickness of the succession gradually increases to the south, as the upper surface

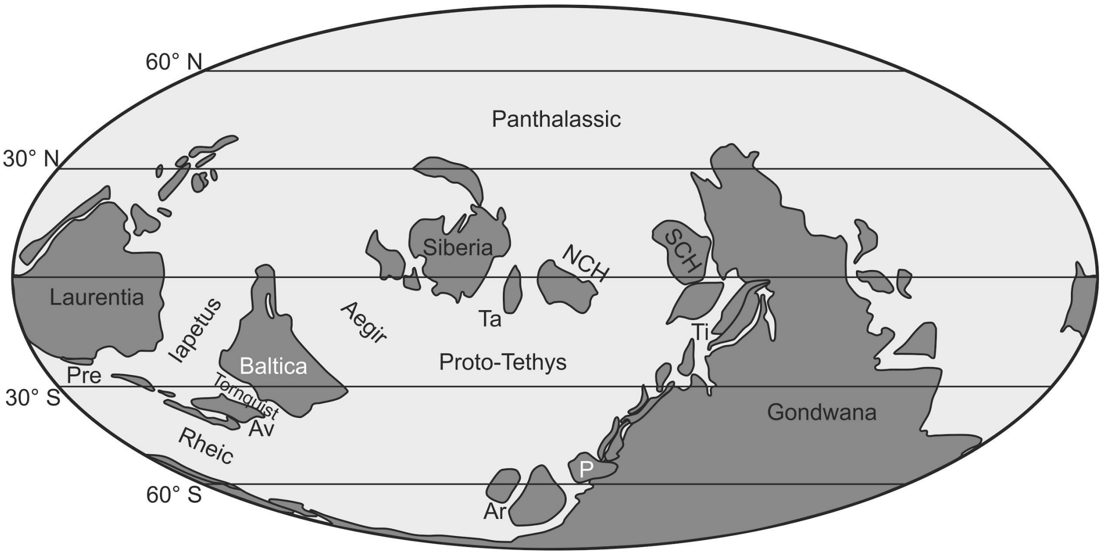

Figure 8: Paleogeographical map for the Late Ordovician highlighting the inferred position of the Perunica microcontinent (microplate) and the Baltica paleocontinent. Modified after Torsvik & Cocks (2017). Abbreviations: Ar=Armorica; Av=Avalonia; NCH=North China; P=Perunica; SCH=South China; Pre=Argentine Precordillera; Ta=Tarim; Ti=Tibet.

of the basement is dipping southwards (Meidla *et al.* 2014).

The late Ediacaran and Cambrian strata (Mens & Pirrus 1997) of Estonia consist from various clastic sediments that originated under relatively cool-water conditions as Baltica was at that time situated in high-latitudes (Cocks & Torsvik 2005). The transition from the terrigenous to carbonate sedimentation is observed within the strata of the Early Ordovician (Floian) age and the first limestone/dolomite unit originated during the early Middle Ordovician (Dapingian) age (Nestor & Einasto 1997; Meidla 1997; Meidla *et al.* 2014). The post-Floian strata are formed by initially cool-water but subsequently warm-water carbonates with rich and diversified fossil fauna (Meidla 1997; Meidla *et al.* 2014). During the Late Ordovician, framework reefs and carbonate mud-mounds for the first time widely expanded across Baltica (Kröger *et al.* 2016b); and appeared in Estonia, as well (Nestor 1995; Hints & Meidla 1997; Nestor & Einasto 1997; Kröger *et al.* 2016b).

The Ordovician strata of Estonia have been studied already during the 19th century (Engelhardt 1820; Strangways 1821; Eichwald 1825; Schmidt 1858) because of the excellent preservation of sedimentary structures and the high fossil content. The limestones, that form the main part of the Ordovician succession in Estonia, have been quarried and widely used as building and decorative stone. Of a great economic and industrial importance has also been the kukersite oil shale (mainly those of the Kukruse Regional Stage, i.e., lower Sandbian Stage), which is the largest exploitable resource of its kind in the world (Bauert & Kattai 1997; Meidla *et al.* 2014).

The Ordovician successions in the outcrop area on the north of Estonia differ lithologically, as well as paleontologically from the stratigraphically corresponding subsurface rocks in the central and southern part of the country (Meidla *et al.*

2014). This has caused complications with correlation and different concepts trying to resolve this problem were offered. Among them are structural-facies zones of Männil (1966) and confacies belts of Jaanusson (1976, 1982; see also Pärnaste *et al.* 2013 and Bergström *et al.* 2013). Newer terminology has been proposed by Harris *et al.* (2004). Recently, the stable carbon isotopic zonation (e.g., Ainsaar *et al.* 2004, 2010; Kaljo *et al.* 2007) proved helpful in respect to the correlation of the Estonian Ordovician.

As mentioned above, the shift in the character of facies reflects the drift of Baltica from high to low and finally equatorial latitudes that gradually progressed during the Early Paleozoic. In the Silurian, the sedimentation of limestones and dolomites continued (Nestor 1997), while in the Devonian, the deposition of sandstones prevailed (Kleesment & Mark-Kurik 1997; Kajak 1997). After the Devonian, the region went through a very long period of erosion that ended as late as after the Quaternary glaciation. The only post-Paleozoic rocks, that are preserved in Estonia, are glacial sediments and various other deposits of the Pleistocene and Holocene age (Raukas & Kajak 1997).

3.5 The geology of the Siljan District, Dalarna, central Sweden

The present-day Sweden is situated on the Fennoscandian or Baltic Shield of the East European Craton. The bedrock is mainly Proterozoic in age but in the northernmost part of the country, Archaean rocks are preserved, as well (e.g., Öhlander *et al.* 1993). The crystalline basement is overlaid by 1) stratigraphically younger sedimentary cover (Gee & Sturt 1985; Lindström *et al.* 2008) and 2) the Scandinavian Caledonides (Gee 1975; Gee & Sturt 1985; Roberts 2003; Gee 2008).

A unique region for the Paleozoic of Sweden is the Siljan District of the Dalarna Province. There, one of the largest impact structures in Europe (Reimold *et al.* 2005; Ebbestad & Högström 2007; Högström *et al.* 2010; Juhlin *et al.* 2012) is preserved (Fig. 9). It reaches a total estimated diameter between 52–75 km (Grieve 1988; von Dalwigk & Kenkmann 2000; Henkel & Aaro 2005), while the diameter of the original crater was estimated to have been up to 85 km (Henkel & Aaro 2005). The impact event occurred in the early Middle Devonian (Frasnian), at about 377 Ma (Reimold *et al.* 2005). The impact origin of the Siljan structure was first proposed by Wickman *et al.* (1963) and Fredriksson & Wickman (1963) and fully recognized in the late 80's (Collini 1988).

The Siljan structure consists of a c. 30 km wide central uplift, which is built mainly by Proterozoic magmatic and Late Proterozoic metamorphosed rocks, and a surrounding irregular ring graben with Paleozoic sediments reaching a maximum width of c. 14 km. No Paleozoic rocks are preserved beyond the ring graben due to later erosion (Ebbestad & Högström 2007).

The Paleozoic rocks of the Siljan structure are tectonically disturbed, often steeply inclined or overturned (Ebbestad & Högström 2007; Högström *et al.* 2010; Juhlin *et al.* 2012) but still well-preserved and stratigraphically important. Some outcrops are type localities, define international biozones or contain marker beds and many of the fossils known from the region are type specimens of various invertebrate taxa (Ebbestad & Högström 2007; Ebbestad *et al.* 2015). The Siljan region has been studied already in the 18th and 19th centuries (Linnaeus

1734, referenced in Hedberg 1988; Törnquist 1871) and the research has been intensive since then (see Ebbestad & Högström 2007 for summary of references).

The oldest Paleozoic strata that crop out in the Siljan ring are of Ordovician age, but Late Cambrian sediments were found in erratic boulders, as well (Puura & Holmer 1993; Ebbestad & Högström 2007). The Ordovician succession starts with the *Obolus* sandstone, but most of the Period is represented by cool-water to warm-water limestones. The Late Ordovician Kullsberg and Boda Limestone formations contain carbonate build-ups (Kröger *et al.* 2016 a, b).

The Silurian of the Siljan district consists of bituminous mudstones with graptolites that are overlain by the fine-grained Orsa Sandstone and younger Devonian sandstones. No Paleozoic sedimentary successions younger than that are preserved in the Siljan structure and in Sweden (Lindström *et al.* 2008).

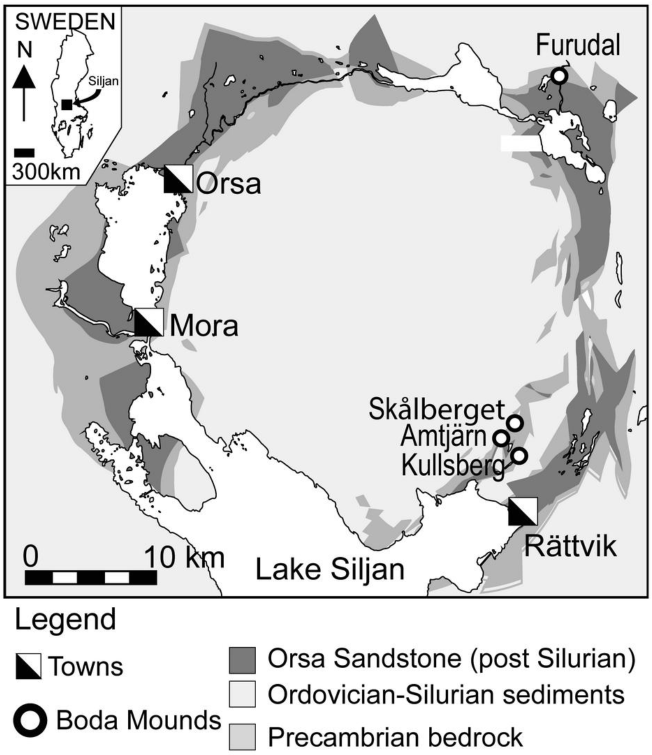

Figure 9: Map of the Siljan impact structure (central Sweden) showing the ring-shaped graben containing Paleozoic rocks. Circles represent selected individual mud mounds of the Kullsberg Limestone Formation (Upper Ordovician; Kröger & Aubrechtová 201X – Appendix 4).

4. Results and discussion

4.1 Middle Ordovician cephalopods of the Prague Basin and their paleogeographic implications

In the Prague Basin, well-preserved, abundant and diverse fossil cephalopod assemblages occur mainly in the low-latitude limestones of Late Silurian and Early Devonian age (see Manda & Frýda 2010 and references therein). By contrast, cephalopods from the stratigraphically older, high to mid-latitude clastic rocks of the Ordovician age, are comparatively less diverse and often cannot be taxonomically determined due to their unfavourable preservation. For these reasons, the group and its paleogeographical and paleoenvironmental significance has not received sufficient attention in the Prague Basin since the detailed works of J. Barrande (1865–1877). The only later publications include a summary by Marek (1999), comprehensive revisions of genera *Bathmoceras* (Marek & Mutvei, *not published*), *Trocholites* (Manda 2008b), *Bactroceras* (Aubrechtová 2015 – Appendix 1) and a recent description of the lituitids (Aubrechtová & Turek 201X – Appendix 5).

The majority of fossil cephalopods from the Ordovician of the Prague Basin are slender longiconic orthocones with relatively narrow, tubular siphuncles and occasional cameral deposits. These forms are representatives of the orders Orthocerida and Pseudorthocerida (Marek 1999) but their exact taxonomic assignment is mostly difficult and out of the scope of the present thesis. However, some of the orthocerid and pseudorthocerid taxa have been briefly discussed, synonymised or re-assigned by, e.g., Dzik (1981), Kröger (2004, 2012), Kröger & Isakar (2006), Evans (2005), Evans *et al.* (2013) and Aubrechtová (2015 – Appendix 1).

Besides the Orthocerida and Pseudorthocerida, other cephalopod orders are represented in the Ordovician of the Prague Basin, as well. It is notable, that these orders are restricted only to rather narrow intervals in the upper Dapingian (Klabava Formation), the Darriwilian (Šárka and Dobrotivá formations) and upper Katian (Králův Dvůr Formation) stages (Fig. 10). During these time intervals, faunal interchanges between the Prague Basin and other regions have been postulated (see summary in Fatka & Mergl 2009).

From the upper part of the Klabava Formation, stratigraphically earliest cephalopods in the Prague Basin were recorded (Kraft & Kraft 1994; Havlíček 1998; Marek 1999). Besides *Bactroceras* and other orthocerids, the cyrtocerinid *Bathmoceras complexum* and lituitid *Rhynchorthoceras* cf. *angelini* are known (Marek 1999; Aubrechtová & Turek 201X – Appendix 5). In the Šárka Formation, *Bathmoceras complexum* (Barrande, 1868; see also Mutvei 2015) is common along with three endocerid species. Also abundant is the peculiar species "*Orthoceras*" *bonum*. Barrande, 1868, which was assigned to the order Actinocerida but this classification is doubtful (Marek 1999; Manda 2008b; Evans *et al.* 2013). Non-orthocerid cephalopods of the Dobrotivá Formation include a single, undetermined endocerid (Turek & Aubrechtová, personal observation), two lituitid genera *Trilacinoceras* and *Lituites* (Aubrechtová & Turek 201X – Appendix 5) and a tarphycerid *Trocholites fugax* Babin & Gutiérrez-Marco, 1992 (=?*Lituites* *primulus* Barrande, 1865), which was studied and discussed by Manda (2008b). In the Upper Ordovician Králův Dvůr Formation, a single actinocerid and an endocerid have been identified (Turek & Aubrechtová, personal observation). In addition, *Diestoceras primum* (Barrande, 1865) is so far the first and only representative of the Oncocerida in the Ordovician of the Prague Basin (cf. Strand 1934; Flower 1946 and Marek 1999).

In the course of the present PhD. research, the orthocerid *Bactroceras* Holm, 1898 and lituitids *Rhynchorthoceras* Remelé, 1882, *Trilacinoceras* Sweet, 1958 and *Lituites* Bertrand, 1763 have been studied (Aubrechtová 2015 – Appendix 1; Aubrechtová & Turek 201X – Appendix 5).

4.2 Early orthocerid *Bactroceras* from the Middle Ordovician of the Prague Basin

Bactroceras Holm, 1898 is evolutionary important as the earliest known orthocerid cephalopod (Kröger & Evans 2011). As all orthocerids, *Bactroceras* has a slender, straight shell and a narrow, tubular siphuncle with orthochoanitic septal necks. The siphuncle is, however, not central (nor subcentral) in position but located in contact or in the proximity to the ventral shell wall. For this reason, previous researchers regarded the species *Bactroceras sandbergeri* (=*Eobactrites* Schindewolf, 1932*)* as the earliest bactritid (Schindewolf 1932, 1933; Erben 1964; Holland 2003; Shevyrev 2006a, b). The collection of *Bactroceras* from the Prague Basin is unique in that it is the largest collection of the genus globally counting up to over one-hundred specimens. Therefore, the Bohemian material significantly extends the knowledge on the morphology and ontogeny of *Bactroceras.* Small, dorsally positioned muscle scars were described for the first time in the genus and one of the specimens even preserves the embryonic shell with the medium-sized, hemispherical initial chamber. Mentioned type of muscle scars (Mutvei 1957, 2002a, b) and initial chamber (Balashov 1957; Ristedt 1968; Kolebaba 1973; Engeser 1996; Kröger 2006; Kröger & Isakar 2006) are additional diagnostic features of order Orthocerida and prove that the similarity of *Bactroceras* and the bactritids is only a convergence (e.g., Sweet 1958; Dzik 1981, 1984; Evans 2005).

Stratigraphically oldest representatives of *Bactroceras* are of the Early Ordovician age; they were reported from the late Tremadocian of France (Kröger & Evans 2011), Iran (Evans *et al.* 2013) and Turkey (Dean & Monod 1970) and from the late Floian of Bolivia (Marek *et al.* 2000; Aubrechtová 2015 – Appendix 1). During the Middle Ordovician, *Bactroceras* is known from the Prague Basin but also from Avalonia (Evans 2005), Baltica (Rüdiger 1889; Holm 1898; Sweet 1958), South China (Xu & Lai 1987; Zou 1987) and even Laurentia (Flower 1968; Evans & King 1990; Evans 2005). In the Late Ordovician, *Bactroceras* occurred in the Prague Basin (Barrande 1870; Aubrechtová 2015 – Appendix 1) and the low latitude/equatorial South China (Lai 1987), Australia (Glenister 1952; Stait *et al.* 1985; Hewitt & Stait 1985) and Indonesia (Crick & Van Ufford 1995). The foregoing paleogeographical distribution of *Bactroceras* implies, that orthocerid cephalopods originated in the high-latitude regions in the Early Ordovician and spread to the mid and even low latitudes later during the Ordovician (Kröger *et al.* 2009b; Kröger & Evans 2011; Kröger 2013a). Second, the occurrence of *Bactroceras sandbergeri* (and other cephalopods, such as *Bathmoceras* and endocerids) in the Šárka Formation of the Prague Basin and in roughly coeval strata of Wales and Baltica shows, that faunal interchanges were possible between these regions at least during the Middle Ordovician (Marek 1999; Fatka & Mergl 2009).

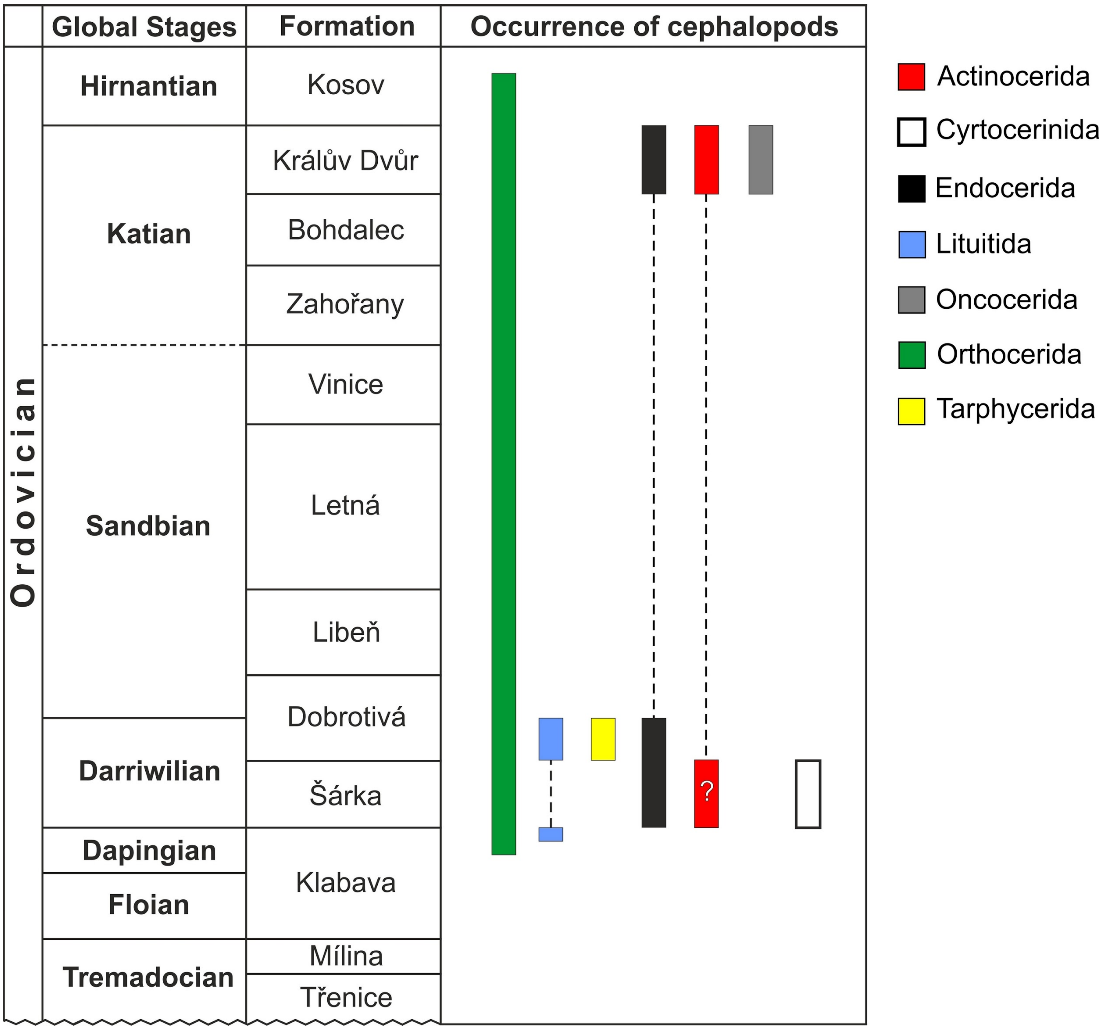

Figure 10: Stratigraphic occurrence of cephalopod orders in the Ordovician of the Prague Basin (generalized with the exception of the Lituitida; see Aubrechtová & Turek 201X – Appendix 5). Modified after Marek (1999) and Lajblová & Kraft (2014).

4.3 Lituitid cephalopods from the Middle Ordovician of the Prague Basin

Occurrences of cephalopods of the order Lituitida in the Prague Basin are also paleobiogeographically significant. During the Ordovician, the lituitids were relatively abundant and widespread in the low-latitude regions, namely Baltica (see Balashov 1953; Sweet 1958 and references therein) and China (North and South China, Tarim, Tibet; e.g., Lai 1986, 1989; Yun 1999, 2002, 2003; Xiao *et al.* 2006; Fang *et al.* 2017a, b) but have been described also from Laurentia (Flower 1975), Siberia (Kröger 2013a), Avalonia (Evans 2005) and the Argentine Precordillera (Kröger *et al.* 2007). By contrast, the lituitids are known only from a handful of specimens from regions, that were in the Ordovician situated in high-latitudes (such as the Prague Basin). Stratigraphically earliest lituitid currently known from the high paleolatitudes is a single fragment assigned by Marek (1999) to the species *Rhynchorthoceras* cf. *angelini* (Boll, 1857). The fragment originates from the upper part of the Klabava Formation (upper Dapingian Stage). The species appearance in the Prague Basin coincides with a time period, when the exchange of nektonic fauna intensified between the Prague Basin and Baltica (e.g., Dzik 1983; Manda 2008b; Kröger 2013a; Aubrechtová 2015 – Appendix 1).

Five specimens assigned to *Lituites lituus* de Montfort, 1808 and one specimen assigned to ?*Trilacinoceras discors* (Holm, 1891) from the Prague Basin (Dobrotivá Formation, late Darriwilian) have been described for the first time in the course of the present thesis (Aubrechtová & Turek 201X – Appendix 5). The only other lituitid known from the high paleolatitudes is a single specimen of *Trilacinoceras*? from roughly coeval strata of the Iberian Peninsula (Guttiérrez-Marco *et al.* 1984; Babin & Guttiérrez-Marco 1992; Sá & Guttiérrez-Marco 2009). The timing of the lituitid appearance in the Prague Basin and Iberia corresponds to a dispersion event of another typically low-latitude cephalopod – the tarphycerid *Trocholites fugax* (Babin & Gutiérrez-Marco, 1992; see also Manda 2008b). Interestingly, lituitids and tarphycerids are entirely missing from the Šárka Formation, a formation preceding the Dobrotivá Formation. In the Šárka Formation (early–mid Darriwilian), fossil cephalopod fauna is comparatively richer and more abundant and several taxa of Baltican affinity are known from there (Manda 2008b; Aubrechtová 2015 – Appendix 1).

4.4 Late Ordovician cephalopods from the reef environments of Baltoscandia

Reefs have existed on Earth ever since the Paleoarchean (Allwood *et al.* 2007). For a long time, the reefs were only microbial (stromatolites, thrombolites). Later, in the Cambrian and early–mid Ordovician, skeletal reef-building organisms appeared, as well, but mostly acted only as subordinate elements (Webby 2002; Riding 2006). Exceptions include large Cambrian archaeocyath reefs (Rowland & Shapiro 2002).

In the latest Middle Ordovician, however, a transition from microbial-dominated to metazoan-dominated (skeletal-dominated) reefs occurred (Webby 2002). Bryozoans and stromatoporoids became the main reef-builders and sponges, echinoderms, corals and algae were common and important components. During the Late Ordovician, the metazoan reefs spread globally and expanded also to the more distant, relatively deeper-water depositional settings (mud-mounds). This fundamental change in the organismal composition and structure of reefs and the subsequent rapid diversification of reef-dwelling faunas is among the key phases of the Great Ordovician Biodiversification Event (the GOBE; Webby 2002; Adachi *et al.* 2011; Kröger *et al.* 2016b).

In Baltoscandia, earliest extensive metazoan-dominated reefs developed during the late Sandbian–early Katian time interval. Framework reefs grew in the proximal, shallow-water depositional settings, while mud-mounds originated in the deeper settings (Tuuling & Flodén 2000; Kröger *et al.* 2016b). This initial phase of bioherm development was followed by another generation of reefs during the mid-Katian and later, between the late Katian and early Hirnantian. A comprehensive description of the development, structure and stratigraphy of reefs and mud-mounds of Baltoscandia has recently been made in the work of Kröger *et al.* (2016a). According to the authors, the main cause of the appearance and expansion of the reefs and mounds on Baltica during the Late Ordovician was probably the drift of the paleocontinent towards low and equatorial paleolatitudes.

Both the framework reefs and mud-mounds were formed natural diversity hotspots. A remarkably rich and diversified, often endemic faunas inhabited them (for summary see Ebbestad & Högström 2007; Kröger & Ebbestad 2014). Cephalopods were important motile constituents of these associations and their fossil remains have potential implications to stratigraphy, paleoecology and paleogeography of the reef settings. Despite existing museum collections held hundreds of fossil cephalopod specimens, the group was not in the past comprehensively investigated or interpreted. Most recently, a series of three papers has been published that analysed fossil cephalopod assemblages of the Late Ordovician reef settings of Baltoscandia. The first of the series is the work of Kröger (2013b), who monographed the late Katian–early Hirnantian fossil cephalopods from the mud-mounds of the Boda Limestone Formation (Siljan District, central Sweden). The other two studies have been completed in the course of the present PhD. project – the fossil cephalopods from the framework reefs of the Vasalemma Formation in northwest Estonia (Kröger & Aubrechtová 2018 – Appendix 3) and the mud-mounds of the Kullsberg Limestone Formation in central Sweden (Kröger & Aubrechtová 201X – Appendix 4), have been revised. Both latter formations are of late Sandbian–early Katian age but originated in different depositional settings within the Baltic Basin, which in turn produced a differing character of the associated cephalopod faunas.

4.5 Cephalopods of the Vasalemma Formation, Estonia

The Vasalemma Formation of northwest Estonia (Fig. 11) is an up to 15 m thick succession of biodetrital grainstones with intercalated reef bodies. The sedimentation occurred on a shallow platform in the central part of North Estonian Confacies Belt (see Kröger *et al.* 2014, 2016b) during the latest Sandbian time interval (Kröger & Aubrechtová 2018 – Appendix 3; Fig. 12 herein). The limestones of the Vasalemma Formation record the rising limb of a major excursion of carbon isotopes (Kröger *et al.* 2014) that has been correlated with the North American Guttenberg Carbon Isotope Excursion (known as the GICE; Ainsaar *et al.* 2010; Bergström *et al.* 2010, 2012). Notably, the same time interval is known for abrupt faunal changes (including the growth of bioherms elsewhere in Baltoscandia), as well as volcanic events, tectonic activity and oceanic and climatic disturbances (see references in Kröger & Aubrechtová 2018 – Appendix 3).

The fossil cephalopods of the Vasalemma Formation have previously been dealt with in some greater detail only by Balashov (1953), Stumbur (1962) and Kröger & Isakar (2006). In this PhD. project, over 300 specimens from older and relatively new museum collections have been studied (Kröger & Aubrechtová 2018 – Appendix 3). The specimens were mostly collected from shell concentrations in synsedimentary cavities that are called “pockets” (see references in Kröger *et al.* 2014 and Kröger & Ebbestad 2014).

The taxonomic composition of the Vasalemma fossil cephalopod assemblage shows a prevalence of small actinocerids of the genus *Orthonybyoceras* Shimizu & Obata, 1935, followed by the annulated orthocerid *Striatocycloceras* Kröger & Isakar, 2006 and the tarphycerid *Discoceras* Barrande, 1867. It is notable, that endocerids are entirely missing from the fossil assemblage. Such a composition of fauna points to a shallow, subtidal environment under warm, sub/tropical climate (Kröger *et al.* 2009b; Kröger 2013a). This conclusion is also supported by a rather high abundance of epibionts (mainly bryozoans), that encrust the cephalopod specimens, and common occurrence of traces of bioerosion (sponge borings).

The cephalopod species of the Vasalemma Formation are mostly endemic, with 17 out of 22 identified species known so far only from the Vasalemma area. Generic and ordeal composition, however, allows for paleogeographical comparisons. It shows high degree of similarity with the late Sandbian faunas of the epicontinental Laurentia. The paleogeographical distribution pattern of the Vasalemma cephalopods is similar to that known in brachiopods (Harper *et al.* 2013; Sohrabi & Jin 2013; Candela 2015), which implies that the spreading and occurrence of both groups is controlled by the sea-water temperature and depositional depth. Some cephalopod genera from the Vasalemma Formation have been reported also from coeval strata of North China and Australia, but to Laurentia, they migrated only later, during the Katian.

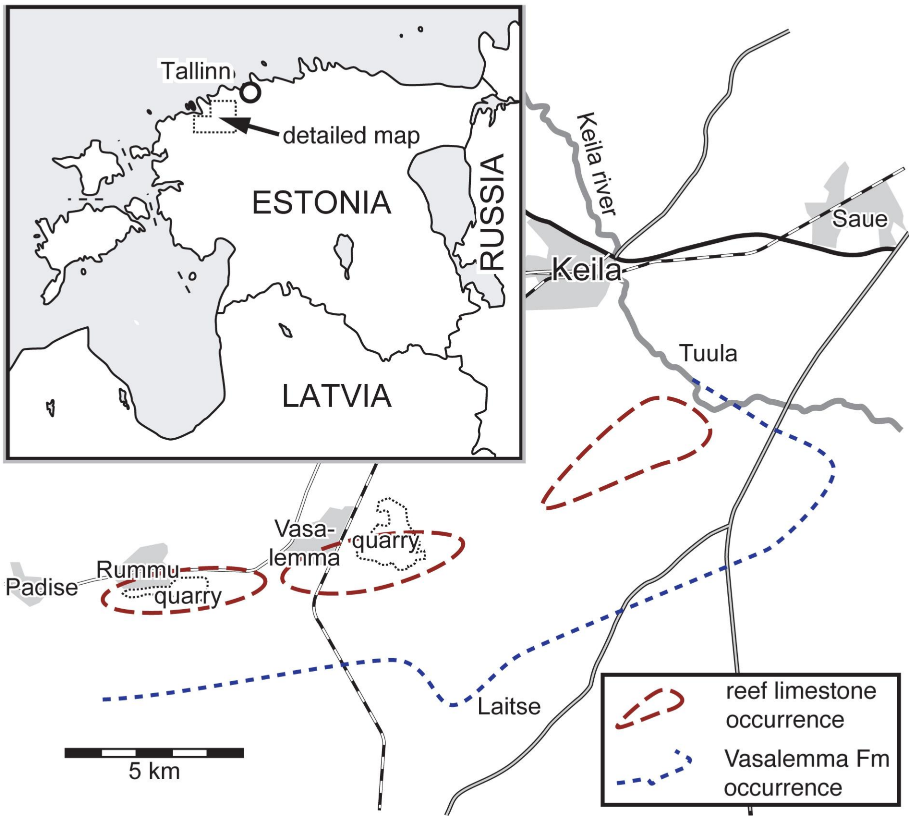

Figure 11: Map of the outcrop area of the Vasalemma Formation in northeastern Estonia with the location of reef limestones. After Kröger & Aubrechtová (2018 – Appendix 3).

4.6 Cephalopods of the Kullsberg Limestone Formation, Sweden

The Kullsberg Limestone Formation in the Siljan District, central Sweden (Fig. 9) consists of carbonate mud-mounds formed by massive, micritic stromatactis limestones with coarse-grained echinoderm limestones along their flanks (see Ebbestad & Högström 2007; Kröger *et al.* 2016a, b for summary and references). The mounds have diameters between 300–350 m and thickness between 40–50 m (Kröger & Aubrechtová 201X – Appendix 4). As discussed above, the Kullsberg mounds are stratigraphically nearly coeval with the reefs of the Vasalemma Formation (Fig. 12), i.e., are of late Sandbian age (but the deposition of the former possibly persisted slightly longer, until the earliest Katian; Kröger & Aubrechtová 201X – Appendix 4). Kröger *et al.* (2016b) argued that the Kullsberg Limestone and Vasalemma formations are additionally nearly coeval with the Mjøsa and Steinvika formations of Norway. The second, stratigraphically younger generation of carbonate mud-mounds in the Siljan region is represented by the Boda Limestone Formation (late Katian–early Hirnantian; Fig. 12). Both mud-mound generations in Siljan represent relatively deeper depositional settings compared to that of the Vasalemma Formation – the deposition depth of the Kullsberg Limestone was estimated up to 50 m (Tobin *et al.* 2005) and of the Boda Limestone between 50–100 m (Kröger & Ebbestad 2014).

The fossil cephalopods from the Kullsberg Limestone Formation have not been studied previously in any detailed manner. Only recently, Kröger & Aubrechtová (201X – Appendix 4) described c. 180 specimens of cephalopods from existing museum collections. As it was the case of the Vasalemma cephalopods, most of the Kullsberg specimens were collected from infillings of synsedimentary cavities called the "pockets" (see references in Kröger *et al.* 2014 and Kröger & Ebbestad 2014).

The Kullsberg fossil cephalopod assemblage is strongly dominated by orthocerids *Ordogeisonoceras* and *Striatocycloceras*, discosorids are the second most abundant group. By contrast to the Vasalemma Formation, the Kullsberg fossil assemblage also contains endocerids, while actinocerids are missing. Epibionts and shell borings have not been observed in any of the specimens, except for a single specimen assigned to the tarphycerid *Discoceras*, which is overgrown by small bryozoan colonies. The taxonomic composition of the Kullsberg fossil cephalopod assemblage and the absence of epibionts/boring organisms supports the interpretation of the Formation as having been developed in a relatively deep-water and distant settings (Tobin *et al.* 2005).

Paleogeographically, the Kullsberg fossil assemblage corresponds to other low-latitude fossil cephalopod assemblages known from North America and South China and supports paleogeographical comparisons based on brachiopod faunas (see references in Kröger & Aubrechtová 2018 – Appendix 3).

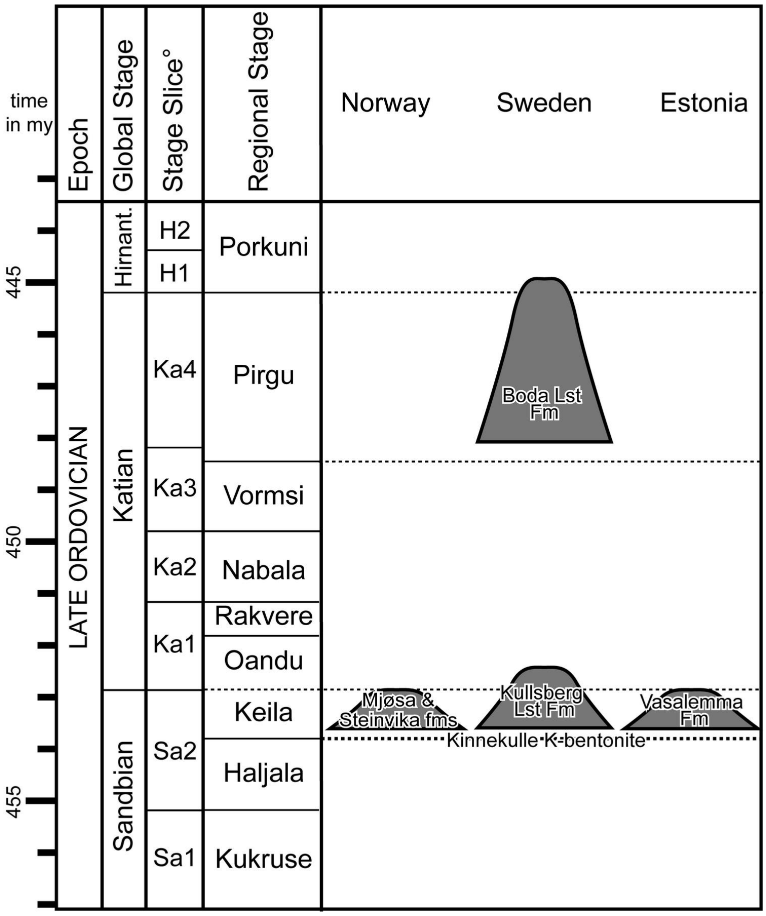

Figure 12: Stratigraphical position of the Late Ordovician reef limestones of Baltica, from which some of the fossil cephalopods studied herein were gathered and compared. After Kröger & Aubrechtová (201X – Appendix 4).

4.7 Late Silurian ascocerid from Estonia and its paleobiogeographical significance

The order Ascocerida consists of rare and morphologically peculiar cephalopods in which shell truncation happened periodically during life (see the chapter Order Ascocerida above). The ascocerids originated during the Ordovician (Flower 1941) and were mostly restricted to mid- to low-latitude Laurentia and Baltica. During the Late Silurian, however, the ascocerids expanded also to Avalonia (Holland 1999) and the Prague Basin (Barrande 1877). The latter occurrence was probably related to the position of Perunica near the Baltica paleocontinent in the relatively low latitudes (Havlíček 1998; Cocks & Torsvik 2006). It is noteworthy, that in the Prague Basin, also other cephalopods have paleogeographical relationships with Baltica during the Late Silurian, namely the phragmoceratids (Manda 2008a).

The largest collections of Silurian ascocerids were collected from Bohemia (Barrande 1855, 1865, 1877) and the Swedish island of Gotland (Lindström 1890). Outside Gotland, the record of Silurian ascocerids in Baltica consists of only a handful of specimens from Poland (Dzik 1984) and the Island of Saaremaa, Estonia (Kaljo 1970; Klaamann 1970). In Aubrechtová & Meidla (2016 – Appendix 2), the stratigraphically earliest ascocerid from the Late Silurian of Estonia (Fig. 13) was identified and described and the locality of the single specimen, the Pähkla Quarry of the Island of Saaremaa, was revised and its current state was documented. The stratigraphic age of the locality and the specimen (Ludlow Series) corresponds to a time interval, when ascocerid cephalopods are the most diverse and have their widest paleogeographic occurrence (see references in Aubrechtová & Meidla 2016 – Appendix 2). The newly identified specimen from Estonia is an important addition to the knowledge on the paleoecology and paleogeography of the group.

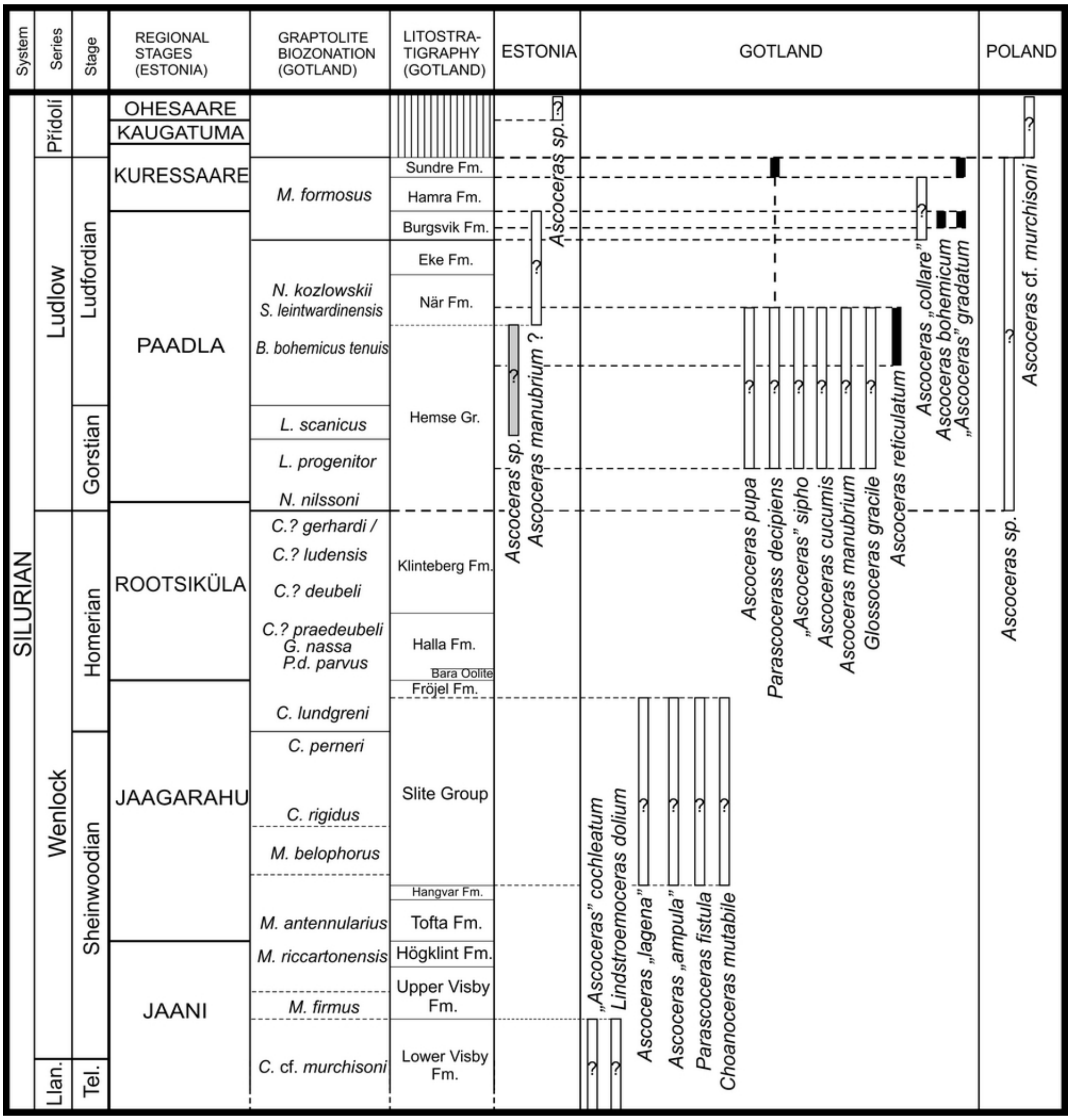

Figure 13: Stratigraphic distribution of ascocerid cephalopods in the Silurian of Baltica showing the position of the herein studied specimen from Estonia (grey bar). After Aubrechtová & Meidla (2016 – Appendix 2).

5. Conclusions

In Aubrechtová (2015 – Appendix 1) the cephalopod genus *Bactroceras* from the Middle Ordovician of the Prague Basin was revised. *Bactroceras* is evolutionary important as the earliest known member of the order Orthocerida. The genus first appeared in the Early Ordovician in the high-latitude margins of peri-Gondwana and later during the Ordovician expanded towards the lower latitudes. From the strata of the Prague Basin, *Bactroceras* has been known from the Klabava (upper Dapingian Stage), Šárka (Darriwilian Stage) and the Králův Dvůr formations (upper Katian Stage). The Bohemian collection of *Bactroceras* is the largest globally, yet any detailed description and revision was lacking for a long time. During the study in Aubrechtová (2015 – Appendix 1), muscle scar imprints were reported the first time in *Bactroceras* and also, the initial chamber was thoroughly described and photographed. The genus was systematically revised and the paleogeographic and stratigraphic distribution of the individual species of *Bactroceras* was summarized. *Bactroceras* appeared in the Prague Basin during time intervals of increased faunal exchanges with other regions, namely Baltica. The study supported results of previously published research regarding the origin of orthocerids during the Early Ordovician in the high-latitude regions and deep-water, pelagic environments and their subsequent expansion to the lower latitudes and occupation of shallow-water and more proximal habitats (Kröger *et al.* 2009b; Kröger 2013a).

Cephalopods of the order Lituitida were characteristic components of mid- and low-latitude faunas during the Middle and Late Ordovician. In the high-latitude regions of peri-Gondwana, they were, by contrast, rather rare. The earliest lituitid known from the high-latitudes is a single specimen of the genus *Rhynchorthoceras* from the Klabava Formation (upper Dapingian Stage) of the Prague Basin, and for a long time, the only lituitid ever recorded in the Ordovician strata of Bohemia. As in the orthocerid *Bactroceras* above, the lituitid *Rhynchorthoceras* occurred in the Prague Basin within faunas with Baltic affinities (Marek 1999). In Aubrechtová & Turek (201X – Appendix 5), *Rhynchorthoceras* was for the first time studied in a detailed manner. Additionally, newly identified specimens belonging to two other lituitid genera, *Lituites* and *Trilacinoceras*, were described from the Dobrotivá Formation (upper Darriwilian Stage). The lituitids of the Dobrotivá Formation are important, because they co-occur there with another typically low-latitude cephalopod, the tarphycerid *Trocholites* (Manda 2008b); they are also coeval with the only other high-latitude occurrence of lituitids, a probable *Trilacinoceras* from the Iberian Peninsula (Sá & Guttiérrez-Marco 2009). Similarly to the orthocerids, the lituitids are thought to have been adapted to the life in relatively distant, deeper-water, pelagic environments and able to migrate over long distances. However, the paleogeographic distribution of lituitids implies that the environmental conditions of the high-latitude regions may have been off their ecological limits.

In Kröger & Aubrechtová (2018 – Appendix 3) and Kröger & Aubrechtová (201X – Appendix 4), two roughly coeval (late Sandbian) fossil cephalopod assemblages were analysed from the reefs of the Vasalemma Formation of northwest Estonia and the mud-mounds of the Kullsberg Limestone Formation of the Siljan District, central Sweden. Both formations differ in the composition of their fossil cephalopod faunas. The Vasalemma fossil assemblage is dominated by actinocerids, orthocerids and tarphycerids and endocerids are missing; the shells are commonly strongly overgrown by epibionts. The Kullberg fossil assemblage is, by contrast, composed of orthocerids, discosorids and endocerids, while actinocerids do not occur and epibionts are extremely rare. The taxonomic overlap between the Vasalemma and Kullsberg cephalopods is low (only one third of the species are common to both fossil assemblages) resulting probably from different bathymetric conditions (see above). The Kullsberg fossil assemblage is in fact much more similar to the stratigraphically younger Boda Limestone Formation, in which orthocerids prevail, as well, and actinocerids are rare or missing. Both latter formations have been interpreted to represent a similar, distant and deeper-water environment, while the Vasalemma formation is interpreted as shallow-water (Ebbestad & Högström 2007; Kröger *et al.* 2016). Cephalopods studied by Kröger (2013b), Kröger & Aubrechtová (2018 – Appendix 3) and Kröger & Aubrechtová (201X – Appendix 4) support these assumptions.

The Late Ordovician fossil cephalopod assemblages from the Prague Basin were very different from those on Baltica described above. The Prague Basin was still situated in the high latitudes during the time interval. Orthocerids and pseudorthocerids dominated, while cephalopods of the low-latitude origin were rare. So far, they have been found only in the strata of the Králův Dvůr Formation (upper Katian Stage; Marek 1999) that represent a time period of an increased faunal interchange between the Prague Basin and mainly Avalonia and Baltica (Fatka & Mergl 2009). The migration of these cephalopods to the Prague Basin may be possibly related to the globally recognized Boda Event (Kröger *et al.* 2016b).

In Aubrechtová & Meidla (2016 – Appendix 2), a single specimen assigned to the enigmatic order Ascocerida was described from the Late Silurian of Estonia. In Baltica, the ascocerids have only rarely been collected from Silurian strata outside the Island of Gotland (Lindström 1890); the Estonian specimen is thus an important addition to the paleogeographic distribution of the group. The age of the specimen also corresponds to a time interval, when the abundance and diversity of ascocerids reached its maximum. Also the paleogeographic extent of the group was at its widest, as the ascocerids for the first time during the Silurian appeared outside the Laurentia–Baltica region, in Avalonia (Holland 1999) and in the Prague Basin (Barrande 1855, 1865, 1877). The expansion of ascocerids in the Prague Basin is possibly related to the position of Perunica near Baltica and in the relatively low latitudes (Cocks & Torsvik 2006).

6. List of References

ADACHI, N., EZAKI, Y. & LIU, J. 2011. Early Ordovician shift in reef construction from microbial to metazoan reefs. *Palaios 26(2)*, 106–114.

AGASSIZ, L. 1847. Lettre sur quelques points de'organisation des animaux rayonnes. *Comptes rendus 25*, 677–682.

AINSAAR, L., MEIDLA, T. & MARTMA, T. 2004. The Middle Caradoc facies and faunal turnover in the Late Ordovician Baltoscandian palaeobasin. *Palaeogeography, Palaeoclimatology, Palaeoecology 210(2–4)*, 119–133.

AINSAAR, L., KALJO, D., MARTMA, T., MEIDLA, T., MÄNNIK, P., NÕLVAK, J. & TINN, O. 2010. Middle and Upper Ordovician carbon isotope chemostratigraphy in Baltoscandia: a correlation standard and clues to environmental history. *Palaeogeography, Palaeoclimatology, Palaeoecology 294*, 189–201.

ALLWOOD, A.C., WALTER, M.R., BURCH, I.W. & KAMBER, B.S. 2007. 3.43 billion-year-old stromatolite reef from the Pilbara Craton of Western Australia: Ecosystem-scale insights to early life on Earth. *Precambrian Research 158*, 198–227.

ANGELIN, N.P. & LINDSTRÖM, G. 1880. *Fragmenta Silurica.* 64 pp. Samson and Wallin, Stockholm.

ARNOLD, J.M., LANDMAN, N.H. & MUTVEI, H. 2010. Development of the Embryonic Shell of *Nautilus*, 373–400. *In* SAUNDERS, W.B. & LANDMAN, N.H. (eds) *Nautilus, Topics in Geobiology 6.* Springer, Dordrecht.

BABIN, C. & GUTIÉRREZ-MARCO, J.C. 1992. Intérêt paléobiogéographique de la présence du genre *Trocholites* (Cephalopoda, Nautiloidea) dans le Dobrotivá (Llandeilo) inférieur d'Espagne. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 9*, 519–541.

BALASHOV, Z.G. 1953. Svernutye i polivernutye nautiloidei ordovika pribaltiki. *Trudy Vsesoyuznogo Neftyanogo Nauchno-Issledovatelskogo Geologo–Razvednoknogo Instituta 78*, 217–268.

BALASHOV, Z.G. 1957. The protoconch of a specimen of the genus *Orthoceras* of the Early Paleozoic. *Doklady Akademii Nauk SSSR 116*, 855–857.

BALASHOV, Z.G. 1962. *Ordovician nautiloids from the Siberian platform.* 205 pp. Leningrad University, Leningrad.

BARRANDE, J. 1855. Sur les *Ascoceras.* Prototype des Nautilides. *Bulletin de la Societé Géologique de France 2*, 157–177.

BARRANDE, J. 1865–1877. *Systéme silurien du centre de la Bohême, Ire partie. Recherches paléontologiques, II. Classe de mollusques, ordre des céphalopodes.* Praha.

BARSKOV, I.S. 1963. Systema i filogenia Pseudorthoceratid. *Bjulletyn Moskoskogo obshestva Ispytately Prirody, Geologia 38*, 149–150.

BAUERT, H. & KATTAI, V. 1997. Kukersite oil shale, 313–327. *In* RAUKAS, A. & TEEDUMÄE, A. (eds) *Geology and Mineral Resources of Estonia.* Estonian Academy Publishers, Tallinn.

BERGSTRÖM, S.M., YOUNG, S. & SCHMITZ, B. 2010. Katian (Upper Ordovician) $_{13}$C chemostratigraphy and sequence stratigraphy in the United States and Baltoscandia: a regional comparison. *Palaeogeography, Palaeoclimatology,* *Palaeoecology 296*, 217–234.

BERGSTRÖM, S.M., LEHNERT, O., CALNER, M. & JOACHIMSKI, M.M. 2012. A new upper Middle Ordovician–Lower Silurian drillcore standard succession from Borenshult in Östergötland, southern Sweden: 2. Significance of $_{13}$C chemostratigraphy. *GFF 134*, 39–63.

BERGSTRÖM, J., PÄRNASTE, H. & ZHIYI, Z. 2013. Trilobites and biofacies in the Early–Middle Ordovician of Baltica and a brief comparison with the Yangtze Plate. *Estonian Journal of Earth Sciences 62(4)*, 205–230.

BERTRAND, E. 1763. *Dictionnaire universel des fossiles propres, et des fossiles accidentels.* 606 pp. Louis Chambeau, Avignon.

BOGOLEPOVA, O.K. 1995. Lower Silurian cephalopod limestones from the Mojero River Section (Eastern Siberia, Russia) and their paleogeographic relationships. *Jahrbuch der geologischen Bundesanstalt 138(2–4)*, 155–160.

BOLL, E. 1857. Beitrag zur Kenntnis der silurischen Cephalopoden im norddeutschen Diluvium und den anstehenden Lagern Schwedens. *Archiv des Vereins der Freunde der Naturgeschichte in Mecklenburg 11*, 58–95.

BOYLE, P. & RODHOUSE, P. 2005. *Cephalopods: Ecologies and Fisheries.* 464 pp. Wiley-Blackwell, Oxford. BRENCHLEY, P.J. & ŠTORCH, P. 1989. Environmental changes in the Hirnantian (upper Ordovician) of the Prague Basin, Czechoslovakia. *Geological Journal 24(3)*, 165–181.

BRETT, C.E., & WALKER, S.E. 2002. Predators and predation in Paleozoic marine environments. *The Paleontological Society Papers 8*, 93–118.

CANDELA, Y. 2015. Evolution of Laurentian brachiopod faunas during the Ordovician Phanerozoic sea level maximum. *Earth-Science Reviews 141*, 27–44.

CHEN, J.-Y. & QI, D.-L. 1982. Upper Cambrian Cephalopoda from Suxian of Anhui Province. *Acta Palaeontologica Sinica 21*, 392–403.

CHEN, T.-E. 1987. Ordovician nautiloids from Xainza, northern Xizang. *Bulletin of Nanjing Institute of Geology and Palaeontology, Academia Sinica 11*, 133–187. [In Chinese, English summary]

CHEN, J.-Y. & TEICHERT, C. 1983. Cambrian Cephalopoda in China. *Palaeontographica A 181*, 1–102.

CHEN, J.-Y., ZOU, X.-P., CHEN, T.-E & QI, D.-L. 1979. Late Cambrian cephalopods of North China – Plectronocerida, Protactinocerida (ord. nov.) and Yanhericerida (ord. nov.). *Acta Palaeontologica Sinica 18*, 1–20. [In Chinese, English summary]

CHERNS, L. & WHEELEY, J.R. 2007. A pre-Hirnantian (Late Ordovician) interval of global cooling – The Boda event re-assessed. *Palaeogeography, Palaeoclimatology, Palaeoecology 251(3–4)*, 449–460.

CHLUPÁČ, I. 1998. Devonian, p. 101–133. *In* Chlupáč, I., Havlíček, V., Kříž, J., Kukal, Z. & Štorch, P. (eds) *Palaeozoic of the Barrandian (Cambrian to Devonian).* Czech Geological Survey, Prague.

CHLUPÁČ, I. & KUKAL, Z. 1988. Possible global events and the stratigraphy of the Paleozoic of the Barrandian (Cambrian–Middle Devonian, Czechoslovakia). *Sborník geologických věd, Geologie 43*, 83–146.

CICHOWOLSKI, M. & VACCARI, N.E. 2011. The oldest record of Eothinoceratidae (Ellesmerocerida, Nautiloidea): Middle Tremadocian of the Cordillera Oriental, NW Argentina. *Geological Journal 46(1)*, 42–51.

CICHOWOLSKI, M., URIZ, N.J., ALFARO, M.B. & GALEANO IN-

CHAUSTI, J.C. 201X. “Ascocerid cephalopods from the Hirnantian?–Llandovery of the southern Paraná Basin (Paraguay, South America): first record from high paleolatitudes”. *Journal of Paleontology*, in press.

CLARKE, M.R. & TRUEMAN, E.R. 2013. *Paleontology and Neontology of Cephalopods.* 382 pp. Elsevier.

COCKS, L.R.M. 2000. The Early Palaeozoic geography of Europe. *Journal of the Geological Society 157(1)*, 1–10.

COCKS, L.R.M. & FORTEY, R.A. 1998. The Lower Palaeozoic margins of Baltica. *Geologiska Föreningens Förhandlingar 120*, 173–179.

COCKS, L.R.M. & TORSVIK, T.H. 2002. Earth geography from 500 to 400 million years ago: a faunal and palaeomagnetic review. *Journal of the Geological Society 159(6)*, 631–644.

COCKS, L.R.M. & TORSVIK, T.H. 2005. Baltica from the late Precambrian to mid-Palaeozoic times: the gain and loss of a terrane’s identity. *Earth-Science Reviews 72(1–2)*, 39–66.

COCKS, L.R.M. & TORSVIK, T.H. 2006. European geography in a global context from the Vendian to the end of the Palaeozoic. *Memoirs – Geological Society Of London 32*, 83–95.

COCKS, L.R.M. & TORSVIK, T.H. 2011. The Palaeozoic geography of Laurentia and western Laurussia: A stable craton with mobile margins. *Earth-Science Reviews 106*, 1–51.

COLLINI, B. 1988. Geological setting of the Siljan ring structure, 349–354. *In* BODÉN, A. & ERIKSSON, K. (eds.) *Deep Drilling in Crystalline Bedrock. Vol 1. The Deep Gas Drilling in the Siljan Impact Structure, Sweden and Astroblemes.* Springer, Berlin.

CRICK, R.E. & VAN UFFORD, Q. 1995. Late Ordovician (Caradoc – Ashgill) ellesmerocerid *Bactroceras* latisiphonatum of Irian Jaya and Australia. *Alcheringa 19*, 235–241.

DEAN, W.T. & MONOD, O. 1970. The Lower Palaeozoic stratigraphy and faunas of the Taurus Mountains near Beysehir, Turkey. I. Stratigraphy. *Bulletin of the British Museum (Natural History), Geology Series 19*, 413–426.

DENTON, E.J. 1974. Croonian Lecture, 1973: on buoyancy and the lives of modern and fossil cephalopods. *Proceedings of the Royal Society of London B: Biological Sciences 185(1080)*, 273–299.

DOGUZHAEVA, L.A., BENGTSON, S., REGUERO, M.A. & MÖRS, T. 2017. An Eocene orthocone from Antarctica shows convergent evolution of internally shelled cephalopods. *PloS one 12(3)*, e0172169.

DOGUZHAEVA, L.A., & MUTVEI, H. 1993. Shell ultrastructure, muscle-scars, and buccal apparatus in ammonoids. *Geobios 26*, 111–119.

DZIK, J. 1981. Origin of the Cephalopoda. *Acta Palaeontologica Polonica 26*, 161–191.

DZIK, J. 1983. Early Ordovician conodonts from the Barrandian and Bohemian–Baltic faunal relationships. *Acta Palaeontologica Polonica 28(3–4)*, 327–368.

DZIK, J. 1984. Phylogeny of the Nautiloidea. *Palaeontologia Polonica 45*, 1–203.

DZIK, J. & KORN, D. 1992. Devonian ancestors of *Nautilus. Paläontologische Zeitschrift 66(1–2)*, 81–98.

EBBESTAD, J.O.R. & HÖGSTRÖM, A.E.S. 2007. Ordovician of the Siljan District, Sweden, 7–9. *In* EBBESTAD, J.O.R., WICKSTRÖM, L. & HÖGSTRÖM, A.E.S. (eds) *WOGOGOB 2007, 9th meeting of the Working Group on Ordovician Geology of Baltoscandia, Field Guide and Abstracts. Rapporter och Meddelanden 128.*

EBBESTAD, J.O.R., HÖGSTRÖM, A.E.S., FRISK, Å.M., MARTMA, T., KALJO, D., KRÖGER, B. & PÄRNASTE, H. 2015. Terminal Ordovician stratigraphy of the Siljan district, Sweden. *GFF 137*, 35–56.

EICHWALD, E. 1825. *Geognostico-zoologicae per Ingriam marisque Baltici provincias nec non de trilobitis observationes.* 58 pp. Casani.

ENGELHARDT, M. 1820. *Darstellung aus dem Felsgebäude Russlands. Erste Lieferung. Geognostischer Umriss von Finland.* 44 pp. Berlin.

ENGESER, T. 1996. The position of the Ammonoidea within the Cephalopoda, 3–19. *In* LANDMAN, N.H., TANABE, K. & DAVIS, R.A. (eds.) *Ammonoid paleobiology. Topics in Geobiology 13.* Plenum Press, New York.

ERBEN, H.K. 1964. Bactritoidea, K491–K505. *In* MOORE, R.C. (ed.) *Treatise on invertebrate paleontology. Part K. Mollusca 3. Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea.* GSA and University of Kansas Press, Lawrence, Kansas, USA.

ERNST, A., KRAFT, P., & ZÁGORŠEK, K. 2014. Trepostome bryozoans from the Zahořany Formation (Upper Ordovician) of Loděnice, Prague Basin, Czech Republic. *Paläontologische Zeitschrift 88*(1), 11–26.

EVANS, D.H. 2005. The Lower and Middle Ordovician Cephalopod Faunas of England and Wales. *Monograph of the Palaeontographical Society 628*, 1–81.

EVANS, D.H. 2007. A Middle Ordovician cephalopod fauna from Cuzco Province, southern Perú and its palaeobiogeographical significance. *Geological Journal 42*, 25–36.

EVANS, D.H. & KING, A.H. 1990. The affinities of early oncocerid nautiloids from the Lower Ordovician of Spitsbergen and Sweden. *Palaeontology 33*, 623–630.

EVANS, D.H. & HOLLAND, C.H. 1995. The nautiloid cephalopod Order Endocerida in the Silurian. *Paläontologische Zeitschrift 69(3–4)*, 343–352.

EVANS, D.H. & KING, A.H. 2012. Resolving polyphyly within the Endocerida: The Bisonocerida nov., a new order of early palaeozoic nautiloids. *Geobios 45(1)*, 19–28.

EVANS, D.H., GHOBADI POUR, M. & POPOV, L.E. 2013. Review of the Early to Mid Ordovician orthoconic cephalopods from Iran. *Bulletin of Geosciences 88(1)*, 21–44.

EVANS, D.H., POUR, M.G., POPOV, L.E., & JAHANGIR, H. 2015. An early Silurian (Aeronian) cephalopod fauna from Kopet-Dagh, north-eastern Iran: including the earliest records of non-orthocerid cephalopods from the Silurian of Northern Gondwana. *Bulletin of Geosciences 90(2)*, 479–507.

FANG, X., ZHANG, YUN., CHEN, T. & ZHANG, YUA. 2017a. A quantitative study of the Ordovician cephalopod species *Sinoceras chinense* (Foord) and its palaeobiogeographic implications. *Alcheringa: An Australasian Journal of Palaeontology 41(3)*, 321–334.

FANG, X., CHEN, T., ZHANG, YUN. & ZHANG, YUA. 2017b. Lituitidae nautiloids from the Datianba Formation (uppermost Darriwilian to Sandbian, Ordovician) in western Hunan Province and its ontogenical study. *Acta Palaeontologica Sinica 56(3)*, 331–346.

FANG, X., CHEN, T., BURRETT, C., WANG, Y., QU, Y., ZHENG, C., ZHANG, Y., ZHANG Y. & LI, W. 2018. Middle Ordovician actinocerid nautiloids (Cephalopoda) from Xainza County, Tibet, western China, and their paleogeographic implications. *Journal of Paleontology 92(3)*, 398–411.

FATKA, O. & MERGL, M. 2009. The „microcontinent“ Perunica – status and story 15 years after its conception. *Geological Society, London, Special Publications 325*, 65–101.

FATKA, O., LEROSEY-AUBRIL, R., BUDIL, P. & RAK, Š. 2013. Fossilised guts in trilobites from the Upper Ordovician Letná Formation (Prague Basin, Czech Republic). *Bulletin of Geosciences*, *88(1)*, 95–104.

FEDOROV, P.V. 2003. Lower Ordovician mud mounds from the St. Petersburg region, northwestern Russia. *Bulletin of the Geological Society of Denmark 50(1)*, 125–137.

FERRETTI, A. & KŘÍŽ, J. 1995. Cephalopod limestone biofacies in the Silurian of the Prague Basin, Bohemia. *Palaios 10(3)*, 240–253.

FIORITO, G., VON PLANTA, C. & SCOTTO, P. 1990. Problem solving ability of Octopus vulgaris lamarck (Mollusca, Cephalopoda). *Behavioral and neural biology 53(2)*, 217–230.

FISCHER, A.G. & TEICHERT, C. 1969. Cameral deposits in cephalopod shells. *The University Of Kansas Paleontological Contributions, Paper 37*, 1–29.

FLOWER, R.H. 1939, Study of the Pseudorthoceratidae. *Palaeontographica Americana 2(10)*, 1–219.

FLOWER, R.H. 1941. Revision and internal structure of *Leurocycloceras. American Journal of Science 239*, 469–488.

FLOWER, R.H. 1946. Ordovician cephalopods from the Cincinnati region. Part 1. *Bulletins of American Paleontology 29(116)*, 3–547.

FLOWER, R.H. 1955. Cameral deposits in orthoconic nautiloids. *Geological Magazine 92*(2), 89–103.

FLOWER, R.H. 1957. Nautiloids of the Paleozoic. *Geological Society of America Memoir 67*, 829–852.

FLOWER, R.H. 1962a. Notes on the Michelinoceratida. *Memoirs of the New Mexico Institute of Mining and Technology 10*, 19–42.

FLOWER, R.H. 1962b. Part 1, Revision of *Buttsoceras*, Part 2, Notes on the Michelinoceratida. *State Bureau of Mines and Mineral Resources, New Mexico Institute of Mining and Technology, Memoir 10*, 1–58.

FLOWER, R.H. 1963. New Ordovician Ascoceratida. *Journal of Paleontology 37(1)*, 69–85.

FLOWER, R.H. 1964. The nautiloid order Ellesmeroceratida (Cephalopoda). *New Mexico Institute of Mining and Technology Memoir 12*, 1–164.

FLOWER, R.H. 1968. Cephalopods from the Tiñu Formation, Oaxaca State, Mexico. *Journal of Paleontology 42*, 804–810.

FLOWER, R.H. 1975. American Lituitidae (Cephalopoda). *Bulletins of American Paleontology 67(287)*, 139–173.

FLOWER, R.H. 1984. *Bodeiceras*, a new Mohawkian oxycone, with revision of the older Barrandeoceratida and discussion of the status of the order. *Journal of Paleontology 58(6)*, 1372–1379.

FLOWER, R.H. 1988. Progress and changing concepts in cephalopod and particularly nautiloid phylogeny and distribution. *Cephalopods Present and Past. Schweizerbart'sche Verlagsbuchhhandlung*, 17–24.

FLOWER, R.H. & KUMMEL, B. 1950. A classification of the Nautiloidea. *Journal of Paleontology 24*, 604–616.

FORTEY, R.A. & COCKS, L.R.M. 2005. Late Ordovician global warming – the Boda event. *Geology 33(5)*, 405–408.

FREDRIKSSON, K. & WICKMAN, F.E. 1963. Meteoriter. *Svensk Naturvetenskap*, 121–157.

FREY, R.C. 1989. Paleoecology of a well-preserved nautiloid assemblage from a Late Ordovician shale unit, southwestern Ohio. *Journal of Paleontology 63(5)*, 604–620.

FREY, R.C. 1995. Middle and Upper Ordovician Cephalopods of the Cincinnati Region of Kentucky, Indiana, and Ohio. *United States Geological Survey Professional Paper 1066P*, 1–119.

FRÝDA, J. 1988. A new species of *Modestospira* (Gastropoda) from the Ordovician of Bohemia. *Věstník Ústředního ústavu geologického 63(4)*, 227–232.

FUCHS, D., KEUPP, H. & KLUG, C. 2018. A critical review of Antarcticeras Doguzhaeva, 2017–teuthid affinities can explain the poorly mineralized phragmocone. *Historical Biology*, 1–6.

FURNISH, W.M. & GLENISTER, B.F. 1964a. Nautiloidea – Ascocerida, K261–K277. *In* MOORE, R.C. (ed.) *Treatise on invertebrate paleontology. Part K. Mollusca 3. Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea.* GSA and University of Kansas Press, Lawrence, Kansas, USA.

FURNISH, W.M. & GLENISTER, B.F. 1964b. Nautiloidea – Tarphycerida, K343–K368. In MOORE, R.C. (ed.) *Treatise on invertebrate paleontology. Part K. Mollusca 3. Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea.* GSA and University of Kansas Press, Lawrence, Kansas, USA.

GEE, D.G. 1975. A tectonic model for the central part of the Scandinavian Caledonides. *American Journal of Science 275(A)*, 468–515.

GEE, D.G. & STURT, B.A. 1985. *The Caledonide orogen: Scandinavia and related areas.* 1266 pp. Wiley.

GEE, D.G., FOSSEN, H., HENRIKSEN, N. & HIGGINS, A.K. 2008. From the early Paleozoic platforms of Baltica and Laurentia to the Caledonide Orogen of Scandinavia and Greenland. *Episodes 31(1)*, 44–51.

GLENISTER, B.F. 1952. Ordovician nautiloids from New South Wales. *Australian Journal of Science 15*, 89–91.

GNOLI, M. 2003. Northern Gondwanan Siluro-Devonian palaeogeography assessed by cephalopods. *Palaeontologia Electronica 5(2)*, 1–19.

GREENWALD, L. & WARD, P.D. 2010. Buoyancy in *Nautilus*, 547–560. *In* SAUNDERS W.B. & LANDMAN N.H. (eds) *Nautilus. Topics in Geobiology 6.* Springer.

GRIEVE, R.A.F., 1988: The formation of large impact structures and constraints on the nature of Siljan, 328–348. *In* BODEN, A. & ERIKSSON, K.G. (eds.) *Deep Drilling in Crystalline Bedrock; Vol. 1: The Deep Gas Drilling in the Siljan Impact Structure, Sweden and Astroblemes. Proceedings of the International Symposium.* Springer Verlag, Berlin.

GUTIÉRREZ-MARCO, J.C., RÁBANO, I., PRIETO, M. & MARTIN, J.

1984. Estudio bioestratigráfico del Llanvirn y Llandeilo (Dobrotiviense) en la parte meridional de la Zona Centroibérica (España). *Cuadernos de Geología Ibèrica 9*, 287–319.

GUTIÉRREZ-MARCO, J.C., RÁBANO, I., SAN JOSÉ, M.A., HERRANZ, P. & SARMIENTO, G.N. 1995. Oretanian and Dobrotivian Stages vs. "Llanvirn–Llandeilo" Series in the Ordovician of the Iberian Peninsula, 55–59. *In* COOPER, J.D., DROSER, M.L. & FINNEY, S.C. (eds) *Ordovician Odyssey: Short papers for the 7th Symposium on the Ordovician System, Las Vegas.* Pacific Section of Society of Sedimentary Geology (SEPM), Fullerton, California, *77*.

GUTIÉRREZ-MARCO, J.C, SÁ, A.A, GARCÍA-BELLIDO, D.C & RÁBANO, I. 2017. The Bohemo-Iberian regional chronostratigraphical scale for the Ordovician System and palaeontological correlations within South Gondwana. *Lethaia 50(2)*, 258–295.

HANLON, R.T. & MESSENGER, J.B. 2018. *Cephalopod Behaviour.* 365 pp. Cambridge University Press, Cambridge.

HARPER, D.A.T., RASMUSSEN, C.M.Ø., LILJEROTH, M., BLODGETT, R.B., CANDELA, Y., JIN, J., PERCIVAL, I.G., RONG, J., VILLAS, E. & ZHAN, R. 2013. Biodiversity, biogeography and phylogeography of Ordovician rhynchonelliform brachiopods. *Geological Society, London, Memoirs 38*, 127–144.

HARPER, D.A., HAMMARLUND, E.U., & RASMUSSEN, C.M. 2014. End Ordovician extinctions: a coincidence of causes. *Gondwana Research 25(4)*, 1294–1307.

HARTZ, E.H. & TORSVIK, T.H. 2002. Baltica upside down: a new plate tectonic model for Rodinia and the Iapetus Ocean. *Geology 30(3)*, 255–258.

HARRIS, M.T., SHEEHAN, P.M., AINSAAR, L., HINTS, L., MÄNNIK, P., NÕLVAK, J., & RUBEL, M. 2004. Upper Ordovician sequences of western Estonia. *Palaeogeography, Palaeoclimatology, Palaeoecology 210*(2–4), 135–148.

HAVLÍČEK, V. 1981. Development of a linear sedimentary depression exemplified by the Prague Basin (Ordovician–Middle Devonian; Barrandian area – central Bohemia). *Sborník geologických věd, Geologie 35*, 7–48.

HAVLÍČEK, V. 1982. Ordovician in Bohemia – development of the Prague Basin and its benthic communities. *Sborník geologických věd, Geologie 37*, 103–136.

HAVLÍČEK, V. 1989. Climatic changes and development of benthic communities through the Mediterranean Ordovician. *Sborník geologických věd, Geologie 44*, 79–116.

HAVLÍČEK, V. 1998. Ordovician, p. 41–79. *In* Chlupáč, I., Havlíček, V., Kříž, J., Kukal, Z. & Štorch, P. (eds) *Palaeozoic of the Barrandian (Cambrian to Devonian).* Czech Geological Survey, Prague.

HAVLÍČEK, V. & VANĚK, J. 1966. The Biostratigraphy of the Ordovician of Bohemia. *Sborník geologických věd, Paleontologie 8*, 7–13.

HAVLÍČEK, V. & MAREK, L. 1973. Bohemian Ordovician and its international correlation. *Časopis pro mineralogii a geologii 18(3)*, 225–232.

HAVLÍČEK, V., VANĚK, J. & FATKA, O. 1994. Perunica microcontinent in the Ordovician (its position within the Mediterranean Province, series division, benthic and pelagic associations). *Sborník geologických věd, Geologie 46*, 23–56.

HEDBERG, H.D. 1988. *The 1740 description by Daniel Tilas of stratigraphy and petroleum occurrence at Osmundsberg in the Siljan region of central Sweden.*

96 pp. The American Association of Petroleum Geologists Foundation, Cincinnati, Ohio.

HENKEL, H. & AARO, S. 2005: Geophysical Investigations of the Siljan Impact Structure – A Short Review, 247–283. *In* KOEBERL, C. & HENKEL, H. (eds.) *Impact Tectonics.* Springer Verlag, Berlin, Heidelberg, New York.

HINTS, L. & MEIDLA, T. 1997. Keila Stage. Oandu Stage. Rakvere Stage. Nabala Stage. Vormsi Stage. Pirgu Stage. Porkuni Stage, 74–88. *In* RAUKAS, A. & TEEDUMÄE, A. (eds) *Geology and Mineral Resources of Estonia.* Estonian Academy Publishers, Tallinn,

HISTON, K. 1993. Primary deposits in nautiloid cephalopods. *Lethaia 26*, 179–181.

HEWITT, R.A. & STAIT, B. 1985. Phosphatic connecting rings and ecology of an Ordovician ellesmerocerid nautiloid. *Alcheringa 26*, 229–243.

HLADIL, J. 1991. The Upper Ordovician dropstones of Central Bohemia and their paleogravity significance. *Věstník ústředního ústavu geologického 66(2)*, 65−76.

HOFFMANN, R., LEMANIS, R., NAGLIK, C. & KLUG, C. 2015. Ammonoid Buoyancy, 613–648. *In* KLUG, C., KORN, D., DE BAETS, K., KRUTA, I. & MAPES, R. (eds) *Ammonoid Paleobiology: From anatomy to ecology. Topics in Geobiology 43.* Springer, Dordrecht.

HÖGSTRÖM, A.E., STURKELL, E., EBBESTAD, J.O.R., LINDSTRÖM, M., & ORMÖ, J. 2010. Concentric impact structures in the Palaeozoic of Sweden – the Lockne and Siljan craters. *GFF 132(1)*, 65–70.

HOLLAND, C.H. 1965. On the nautiloid *Leurocycloceras* from the Ludlovian of Wales and the Welsh borderland. *Palaeontology 7(4)*, 525–540.

HOLLAND, C.H. 1987. The nautiloid cephalopods: a strange success: President's anniversary address 1986. *Journal of the Geological Society 144(1)*, 1–15.

HOLLAND, C.H. 1999. The nautiloid cephalopod order Ascocerida in the British Silurian. *Palaeontology 42(4)*, 683–689.

HOLLAND, C.H. 2003. Some observations on bactritid cephalopods. *Bulletin of Geosciences 78*, 369–372.

HOLM, G. 1891. Om mynningen *Lituites. Geologiska Föreningens i Stockholm Förhandlingar 13*, 736–776.

HOLM, G. 1898. Om ett par *Bactrites*-liknande Undersiluriska Orthocerformer, 354–366. In HOLM, G. (ed.) *Palæontologiska notiser 179, Sveriges geologiska undersökning, ser. C.*

HYATT, A. 1900. Cephalopoda, 502–592. *In* VON ZITTEL, K.A. (ed.) *Textbook of Paleontology*, translated and edited by EASTMANN, C.R.. Macmillan and Co., London.

ISBERG, O. 1934. *Studien über die Lamellibranchiaten des Leptaenakalkes in Dalarna.* 429 pp. Häkan Ohlssons Boktryckeri, Lund.

JAANUSSON, V. 1976. Faunal dynamics in the Middle Ordovician (Viruan) of Baltoscandia, 301–326. *In* Bassett, M.G. (ed.) *The Ordovician System. Proceedings of a Palaeontological Association Symposium, Birmingham.* University of Wales Press, Cardiff.

JAANUSSON, V. 1973. Aspects of carbonate sedimentation in the Ordovician of Baltoscandia. *Lethaia 6(1)*, 11–34.

JAANUSSON, V. 1982. Introduction to the Ordovician of Sweden, 1–9.

In Bruton, D.L. & Williams, S.H. (eds) *IVth International Symposium on the Ordovician System, Field Excursion Guide*, *Paleontological Contributions from the University of Oslo 279.*

JENKYNS, H.C. 1975. Origin of Red Nodular Limestones (Ammonitico Rosso, Knollenkalke) in the Mediterranean Jurassic: A Diagenetic Model. *In* HSÜ, K.J. & JENKYNS, H.C. (eds) *Pelagic Sediments: on Land and under the Sea.* Blackwell Publishing Ltd., Oxford, UK.

JUHLIN, C., STURKELL, E., EBBESTAD, J.O.R., LEHNERT, O., HÖGSTRÖM, A.E., & MEINHOLD, G. 2012. A new interpretation of the sedimentary cover in the western Siljan Ring area, central Sweden, based on seismic data. *Tectonophysics 580*, 88–99.

KÁCHA, P., & ŠARIČ, R. 2009. Host preferences in Late Ordovician (Sandbian) epibenthic bryozoans: example from the Zahořany Formation of Prague Basin. *Bulletin of Geosciences 84* (1), 169–178.

KAJAK, K. 1997. Upper Devonian, 121–123. *In* RAUKAS, A. & TEEDUMÄE, A. (eds) *Geology and mineral resources of Estonia.* Estonian Academy Publishers, Tallinn.

KALJO, D. 1970. Mollusks, 150–153. In KALJO, D. (ed.) *The Silurian of Estonia.* Valgus, Tallinn. [In Russian]

KALJO, D., MARTMA, T. & SAADRE, T. 2007. Post-Hunnebergian Ordovician carbon isotope trend in Baltoscandia, its environmental implications and some similarities with that of Nevada. *Palaeogeography, Palaeoclimatology, Palaeoecology 245*, 138–155.

KLAAMANN, E. 1970. The Paadla Stage, 276–286. In KALJO, D. (ed.) *The Silurian of Estonia.* Valgus, Tallinn. [In Russian]

KLEESMENT, A. & MARK-KURIK, E. 1997. Lower Devonian, Middle Devonian, 107– 121. *In* RAUKAS, A. & TEEDUMÄE, A. (eds) *Geology and mineral resources of Estonia.* Estonian Academy Publishers, Tallinn.

KLUG, C., KRÖGER, B., KIESSLING, W., MULLINS, G.L., SERVAIS, T., FRÝDA, J., KORN, D. & TURNER, S. 2010. The Devonian nekton revolution. *Lethaia 43(4)*, 465–477.

KLUG, C., KRÖGER, B., VINTHER, J., FUCHS, D. & DE BAETS, K. 2015. Ancestry, origin and early evolution of ammonoids, 3–24. *In* LANDMAN, N., TANABE, K. & DAVIS, R.A. (eds.) *Ammonoid Paleobiology.* Plenum Press, New York.

KOLEBABA, I. 1973. Embryonální stádia hlavonožců ze svrchních poloh Liteňského souvrství (silur, spodní wenlock). *Časopis Národního muzea, Oddíl přírodovědný 142*, 28–40.

KOLEBABA, I. 1999a. Sipho-cameral structures in some Silurian cephalopods from the Barrandian area. *Sborník Národního muzea v Praze, Řada B – přírodní vědy 55*, 1–15.

KOLEBABA, I. 1999b. Gradual opening of the siphonal tube in an orthoconic cephalopod from the Silurian of Central Bohemia (Czech Republic). *Journal of the Czech Geological Society 44*, 131–136.

KOLEBABA, I. 2002. A contribution to the theory of the cameral mantle in some Silurian Nautiloidea (Mollusca, Cephalopoda). *Bulletin of the Czech Geological Survey 77*, 183–186.

KORN, D. 2010. A key for the description of Palaeozoic ammonoids. *Fossil*

Record 13(1), 5–12.

KRAFT, J. & KRAFT, P. 1994. The *Azygograptus-Tetragraptus* (*reclinatus* group) Biozone (Klabava Formation, Ordovician of the Prague Basin). *Folia Musei Rerum Naturalium Bohemia Occidentalis, Geologica 40*, 1–36.

KRÖGER, B. 2002: On the efficiency of the buoyancy apparatus in ammonoids: evidences from sublethal shell injuries. *Lethaia 35*, 61–70.

KRÖGER, B. 2003. The size of the siphuncle in cephalopod evolution. *Senckenbergiana lethaea 83(1–2)*, 39–52.

KRÖGER, B. 2004. Revision of Middle Ordovician orthoceratacean nautiloids from Baltoscandia. *Acta Palaeontologica Polonica 49(1)*, 57–74.

KRÖGER, B. 2006. Early growth-stages and classification of orthoceridan Cephalopods of the Darriwillian (Middle Ordovician) of Baltoscandia. *Lethaia 39*, 129–139.

KRÖGER, B. 2007. Some lesser known features of the ancient cephalopod order Ellesmerocerida (Nautiloidea, Cephalopoda). *Palaeontology 50*(3), 565–572.

KRÖGER, B. 2008. Nautiloids before and during the origin of ammonoids in a Siluro-Devonian section of the Tafilalt, Anti-Atlas, Morocco. *Special Papers in Palaeontology 79*, 1–110.

KRÖGER, B. 2012. The "Vaginaten": the dominant cephalopods of the Baltoscandian Mid Ordovician endocerid limestone. *GFF 134(2)*, 115–132.

KRÖGER, B. 2013a. Cambrian–Ordovician cephalopod palaeogeography and diversity, 429–448. *In* HARPER, D.A.T. & SERVAIS, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography. Geological Society, London, Memoirs 38.*

KRÖGER, B. 2013b. The cephalopods of the Boda Limestone, Late Ordovician, of Dalarna, Sweden. *European Journal of Taxonomy 41*, 1–110.

KRÖGER, B. & MUTVEI, H. 2005. Nautiloids with multiple paired muscle scars from Lower–Middle Ordovician of Baltoscandia. *Palaeontology 48(4)*, 781–791.

KRÖGER, B. & ISAKAR, M. 2006. Revision of annulated orthoceridan cephalopods of the Baltoscandic Ordovician. *Fossil Record 9(1)*, 137–163.

KRÖGER, B. & MAPES, R. 2007. Carboniferous actinoceratoid Nautiloidea (Cephalopoda) – A new perspective. *Journal of Paleontology 81(4)*, 714–724.

KRÖGER, B. & LANDING, E. 2008. Onset of the Ordovician cephalopod radiation-evidence from the Rochdale Formation (middle Early Ordovician, Stairsian) in eastern New York. *Geological Magazine 145(4)*, 490–520.

KRÖGER, B. & ZHANG, Y. 2009. Pulsed cephalopod diversification during the Ordovician. *Palaeogeography, Palaeoclimatology, Palaeoecology 273*, 174–183.

KRÖGER, B. & EVANS, D.H. 2011. Review and palaeoecological analysis of the late Tremadocian–early Floian (Early Ordovician) cephalopod fauna of the Montagne Noire, France. *Fossil Record 14*, 5–34.

KRÖGER, B. & LEFEBVRE, B. 2012. Palaeogeography and palaeoecology of early Floian (Early Ordovician) cephalopods from the Upper Fezouata Formation, Anti-Atlas, Morocco. *Fossil Record 15(2)*, 61–75.

KRÖGER, B. & EBBESTAD, J.O.R. 2014. Palaeoecology and palaeogeography of Late Ordovician (Katian–Hirnantian) cephalopods of the Boda Limestone, Siljan district, Sweden. *Lethaia 47*, 15–30.

KRÖGER, B. & RASMUSSEN, J.A. 2014. Middle Ordovician cephalopod biofacies and palaeoenvironments of Baltoscandia. *Lethaia 47(2)*, 275–295.

KRÖGER, B., BERESI, M.S. & LANDING, E. 2007. Early orthoceratoid cephalopods from the Argentine Precordillera (Lower–Middle Ordovician). *Journal of Paleontology 81(6)*, 1266–1283.

KRÖGER, B., ZHANG, Y. & ISAKAR, M. 2009a. Discosorids and Oncocerids (Cephalopoda) of the Middle Ordovician Kunda and Aseri Regional Stages of Baltoscandia and the early evolution of these groups. *Geobios 42(3)*, 273–292.

KRÖGER, B., SERVAIS, T. & ZHANG, Y. 2009b. The Origin and Initial Rise of Pelagic Cephalopods in the Ordovician. *PloS ONE 4*, e7262.

KRÖGER, B., VINTHER, J. & FUCHS, D. 2011. Cephalopod origin and evolution: a congruent picture emerging from fossils, development and molecules. *BioEssays 33*, 602–613.

KRÖGER, B., HINTS, L. & LEHNERT, O. 2014. Age, facies, and geometry of the Sandbian/Katian (Upper Ordovician) pelmatozoan-bryozoan-receptaculitid reefs of the Vasalemma Formation, northern Estonia. *Facies 60*, 963–86.

KRÖGER, B., EBBESTAD, J.O.R. & LEHNERT, O. 2016a. Accretionary mechanisms and temporal sequence of formation of the Boda Limestone Mud Mounds (Upper Ordovician), Siljan District, Sweden. *Journal of Sedimentary Research 86(4)*, 363–379.

KRÖGER, B., HINTS, L. & LEHNERT, O. 2016b. Ordovician reef and mound evolution: the Baltoscandian picture. *Geological Magazine 154(4)*, 683–706.

KŘÍŽ, J. 1998. Silurian, p. 79–98. *In* Chlupáč, I., Havlíček, V., Kříž, J., Kukal, Z. & Štorch, P. (eds) *Palaeozoic of the Barrandian (Cambrian to Devonian).* Czech Geological Survey, Prague.

KUHN, O. 1940. *Paläozoologie in Tabellen.* 50 pp. Fischer Verlag, Jena.

KUHN, O. 1949. *Lehrbuch der Paläozoologie.* 326 pp. E. Schweizerbart, Stuttgart.

KUKAL, Z. 1962. A petrographical investigation of the Ordovician Šárka Beds in the Barrandian area. *Sborník Ústředního ústavu geologického, odd. Geologie 27(1)*, 175–214. [English summary]

LAI, C. 1986. On Lituitidae. *Bulletin of the Chinese Academy of Geological Sciences 12*, 107–126.

LAI, C.-G. 1987. Ordovician cephalopods from Mt. Querquerk (Mt. Charchag), Xinjiang. *Professional Papers in Stratigraphy and Palaeontology 17*, 227–246. [In Chinese]

LAI, C. 1989. Biogeography of the Ordovician cephalopods from China. *Journal of Southeast Asian Earth Sciences 3(1–4)*, 125–130.

LAJBLOVÁ, K. & KRAFT, P. 2014. The earliest ostracods from the Ordovician of the Prague Basin, Czech Republic. *Acta Geologica Polonica 64(4)*, 367–392.

LANDING, E. & KRÖGER, B. 2009. The oldest cephalopods from east Laurentia. *Journal of Paleontology 83*, 89–93.

LANGRIDGE, K.V., BROOM, M. & OSORIO, D. 2007. Selective signalling by cuttlefish to predators. *Current Biology 17(24)*, R1044–R1045.

LI, L.-Z. 1983. Cephalopods from the Upper Cambrian Siyangshan Formation of western Zhejiang. *Papers for the Symposium on the Cambrian–Ordovician and*

Ordovician–Silurian boundaries, Nanjing, October 1983, 14–17.

LINDSTRÖM, G. 1890. The Ascoceratidae and the Lituitidae of the Upper Silurian formation of Gotland. *Kungliga Svenska Vetenskaps-Akademiens Handlingar 23*, 1–54.

LINDSTRÖM, M., SCHMITZ, B., STURKELL, E. & ORMÖ, J. 2008. Palaeozoic impact craters. *In 33rd international geological congress, Oslo. Excursion guide* (No. 10, p. 54).

LINNÆUS, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Laurentii Salvii, Holmiae. Vol. Tomus I, Editio decima, reformata.* 824 pp.

LUKENEDER, A., HARZHAUSER, M., MÜLLEGGER, S. & PILLER, W.E. 2010. Ontogeny and habitat change in Mesozoic cephalopods revealed by stable isotopes ($_{18}$O, $_{13}$C). *Earth and Planetary Science Letters 296(1–2)*, 103–114.

MANDA, Š. 2008a. Palaeoecology and palaeogeographic relations of the Silurian phragmoceratids (Nautiloidea, Cephalopoda) of the Prague Basin (Bohemia). *Bulletin of Geosciences 83(1)*, 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(3)*, 327–334.

MANDA, Š. & KŘÍŽ, J. 2006. Environmental and biotic changes in subtropical isolated carbonate platforms during the Late Silurian *Kozlowskii* Event, Prague Basin. *GFF 128(2)*, 161–168.

MANDA, Š. & KŘÍŽ, J. 2007. New cephalopod limestone horizon in the Ludlow (Gorstian, lower *L. scanicus* Biozone) of the Prague Basin (Bohemia, Perunica). *Bollettino-società Paleontologica Italiana 46(1)*, 33–45.

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.

MANDA, Š. & TUREK, V. 2011. Late Emsian Rutoceratoidea (Nautiloidea) from the Prague Basin, Czech Republic: morphology, diversity and palaeoecology. *Palaeontology 54(5)*, 999–1024.

MANDA, Š. & TUREK, V. 2018. Silurian tarphycerid *Discoceras* (Cephalopoda, Nautiloidea): systematics, embryonic development and paleoecology. *Journal of Paleontology 92(3)*, 412–431.

MÄNNIL, R., 1966. Evolution of the Baltic Basin during the Ordovician. 200 pp. Valgus, Tallinn. [In Russian with English summary]

MATHER J.A. 2004. Cephalopod skin displays: from concealment to communication, 193–214. *In* KIMBROUGH OLLER, D. & GRIEBEL, U. (eds) *Evolution of communication systems: a comparative approach.* MIT Press, Cambridge.

MATHER, J.A. 2008. Cephalopod consciousness: behavioural evidence. *Consciousness and Cognition 17(1)*, 37–48.

MAREK, L. 1952. Příspěvek ke stratigrafii a fauně nejvyšší části břidlic králodvorských (dζ1). *Sborník Ústředního ústavu geologického, odd. Paleontologie 19*, 449−455.

MAREK, J. 1999. Ordovician cephalopods of the Prague Basin (Barrandian area, Czech Republic): a review. *Acta Universitatis Carolinae – geologica 43*, 413–416.

MAREK, J., WEBER, B., SCHÖNIAN, F., EGENHOFF, S.O., ERDT-

MANN, D. 2000. Arenig cephalopods from Bolivia. *Palaeontology down-under 2000, 61, Geological Society of Australia, Abstracts*, 56–57.

McCOY, F. 1844. *A synopsis of the characters of the Carboniferous Limestone fossils of Ireland.* 274 pp. Dublin University Press, Dublin.

MEIDLA, T. 1997. Hunneberg Stage. Billingen Stage. Volkhov Stage. Kunda Stage, 58–65. *In* RAUKAS, A. & TEEDUMÄE, A. (eds) *Geology and Mineral Resources of Estonia.* Estonian Academy Publishers, Tallinn.

MEIDLA, T., AINSAAR, L. & HINTS, O. 2014. The Ordovician System in Estonia, 116–122. In BAUERT, H., HINTS, O., MEIDLA, T. & MÄNNIK, P. (eds) *4th Annual Meeting of IGCP 591, The Early to Middle Paleozoic Revolution Estonia, 10–19 June 2014, Abstracts & Field Guide.* Tartu.

MELCHIN, M.J., MITCHELL, C.E., HOLMDEN, C. & ŠTORCH, P. 2013. Environmental changes in the Late Ordovician–early Silurian: Review and new insights from black shales and nitrogen isotopes. *GSA Bulletin 125(11–12)*, 1635–1670.

MENS, K. & PIRRUS, E. 1997. Vendian. Cambrian, 25–51. *In* RAUKAS, A. & TEEDUMÄE, A. (eds) *Geology and Mineral Resources of Estonia.* Estonian Academy Publishers, Tallinn.

MERGL, M. 2004. The earliest brachiopod-bryozoan dominated community in the Ordovician of peri-Gondwana and its ancestors: a case study from the Klabava Formation (Arenigian) of the Barrandian, Bohemia. *Journal of the Czech Geological Society 49(3/4)*, 127–136.

MERGL, M. 2011a. Diverzita mechovek (Bryozoa) v nejvyšší části králodvorského souvrství (ordovik, svrchní katian) pražské pánve České republiky. *Zprávy o geologických výzkumech v roce 2010 (44), 100–102.*

MERGL, M. 2011b. Earliest occurrence of the Hirnantia Fauna in the Prague Basin (Czech Republic). *Bulletin of Geosciences 86(1)*, 63–70.

MIKULÁŠ, R. 1990. Trace fossils from the Zahořany Formation (Upper Ordovician, Bohemia). *Acta Universitatis Carolinae, Geologica 3*, 303– 335.

MOORE, R.C. 1957. *Treatise on invertebrate paleontology. Part K. Mollusca 4. Cephalopoda – Ammonoidea.* 490 pp. GSA and University of Kansas Press, Lawrence, Kansas, USA.

MOORE, R.C. 1964. *Treatise on invertebrate paleontology. Part K. Mollusca 3. Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea.* 519 pp. GSA and University of Kansas Press, Lawrence, Kansas, USA.

MUTVEI, H. 1957. On the relations of the principal muscles to the shell in *Nautilus* and some fossil nautiloids. *Arkiv for mineralogi och geologi 2*, 219–254.

MUTVEI, H. 1964. Remarks on the anatomy of Recent and fossil Cephalopoda. *Stockholm Contributions on Geology 11*, 79–102.

MUTVEI, H. 1996. Characterization of actinoceratoid cephalopods by their siphuncular structure. *Lethaia 29(4)*, 339–348.

MUTVEI, H. 1997. Siphuncular structure in Ordovician endocerid cephalopods. *Acta Palaeontologica Polonica 42(3)*, 375–390.

MUTVEI, H. 2002a. Connecting ring structure and its significance for classification of the orthoceratid cephalopods. *Acta Palaeontologica Polonica 47*, 157–168.

MUTVEI, H. 2002b. Nautiloid systematics based on siphuncular structure and position of muscle scars. *Abhandlungen der geologischen Bundesanstalt 57*, 379–392.

MUTVEI, H. 2013. Characterization of nautiloid orders Ellesmerocerida, Oncocerida, Tarphycerida, Discosorida and Ascocerida: new superorder Multiceratoidea. *GFF 135*(2), 171–183.

MUTVEI, H. 2015. Characterization of two new superorders Nautilosiphonata and Calciosiphonata and a new order Cyrtocerinida of the subclass Nautiloidea; siphuncular structure in the Ordovician nautiloid *Bathmoceras* (Cephalopoda). *GFF 137(3)*, 164–174.

MUTVEI, H. & DUNCA, E. 2011. Siphuncular structure in the orders Tarphycerida and Barrandeocerida (Cephalopoda: Nautiloidea). *Palaeontology 54(3)*, 705–710.

MUTVEI, H., ARNOLD, J.M. & LANDMANN, N.H. 1993. Muscles and attachment of the body to the shell in embryos and adults of *Nautilus belauensis* (Cephalopoda). *American Museum novitates no. 3059*, 1–15.

MUTVEI, H., ZHANG, Y-b. & DUNCA, E. 2007. Late Cambrian plectronocerid nautiloids and their role in cephalopod evolution. *Palaeontology 50*, 1327–1333.

NESIS, K.N. 1987. *Cephalopods of the world: squids, cuttlefishes, octopuses, and allies.* 351 pp. TFH Publications, New Jersey.

NESTOR, H. 1995. Ordovician and Silurian reefs in the Baltic area. *Publications du Service Géologique de Luxembourg 29*, 39–47.

NESTOR, H. & EINASTO, R. 1997. Ordovician and Silurian carbonate sedimentation basin, 192–204. *In* RAUKAS, A. & TEEDUMÄE, A. (eds) *Geology and mineral resources of Estonia.* Estonian Academy Publishers, Tallinn.

NIXON, M. & YOUNG, J.Z. 2003. *The brain and lives of cephalopods.* 448 pp. Oxford University Press, Oxford.

ÖHLANDER, B., SKIÖLD, T., ELMING, S.Å., CLAESSON, S. & NISCA, D.H. 1993. Delineation and character of the Archaean – Proterozoic boundary in northern Sweden. *Precambrian Research 64(1–4)*, 67–84.

PACKARD, A. 1972. Cephalopods and fish: the limits of convergence. *Biological Reviews 47(2)*, 241–307.

PARIS, F. & MERGL, M. 1984. Arenigian chitinozoans from the Klabava formation, Bohemia. *Review of Palaeobotany and Palynology 43(1–3)*, 33–65.

PÄRNASTE, H. & BERGSTRÖM, J. (2013). The asaphid trilobite fauna: Its rise and fall in Baltica. *Palaeogeography, Palaeoclimatology, Palaeoecology 389*, 64–77.

POLECHOVÁ, M. 2013. Bivalves from the Middle Ordovician Šárka Formation (Prague Basin, Czech Republic). *Bulletin of Geosciences 88(2)*, 427–461.

PUURA, I. & HOLMER, L.E. 1993. Lingulate brachiopods from the Cambrian – Ordovician boundary beds in Sweden. *Geologiska Föreningen i Stockholm Förhandlingar 115(3)*, 215–237.

PUURA, V., KLEIN, V., KOPPELMAA, H. & NIIN, M. 1997. Precambrian basement, 27–34. *In* RAUKAS, A. & TEEDUMÄE, A. (eds). *Geology and mineral resources of Estonia.* Estonian Academy Publishers, Tallinn.

RAK, S., BERGSTRÖM, J., FATKA, O. & BUDIL, P. 2009. The Upper Ordovician arthropod *Zonozoe drabowiensis* Barrande (Libeň and Letná formations, Sandbian, Barrandian area, Czech Republic). *Bulletin of Geosciences 84*, 185–188.

RAUKAS, A. & KAJAK, K. 1997. Quaternary cover, 125–136. *In* RAUKAS, A. & TEEDUMÄE, A. (eds). *Geology and mineral resources of Estonia.* Estonian Academy Publishers, Tallinn.

REIMOLD, W.U., KELLEY, S.P., SHERLOCK, S.C., HENKEL, H. & KOEBERL, C. 2005. Laser argon dating of melt breccias from the Siljan impact structure, Sweden: Implications for a possible relationship to Late Devonian extinction events. *Meteoritics & Planetary Science 40(4)*, 591–607.

REMELÉ, A. 1882. Ueber einige gekrümmte untersilurische Cephalopoden. *Zeitschrift der deutschen geologischen Gesellschaft 34*, 116–138.

RIDING, R. 2006. Microbial carbonate abundance compared with fluctuations in metazoan diversity over geological time. *Sedimentary Geology 185*, 229–238.

RISTEDT, H. 1968. *Zur Revision der Orthoceratidae.* Akademie der Wissenschaften und Literatur in Mainz. Abhandlungen der mathematisch-naturwissenschaftlichen Klasse.

ROBERTS, D. 2003. The Scandinavian Caledonides: event chronology, palaeogeographic settings and likely modern analogues. *Tectonophysics 365(1–4)*, 283–299.

ROWLAND, S.M. & SHAPIRO, R.S. 2002, Reef patterns and environmental influences in the Cambrian and Early Ordovician, 95–128. *In* KIESSLING, W., FLÜGEL, E. & GOLONKA, J. (eds.) *Phanerozoic Reef Patterns, Society for Sedimentary Geology, Special Publication 72.* Tulsa, Oklahoma.

RÜDIGER, H. 1889. *Über die Silur-Cephalopoden aus den mecklenburgischen Diluvialgeschieben.* 86 pp. Inaugural-Dissertation. Philosophischen Facultät der Universität Rostock, Güstrow.

RUZHENCEV, V.E. 1962. *Fundamentals of Palaeontology, Mollusca – Cephalopoda I Nautiloidea, Endoceratoidea, Actinoceratoidea, Bactritoidea, Ammonoidea (Agoniatitida, Goniatitida, Clymeniida).* 877 pp. Izd. ANSSSR, Moscow. [In Russian]

SÁ, A.A. & GUTIÉRREZ MARCO, J.C. 2009. Middle Ordovician cephalopods from the Valongo Formation, northern Portugal. *Geogaceta 47*, 9–12. [In Spanish]

SCHINDEWOLF, O.H. 1932. Zur Stammesgeschichte der Ammoneen. *Palaeontologische Zeitschrift 14*, 173–174.

SCHINDEWOLF, O.H. 1933. Vergleichende Morphologie und Phylogenie der Anfangskammern tetrabranchiater Cephalopoden. Eine Studie über Herkunft, Stammesentwicklung und System der niederen Ammoneen. *Preubischen Geologischen Landesanstalt 148*, 67–73.

SCHINDEWOLF, O.H. 1944. Über das Apikalende der Actinoceren. *Jahrbuch des Reichsamtes für Bodenforschung 62*, 207–247.

SCHMIDT, F. 1858. Untersuchungen über die Silurische Formation von Ehstland, Nord-Livland und Oesel. Archiv für die Naturkunde Liv- Ehst- and Kurlands 1–2, 1–248.

SEPKOSKI, J.J., Jr. 1978. A kinetic mode of Phanerozoic taxonomic diversity. I. Analysis of marine orders. *Paleobiology 4*, 223–251.

SEPKOSKI, J.J., Jr. 1979. A kinetic model of Phanerozoic taxonomic diversity, II. Early Phanerozoic families and multiple equilibria. *Paleobiology 5*, 222–251.

SEPKOSKI, J.J., Jr. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology 7*, 36–53.

SEPKOSKI, J.J., Jr. 1984. A kinetic model of Phanerozoic taxonomic diversity. Part 3, Post-Paleozoic families and multiple equilibria. *Paleobiology 10*, 246–267.

SERVAIS, T. & FATKA, O. 1997. Recognition of the Trans-European-Suture-Zone (TESZ) by the palaeobiogeographical distribution pattern of Early to Middle Ordovician acritarchs. *Geological Magazine 134 (5)*, 617–625.

SERVAIS, T. & SINTUBIN, M. 2009. Avalonia, Armorica, Perunica: terranes, microcontinents, microplates or palaeobiogeographical provinces?. *Geological Society, London, Special Publications 325*, 103–115.

SERVAIS, T. & HARPER, D.A. 2018. The Great Ordovician Biodiversification Event (GOBE): definition, concept and duration. *Lethaia 51(2)*, 151–164.

SERVAIS, T., LEHNERT, O., LI, J., MULLINS, G.L., MUNNECKE, A. & VECOLI, M. 2008a. The Ordovician biodiversification: revolution in the oceanic trophic chain. *Lethaia 41*, 99–109.

SERVAIS, T., DZIK, J., FATKA, O., HEUSE, T., VECOLI, M. & VERNIERS, J. 2008b. Ordovician, 203–248. *In* McCANN, T. (ed) *The Geology of Central Europe, Volume 1: Precambrian and Palaeozoic.* Geological Society, London.

SERVAIS, T., OWEN, A.W., HARPER, D.A.T., KRÖGER, B. & MUNNECKE, A. 2010. The Great Ordovician Biodiversification Event (GOBE): the palaeoecological dimension. *Palaeogeography, Palaeoclimatology, Palaeoecology 294*, 99–119.

SHEVYREV, A.A. 2006a. The cephalopod macrosystem: A historical review, the present state of knowledge, and unsolved problems: 2. Classification of nautiloid cephalopods. *Paleontological Journal 40*, 46–54.

SHEVYREV, A.A. 2006b. The Cephalopod macrosystem: A historical review, the present state of knowledge, and unsolved problems: 3. Classification of Bactritoidea and Ammonoidea. *Paleontological Journal 40(2)*, 150–161.

SHIMANSKY, V.N. & ZHURAVLEVA, F.A. 1961, Fundamental questions of the systematics of the nautiloids and the relationship of this group. *Trudy Paleontologitscheskogo Instituta Akademii Nauk 90*, 1–175. [In Russian]

SHIMIZU, S. & OBATA, T. 1935. On some new genera of Ordovician nautiloids from East Asia. *The Journal of the Shanghai Science Institute 2(2)*, 11–25.

SOHRABI, A. & JIN, J. 2013. Global palaeobiogeography of brachiopod faunas during the early Katian (Late Ordovician) greenhouse episode. *Palaeogeography, Palaeoclimatology, Palaeoecology 389*, 78–86.

STAROBOGATOV, Y.I. 1983. The System of Cephalopod Mollusks. Systematics and Ecology of Cephalopod Mollusks. *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR*, 4–7. [In Russian]

STAIT, B., WEBBY, B.D. & PERCIVAL, I.G. 1985. Late Ordovician nautiloids from Central New South Wales, Australia. *Alcheringa 9*, 143–157.

ŠTORCH, P. & MERGL, M. 1989. Králodvor/Kosov Boundary and the late Ordovician environmental changes in the Prague Basin (Barrandian area, Bohemia). *Sborník geologických věd, Geologie 44*, 117—153.

STRANGWAYS, W.T.H.F. 1821. Geological sketch of the environs of Petersburg. *Transactions of the Geological Society of London 5*, 392–458.

STRENZEL, H.B. 1964. Living *Nautilus*, K59–K93. In MOORE, R.C. (ed.) *Treatise on invertebrate paleontology. Part K. Mollusca 3. Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea.* GSA and University of Kansas Press, Lawrence, Kansas, USA.

STRAND, T. 1934. The Upper Ordovician Cephalopods of the Oslo Area. *Norsk geologiske Tidsskrift 14*, 1–117.

STRIDSBERG, S. 1985. Silurian oncocerid cephalopods from Gotland. *Fossils and Strata 18*, 1–65.

STUMBUR, H.A. 1962. Rasprostranenie nautiloidei v ordovike Estonii (s opisaniem nekotorykh novykh rodov). *Trudy Instituta Geologii Akademii Nauk Estonskoi SSR (ENSV Teaduste Akadeemia Geoloogia Instituudi Uurimused) 10*, 131–147. [In Russian]

SWEET, W.C. 1958. The middle Ordovician of the Oslo region, Norway. 10. Nautiloid cephalopods. *Norsk Geologisk Tidsskrift 38*, 1–176.

SWEET, W.C. 1959. Muscle attachment impressions of some Paleozoic nautiloid cephalopods. *Journal of Paleontology 33*, 293–305.

SWEET, W. 1964. Nautiloidea – Orthocerida, 216–261. In MOORE, R.C. (ed.) *Treatise on Invertebrate Paleontology, Part K, Mollusca.* Geological Society of America, Lawrence.

SWEET, W., TEICHERT, C. & KUMMEL, B. 1964. Phylogeny and Evolution, K106–116. In MOORE, R.C. (ed.) *Treatise on Invertebrate Paleontology, Part K, Mollusca.* Geological Society of America, Lawrence.

TEICHERT, C. 1933. Der Bau der Actinoceroiden Cephalopoden. *Palaeontographica A 78*, 111–230.

TEICHERT, C. 1964a. Morphology of Hard Parts, K13–K59. In MOORE, R.C. (ed.) *Treatise on invertebrate paleontology. Part K. Mollusca 3. Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea.* GSA and University of Kansas Press, Lawrence, Kansas, USA.

TEICHERT, C. 1964b. Actinoceratoidea, K190–K216. In MOORE, R.C. (ed.) *Treatise on invertebrate paleontology. Part K. Mollusca 3. Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea.* GSA and University of Kansas Press, Lawrence, Kansas, USA.

TEICHERT, C. 1988. Main features of cephalopod evolution, 11–79. *In* CLARKE, M.R. & TRUEMAN, E.R. (eds) *The Mollusca.* Academic Press, San Diego.

TEICHERT, C. & KUMMEL, B. 1960. *Size of endoceroid cephalopods.* Harvard University, Museum of Comparative Zoology.

TOBIN, K., BERGSTRÖM, S.M. & DE LA GARZA, P. 2005. A mid-Caradocian (453 Ma) drawdown in atmospheric pCO2 without ice sheet development?. *Palaeogeography, Palaeoclimatology, Palaeoecology 226(3–4)*, 187–204.

TÖRNQUIST, S.L. 1871. Geologiska iakttagelser öfver den kambriska och siluriska lagföljden i Siljanstrakten. *Öfversigt af Kongliga Vetenskapsakademiens Förhandlingar 28*, 83–129.

TORSVIK, T. 1998. Palaeozoic palaeogeography: a North Atlantic viewpoint. *Geologiska Foreningens Forhandlinger 120*, 109–118.

TORSVIK, T.H. & COCKS, L.R.M. 2005. Norway in space and time: a centennial cavalcade. *Norwegian Journal of Geology (Norsk Geologisk Forening) 85*, 73–86.

TORSVIK, T.H. & COCKS, L.R.M. 2013. Gondwana from top to base in space and time. *Gondwana Research 24*, 999–1030.

TORSVIK, T.H. & COCKS, L.R.M. 2017. *Earth History and Palaeogeography.* Cambridge University Press. Cambridge.

TUREK, V. & MANDA, Š. 2012. "An endocochleate experiment" in the Silurian straight-shelled cephalopod *Sphooceras*. *Bulletin of Geosciences 87*, 767–813.

TUULING, I. & FLODÉN, T. 2000. Late Ordovician carbonate buildups and erosional features northeast of Gotland, northern Baltic Sea. *GFF 122*, 237–49.

VON DALWIGK, I. & KENKMANN T., 2000: The Siljan impact structure: New constraints for a diameter reconstruction. *Proceedings, 23rd Nordic Geological Winter Meeting, 24.*

WALCOTT, C.D. 1905. Cambrian faunas of China. *US National Museum, Proceedings 29*, 1–106.

WATKINS, R. 1991. Guild structure and tiering in a high-diversity Silurian community, Milwaukee County, Wisconsin. *Palaios 6*, 465–478.

WARD, P. 1982. The relationship of siphuncle size to emptying rates in chambered cephalopods: implications for cephalopod paleobiology. *Paleobiology 8(4)*, 426–433.

WARD, P.D. & SAUNDERS, B. 1997. *Allonautilus*: a new genus of living nautiloid cephalopod and its bearing on phylogeny of the Nautilida. *Journal of Paleontology 71(6)*, 1054–1064.

WEBBY, B.D. 1984. Ordovician reefs and climate: a review, 89–100. In BRUTON. D.L. (ed.) *Aspects of the Ordovician System. Palaeontological Contributions from the University of Oslo 295.* Universitetsforlaget.

WEBBY, B.D. 2002. Patterns of Ordovician reef development, 129–179. *In* KIESSLING, W., FLÜGEL, E. & GOLONKA, J. (eds) *Phanerozoic Reef Patterns, Society for Sedimentary Geology Special Publication 72.* Tulsa, Oklahoma.

WEBBY, B.D., PARIS, F., DROSER, M.L., & PERCIVAL, I.G. 2004. *The Great Ordovician Biodiversification Event.* 484 pp. Columbia University Press. New York.

WEBERS, G.F., POJETA, J. & YOCHELSON, E.L. 1992. Cambrian mollusks from the Minaret Formation, p. 181–294. *In* WEBERS, G.F., CRADDOCK, C. & SPLETTOESSER J. F. (eds.) *Geology and paleontology of the Ellsworth Mountains, West Antarctica. Geological Society of America Memoir 170.*

WESTERMANN, G.E.G. 1977. Form and function of orthoconic cephalopod shells with concave septa. *Paleobiology 3(3)*, 300–321.

WESTERMANN, G.E.G. 1998. Life habits of nautiloids, 263–298. *In* Savazzi, E. (ed.) *Functional morphology of the invertebrate skeleton.* Wiley and Sons, New York.

WICKMAN, F.E., BLOMQVIST N.G., GEIJER P., PARWEL A.V., UBISCH H. & WELIN E. 1963. Isotopic constitution of ore lead in Sweden. *Arkiv för Mineralogi och Geologi 3*, 193–257.

WIERZBOWSKI, H. 2004. Carbon and oxygen isotope composition of Oxfordian–Early Kimmeridgian belemnite rostra: palaeoenvironmental implications for Late Jurassic seas. *Palaeogeography, Palaeoclimatology, Palaeoecology 203(1–2)*, 153–168.

XIAO, C., CHEN, Z., LIU, L. & HE, Y. 2006. Ordovician cephalopod biofacies of South China and its provincialization. *Journal of China University of Geoscience 17*, 221–230.

XU, G.-h. & LAI, C.-g. 1983. Cephalopods from the Sanyoudong Group of Yichang, Hubei Province. *Bulletin of the Yichang Institute of Geology and Mineral Resources 6*, 183–209. [In Chinese]

XU, G.-h. & LAI, C.-g. 1987. Cephalopods, 245–293. *In* XIAOFENG, W. (ed.) *Biostratigraphy of the Yangtze Gorge area, Volume 2, Early Palaeozoic area.* Geological Publishing House, Beijing.

YOCHELSON, E.L., FLOWER, R.H. & WEBERS, G.F. 1973. The bearing of the new Late Cambrian monoplacophoran genus *Knightoconus* upon the origin of the Cephalopoda. *Lethaia 6*, 275–310.

YUN, CH.-s. 1999. Three Ordovician cephalopods from the Jigusan Formation of Korea. *Paleontological Research 3(2)*, 65–80.

YUN, CH.-s. 2002. Faunal and Biogeographical Characteristics of the Ordovician Cephalopods from Korea. *Abhandlungen der geologischen Bundesanstalt 57*, 555–569.

YUN, CH.-s. 2003. Further study of the Middle Ordovician cephalopod Holmiceras coreanicum with a revision of two Geisonoceras species from Korea. *Paleontological Research, Short Notes 7(4)*, 363–366.

ZHURAVLEVA, F.A. 1972. Devonskie nautiloidei Otrjad Discosorida. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR 134*, 1–320.

ZHURAVLEVA, F.A. & BALASHOV, Z.G. 1981. On the early ontogenesis of the actinoceroids. *Paleontological Journal 15*:14–27.

ZHURAVLEVA, F.A. 1994. The order Dissodocerida (Cephalopoda). *Paleontological Journal 28(1)*,115–133.

ZIEGLER, P.A. 1989. *Evolution of Laurussia – a study in Late Palaeozoic plate tectonics.* 102 pp. Kluwer, Dordrecht.

ZIEGLER, P.A. 1990. *Geological atlas of western and central Europe.* Geological Society of London.

ZOU, X.-p. 1987. Ordovician nautiloid faunas of Yuhang and lin'an, Zhejiang Province. *Bulletin of the Nanjing Institute of Geology and Paleontology 12*, 231–289. [In Chinese]

7. List of Appendices

Appendix 1:
Aubrechtová, M. 2015. A revision of the Ordovician cephalopod *Bactrites sandbergeri* Barrande: systematic position and palaeobiogeography of *Bactroceras*. *Geobios 48(3)*, 193–211. DOI: 10.1016/j.geobios.2015.03.002

Appendix 2:
Aubrechtová, M. & **Meidla, T. 2016**. The oldest ascocerid cephalopod from the Silurian of Estonia and notes on the biogeography of the order Ascocerida (class Cephalopoda). *Estonian Journal of Earth Sciences 65(2)*, 98–104. DOI: 10.3176/earth.2016.07

Appendix 3:
Kröger, B. & **Aubrechtová, M. 2018.** Cephalopods from reef limestone of the Vasalemma Formation, northern Estonia (latest Sandbian, Upper Ordovician) and the establishment of a local warm-water fauna. *Journal of Systematic Palaeontology 16(10)*, 799–839. DOI: 10.1080/14772019.2017.1347212

Appendix 4:
Kröger, B. & **Aubrechtová, M. 201X**. The cephalopods of the Kullsberg Limestone Formation, Upper Ordovician, central Sweden and the effects of reef diversification on cephalopod diversity. *Journal of Systematic Palaeontology*, accepted. DOI: 10.1080/14772019.2018.1491899

Appendix 5:
Aubrechtová, M. & **Turek, V. 201X**. Lituitid nautiloids from the Middle Ordovician of Bohemia and their paleobiogeographic affinities. *Bulletin of Geosciences*, accepted.