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Belemniti spodní křídy (a hraničního intervalu hranice J/K) oblasti severozápadní Tethydy, biostratigrafie, paleobiogeografie a paleoekologie

Lower Cretaceous belemnites (including J/K boundary interval) in the NW Tethys, biostratigraphy, palaeobiogeography and palaeoecology

Typ závěrečné práce:

Disertační práce

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doc. RNDr. Martin Košťák, Ph.D.

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Předkládaná disertační práce se zabývá belemnitovou faunou z oblasti Vnějších Západních Karpat, jejím systematickým určením a stratigrafickým a paleogeografickým zhodnocením. Spolu s izotopovými analýzami, zahrnujícími jak stabilní izotopy kyslíku a uhlíku, tak izotopy stroncia, vytváří komplexní obraz paleoekologických podmínek v období jursko-křídové hranice a spodní křídy. Belemniti nejsvrchnějšího tithonu a hraničního intervalu J/K nejsou obecně příliš dobře prostudovaní, jelikož se na studovaných profilech vyskytují zřídka, nebo sedimentární podmínky nejsou vhodné pro jejich zachování. Rostra belemnitů jsou tak v mediteránní provincii popsána pouze z několika lokalit. Na základě posledních výzkumů byl stratigrafický rozsah některých původně tithonských druhů rozšířen o nejspodnější křídu. Oproti tomu jsou spodnokřídoví belemniti (od pozdního berriasu) relativně rozšíření. V tethydní říši je možné studovat spodnokřídovou belemnitovou faunu v dobrém detailu a dle jejich četného zachování, také stanovit jednotlivá společenstva odpovídajcí stratigrafickým intervalům. Navíc lze modelovat jejich palebiogeografické rozšíření a případné migrace. Specifické podmínky a typ sedimentární asociace, ve které bylo rostrum uloženo, nabízí možnost zkoumání ekologických preferencí, které jednotlivé druhy upřednostňovaly během života. Studium izotopových poměrů z kalcitových (nízkohořečnatých) roster navíc dokreslí celkový obraz, kde jednotlivé poměry odráží chemické složení mořské vody. Studované společenstvo poukazuje na vysoký stupeň diverzity belemnitové fauny žijící v oblasti severovýchodního okraje oceánu Tethys. Taxonomickému zhodnocení bylo podrobeno více než 10,000 roster belemnitů, z nichž bylo identifikováno společenstvo zahrnující dvě čeledi a 28 druhů s 12 blíže neurčenými taxony. Stratigrafický rozsah studovaných roster zaujímá stupně spodní tithon až střední barrem, kde naprostá většina materiálu tvořila akumulace belemnitů různého stáří a paleprostředí. Podle charakteristiky jednotlivých asociací se podařilo stanovit jednotlivé stratigrafické stupně a v závislosti na batymetrických nárocích také vymodelovat vývoj studované oblasti Vnějších Západních Karpat. Bylo zjištěno, že po relativně mělkovodním období panujícím ve studované oblasti od tithonu do berriasu, došlo ve valanginu a pravděpodobně také v ?hauterivu k nastolení hlubokovodního režimu, který byl následně změlčen opět v období barremu. Paleogeograficky odpovídají určení belemniti mediteránní provincii a během hauterivu a barremu pak studovaná fauna vykazuje afinitu k francouzsko-bulharské subprovincii. Mimo tyto dvě lokace jsou belemniti Vnějších Západních Karpat nejvíce podobní materiálu ze Španělska, Francie, Maroka, Maďarska a Itálie. Izotopy stroncia se ukázaly obzvláště přínosné při deteminaci stáří jednotky, kde hodnoty vykazovaly stáří nejspodnějšího berriasu a na studované sekvenci vyvrátili

přítomnost tithonu. Stabilní izotopy kyslíku a uhlíku pak vykazují srovnatelný negativní trend bez výrazných odchylek, klasický pro oblast severní tethydní říše.

Abstract

This thesis deals with the belemnite fauna from the Outer Western Carpathians Klippen, its systematic classification, stratigraphical and palaeogeographical evaluation. The palaeontological/palaeobiological approach, together with isotope analyses, including of carbon and oxygen stable isotopes and of strontium isotopes, enabled an integrated investigation of the palaeoecological conditions during the Jurassic/Cretaceous (J/K) boundary interval and the Early Cretaceous age. The Tethyan belemnites are not intensively studied in detail in the J/K interval, as they occur rather rarely in the sections, and/or sedimentary conditions were not suitable for their preservation. Therefore, belemnites are described only from a few sites in the Mediterranean Province. On the basis of recent research, the stratigraphic range of several species previously considered to be from the Tithonian age was extended to the earliest Cretaceous. By contrast, the Lower Cretaceous belemnites (since the late Berriasian) are more abundant. In the classical areas of the Tethyan Realm, it is possible to study the Lower Cretaceous belemnites in great detail and, according to their higher abundance, to determine an individual assemblage corresponding to stratigraphical intervals. Their occurrence is also an important basement for palaeobiogeography and for recognition of migration patterns. Belemnite original habitats offer further evaluation of ecological preferences. Additionally, the study of isotope ratios from calcitic (Mg-low) rostra significantly helps with interpretation of the palaeoenvironment. The studied assemblages show a relatively high belemnite diversity of the NW edge of the Tethys Ocean. For taxonomic evaluation, more than 10,000 belemnite rostra were systematically studied: two families, six genera and 28 species with 12 taxa in open nomenclature were identified. Stratigraphic range of the studied rostra ranges from the Lower Tithonian to the late early/early late Barremian. The majority of material represents allochtonous accumulations of belemnites originating at different stratigraphical levels and palaeoenvironmental habitats. According to determined belemnites at species levels, individual stratigraphic intervals were confirmed. Individual taxa are more or less bathymetrically dependent, therefore they have been used for reconstruction of the geological/environmental history of a Klippen part of the Outer Western Carpathians. After a relatively shallow water period in the Tithonian to Berriasian interval, deeper water conditions were established during the Valanginian and probably the ?Hauterivian. After the Barremian, the area turned to shallow-water conditions again. Palaeobiogeographically determined

belemnite rostra correspond to the Mediterranean Province and to the French-Bulgarian Subprovince established since the Hauterivian. Belemnites from the Outer Western Carpathians show the closest similarity to Spanish, French, Moroccan, Hungarian and Italian belemnite faunas. The strontium isotope values obtained from belemnite rostra at Štramberk clearly proved the early Berriasian age and refute the presumption of the Tithonian strata in the studied sections. Carbon and oxygen stable isotopes follow a comparable negative trend without significant deviations, typical for the northern Tethyan Realm.

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Contents

1. Introduction

Belemnites were rather shallower water/shelf animals, morphologically resembling Recent squids (e.g. Hoffmann and Stevens, 2020). They were active predators with great locomotion, torpedo-shape bodies, and a unique buoyancy system (Spaeth, 1975; Monks et al., 1996; Rexfort and Mutterlose, 2009; Stevens et al., 2014, etc.). Belemnites formed an important component in the trophic chain of the Jurassic and Cretaceous seas. In the course of favourable conditions, belemnites migrated from warm water areas into the cooler water regions of the Boreal Realm (e.g. Mutterlose, 1979; Alsen and Mutterlose, 2009); however, opposite trends are also reported. Generally, belemnites are considered to be stenohaline animals living in well oxygenated waters (e.g. Hoffmann and Stevens, 2020). During their lifetime, they formed a conical calcitic internal shell (rostrum), composed by horizontal alternating laminae intersected by a radial crystal structure. The rostrum is the most commonly preserved part of the belemnite inner shell, and systematic classification is based on its morphology.

Belemnites represent stratigraphically and palaeogeographically important fossils, and are also used as an index fossil. In addition, belemnite rostra serve as archives of environmental changes, thanks to their ability to record a signal of conditions of ambient seawater during belemnite growth/life (e.g. Wierzbowski and Joachimski, 2009; Armendáriz et al., 2012; Ullmann et al., 2014; Stevens et al., 2017). Calcitic rostrum has been processed for the first time as a material for analysing stable isotope data by Urey (1948). Recently, the isotope methods are abundantly used mainly for palaeoenvironmental reconstructions and chemostratigraphy (van de Schootbrugge et al., 2000; McArthur et al., 2004, 2007a; Bodin et al., 2009; Mutterlose et al., 2010; Žák et al., 2011; Price et al., 2011, 2016, etc.). The strontium isotopes represent chemostratigraphical potential, and the global Sr curve is refined based mainly on belemnite rostra (e.g. Jones et al., 1994; Price and Gröcke, 2002; Wierzbowski et al., 2017). Therefore, belemnites constitute an important stratigraphical marker (Podlaha et al., 1998; McArthur et al., 2007a, b; Bodin et al., 2009, 2015, etc.).

In contrast to the Jurassic–Cretaceous boundary interval, the Lower Cretaceous belemnites are relatively well investigated in the northern Tethyan Realm (e.g. Krimholz, 1939; Combémorel, 1973; Combémorel and Mariotti, 1986a, b, 1990; Doyle and Mariotti, 1991; Weiss, 1991; Janssen, 1997; Főzy et al., 2011; Hoedemaeker et al., 2016). According to extensive material studied in recent decades, mainly from France, Spain, Bulgaria, Morocco and Hungary (Stoyanova-Vergilova, 1963, 1965a, b, 1970; Janssen, 1997, 2003, 2009, 2010, 2018, 2020; Clément, 1999, 2000; Janssen and Clément, 2002; Janssen and Főzy, 2004, 2005; Mutterlose and Wiedenroth, 2008; Főzy and Janssen, 2009; Főzy et al., 2010, 2011; Janssen et al., 2012; Hoedemaeker et al., 2016, etc.), modern taxonomic classifications with several palaeoecological implications were provided. In the Outer Western Carpathians, however, only a few papers dealing with belemnites were published in the past (Oppel, 1865; Zittel, 1868; Uhlig, 1883, 1902; Vašíček, 1978; Horák, 1988; Michalík and Vašíček, 1989; Vašíček et al., 1994). Despite a huge number of recorded belemnite rostra, a detailed stratigraphic determination as well as the palaeobiogeographic framework were not investigated in great detail. Accumulations of rostra in complicated geological structures with intensive and repeated tectonic history make our investigations difficult. However, according to recent works and comparison with bed-by-bed sampled sections (Janssen and Clément, 2002; Janssen 2003, 2009, 2020; Mutterlose and Wiedenroth 2008; Főzy et al., 2010; Janssen et al., 2012), a modern taxonomic evaluation in relation to stratigraphic identification could be applied.

At the Štramberk locality, extensive geological/stratigraphical investigations concerning the development of this area have been performed (Vašíček and Skupien 2004, 2005 and references therein). This famous locality with the still working Kotouč Quarry was studied mainly by palaeontological methods (macro- and micro-fossils) (Vašíček, 1978; Houša, 1990; Houša and Vašíček, 2005, Svobodová et al., 2011; Vašíček and Skupien, 2016, etc.) and partly by magnetostratigraphy (Houša et al., 1992, unpublished report). However, an accurate age of the Štramberk Limestone unit was not deciphered, but thanks to newly investigated belemnite rostra, this question has already been partly refined. Moreover, the individual belemnite taxa provided important information reflecting palaeoenvironmental conditions and changes. At the Kurovice locality, belemnites are rather scarce, but they are exclusively preserved in the deeper carbonate sediments, below the ACD (Eliáš et al., 1996; Košťák et al., 2018). The Kurovice Quarry has been the subject of investigations, mainly for the speculative mutual occurrence of Jurassic and Cretaceous fossils in the past (*see* Eliáš et al., 1996 and references therein). The Kurovice section has also been selected as one of the possible stratotype of the J/K boundary by GSSP and the Berriasian Working Group (Elbra et al., 2018; Svobodová et al., 2019; Wimbledon et al., 2020a).

The aim of the belemnite research in the NW Tethys area was to provide a modern taxonomic evaluation of belemnites, including detailed morphological and ontogenetical studies. Based on these investigations, we were able to compare these belemnites within other

Tethyan areas and sections. Subsequently, according to detailed biostratigraphy known from other sites and from palaeobiogeographic distributions, we have partly deciphered a complicated geological history of the studied area. On the basis of bathymetric preferences of taxa, we have introduced the palaeoenvironmental model into which we integrate the Outer Western Carpathians in a broader context. However, this hypothesis needs to be tested in the future. Finally, based on geochemical analyses of oxygen and carbon stable isotopes and of strontium isotopes from belemnite rostra, we have provided a refinement of palaeoecological conditions and stratigraphic interpretations in this Klippen part of the Outer Western Carpathians.

1.1 Full publication list

Publications included in this thesis:

This Ph.D. thesis is based on following publications, referred further in Roman numerals in bold.

I. Košťák, M., **Vaňková, L.**, Mazuch, M., Bubík, M., Reháková, D., **2018**. Cephalopods, small vertebrate fauna and stable isotope ($\delta^{13}C$, $\delta^{18}O$) record from the Jurassic-Cretaceous transition (uppermost Crassicollaria through Calpionella Zones) of the Outer Western Carpathians, Kurovice quarry (Czechia). *Cretaceous Research* 92, 43-65.

II. Vaňková, L., Elbra, T., Pruner, P., Vašíček, Z., Skupien, P., Reháková, D., Schnabl, P., Košťák, M., Švábenická, L., Svobodová, A., Bubík, M., Mazuch, M., Čížková, K., Kdýr, Š., **2019**. Integrated stratigraphy and palaeoenvironment of the Berriasian peri-reefal limestones at Štramberk (Outer Western Carpathians, Czech Republic). *Palaeogeography, Palaeoclimatology, Palaeoecology* 532, 109256. https://doi.org/10.1016/j.palaeo.2019.109256

III. Wimbledon, W.A.P., Reháková, D., Svobodová, A., Elbra, T., Schnabl, P., Pruner, P., Šifnerová, K., Kdýr, Š., Dzyuba, O., Schnyder, J., Galbrun, B., Košťák, M., **Vaňková, L.**, Copestake, P., Hunt, C.O., Riccardi, A., Poulton, T.P., Bulot, J.G., Frau, C., De Lena, L., **2020a**. The proposal of a GSSP for the Berriasian Stage (Cretaceous System): Part 1. *Volumina Jurassica* XVIII, 53-106.

IV. Vaňková, L., Košťák, M., Mazuch, M., **2021**. Lower Cretaceous belemnites of Štramberk klippen (Czech Republic): Implications for geological history of the Outer Western Carpathians. *Cretaceous Research*, in review.

Publication on related topic but not included in this thesis:

Wimbledon, W.A.P., Reháková, D., Svobodová, A., Elbra, T., Schnabl, P., Pruner, P., Šifnerová, K., Kdýr, Š., Frau, C., Schnyder, J., Galbrun, B., **Vaňková, L.**, Dzyuba, O., Copestake, P., Hunt, C.O., Riccardi, A., Poulton, T.P., Bulot, J.G., De Lena, L., **2020b**. The proposal of a GSSP for the Berriasian Stage (Cretaceous System): Part 2. *Volumina Jurassica* XVIII (2), 119-158.

Focus of included studies:

Study I. Deep water environment with submarine slump from shallow water areas, Kurovice section, J/K boundary and the lowermost Berriasian

This study is focused on macro-faunal composition from several beds and a 'tsunamite-like' episode in the lowermost Berriasian. Environmental changes (investigation based on variations of the $\delta^{13}C_{carb}$, $\delta^{18}O_{carb}$) through the J/K boundary interval helped provide an understanding of conditions in a deep carbonate sedimentation below the aragonite compensation depth (ACD). According to well calibrated calpionellid stratigraphy, it was possible to precisely identify individual levels and significant changes in the sedimentary record. Macrofossils were analysed by modern taxonomic methods with a focus on palaeoecological dependences. The author was responsible for systematic determination of belemnite rostra, and their palaeoecological and palaeobiogeographical interpretations. Stratigraphic distribution of belemnites was highly desirable for age determination of the turbidite structure.

Study II. Carbonate platform and reef slope/talus, Kotouč Quarry sections, lower Berriasian

This study represents a multiproxy research of two profiles in a shallow water environment. Peri-reefal limestones have been intensively reviewed by numerous stratigraphical methods concerning micro- and macrofossil markers, magnetostratigraphy and geochemical data. A thorough microfacies analysis in combination with fossil content and isotopic evaluation resulted in complex palaeoecological and palaeoenvironmental assessment. Unique use of strontium isotopes ($^{87}Sr/^{86}Sr$, their respective values) from belemnite rostra fully demonstrated an early Berriasian age. The author was responsible for the entire preparation setup of belemnite rostra, its taxonomic evaluation and application of isotope methodologies. The laboratory work involved several procedures, from the collection of material, sample preparation, selection of suitable samples and participation during its analysing to stratigraphical and palaeoecological interpretation of results. The author also significantly contributed to the overall evaluation of the results and final summary and conclusions.

Study III. Various sedimentation environments, Tethyan Realm, J/K boundary

This study summarised several years of research of the Tithonian–Berriasian interval from numerous key localities. Possibilities for correlations were set mainly by magnetostratigraphy and biostratigraphy (mostly calpionellid data) with several secondary markers and proxies, e.g. radiometric dating, stable isotope records and Sr analyses. The combination of methods provided a complete overview of palaeoenvironmental changes in the J/K interval and their comparison within the studied profiles. The author was responsible for the study and interpretation of strontium isotopes obtained from belemnite rostra of the Tethyan Realm. Also, comparison of isotopic values from the Tethyan belemnite rostra with those from the Boreal Realm was performed by the author.

Study IV. Shelf–pelagic sedimentation in several environments, Kotouč Quarry, ?latest Tithonian–'mid' Barremian

This study deals with a huge and abnormal quantity of belemnite rostra accumulated at one place (Š-12 pocket). Detailed analyses of belemnite assemblage proved diversified fauna and, surprisingly, also a long sedimentation interval with several reworking episodes during the Lower Cretaceous. A combination of systematic, stratigraphic, palaeogeographic and sedimentary research (infills of belemnite alveolas) resulted in a broad overview of palaeoenvironmental conditions in studied intervals and served as a key to the history of the development of the Štramberk area. The research is given in the context of other localities, especially within the Tethyan Realm. The author was responsible for taxonomic classification, morphological analyses, palaeobiogeographical and palaeoecological interpretations. Stratigraphic outputs and modelling of sedimentation area development were also performed by the author. Moreover, the author was highly involved in final decisions and the interpretation of results.

The presented studies are based on high-quality modern taxonomic classification containing morphometry, an understanding of morphological changes with intraspecific variability, ontogeny and potential sexual dimorphism of some species. The genera and species present are compared and consulted with numerous other localities within the Tethys Ocean and have also been studied in relation to the Boreal Realm. Overall, the most important parameters obtained from the belemnite rostra used are systematic and taxonomy, biostratigraphy levels and recognition of palaeoenvironmental/geological events. According to specific fauna occurrence, the palaeobiogeographic distribution of species and the relation to an exact bioprovince (subprovince) has been clarified. The identified palaeoenvironmental changes and associated geological development were highly beneficial, even in the case where standard methods reached their limits. Therefore, belemnite rostra represent a great marker for refining the slump structure and/or for multiple reworking processes. Palaeoecological interpretation was also possible, on the basis of geochemical analyses that focused on the stable isotopes of oxygen and carbon, and on the strontium isotopes. All studied belemnite rostra are of the Late Jurassic (Tithonian) to Early Cretaceous (Berriasian–Barremian) age and come from the NE Tethys (Circum-Mediterranean Province and French-Bulgarian belemnite Subprovince). Belemnites were collected from two different (shallow and deep water) environments recently located in the Outer Western Carpathians.

1.2 Conference contributions

Vaňková, L., 2016. Early Cretaceous belemnites from locality Štramberk (taxonomy, stratigraphy and palaeoecology). 17th Czech-Slovak-Polish Palaeontological Conference, Kraków. Abstracts volume, *Polish Geological Institute*, ISBN 978-83-7863-666-3, p. 88.

Vaňková, L., 2017. Taxonomy and stratigraphy of the Lower Cretaceous belemnites from Štramberk (Czech Republic, Outer Western Carpathians) In: Sames, B. (Ed): 10th International Symposium on the Cretaceous. Vienna. Abstracts volume, *Berichte der Geologischen Bundesanstalt*, 120, 102, Vienna, ISSN 1017-8880, p. 267.

Košťák, M., **Vaňková, L.,** Mazuch, M., 2017. Stable isotope record ($\delta^{13}C$, $\delta^{18}O$), invertebrates and small vertebrate fauna from the Jurassic-Cretaceous transition of the Kurovice quarry (Czech Republic, Outer Western Carpathians) In: Sames, B. (Ed): 10th International Symposium on the Cretaceous. Vienna. Abstracts volume, *Berichte der Geologischen Bundesanstalt*, 120, 102, Vienna, ISSN 1017-8880, p. 147.

Vaňková, L., Košťák, M., 2017. The earliest Cretaceous (Berriasian) belemnites from Štramberk (Silesian Unit, Outer Western Carpathians), stratigraphy and stable isotope record. In: Šimon et al. (Ed): Zborník abstraktov a exkurzný sprievodca Otvoreného geologického kongresu Vysoké Tatry 2017. Open geological congress Vysoké Tatry + 18th Czech-Slovak-Polish Paleontological Conference, Stará Lesná. Abstract volume, *Mente et Malleo (MEM, Spravodajca slovenskej geologickej spoločnosti)*, ISSN 2453-096X, p. 109.

Vaňková, L., Košťák, M., Mazuch, M., 2018. Belemnite diversity of the J/K boundary interval in the NE Tethys (Outer Western Carpathians, Czech Republic) and their implication for palaeoecology and stratigraphy. 10th International Symposium "Cephalopods – Present and Past", Fes. Abstracts volume, *Münstersche Forschungen Zur Geologie Und Paläontologie*, 110, ISSN 0368-9654, pp. 103-104.

Košťák, M., **Vaňková, L.,** Mazuch, M., Bubík, M., Reháková, D., 2018. Macrofauna and stable isotope record ($\delta^{13}C$, $\delta^{18}O$) from the J/K transition of the Kurovice section (Outer Western Carpathians). Workshop of the ICS Berriasian Working Group, Kroměříž.

Vaňková, L., 2018. Taxonomy and stratigraphy of the Lower Cretaceous belemnites from Štramberk (Czech Republic, Outer Western Carpathians). 19th Czech-Slovak-Polish Palaeontological Conference, Prague. Abstracts volume, *Folia Musei rerum naturalium Bohemiae occidentalis. Geologica et paleobiologica* 52 *(Special volume)*, ISSN 1805-2371, p. 92.

Vaňková, L., 2018. Taxonomy and palaeoecological implications of the J/K interval belemnites (Outer Western Carpathians, Czech Republic). In: Leonova, T.B,, Barskov, I.S., Mitta, V.V. (eds), Contributions to current cephalopod research: Morphology, Systematics, Evolution, Ecology and Biostratigraphy, 5. 5th All Russian Conference – Contributions to current cephalopod research: Morphology, Systematics, Evolution, Ecology and Biostratigraphy, Moscow. Abstract volume, *Russian Academy of Sciences, Borissiak Paleontological Institute*, ISBN 978-5-6040412-6-7, pp. 31-32.

Vaňková, L., Košťák, M., 2019. Upper Jurassic–Lower Cretaceous belemnites reveal the geological history of the Outer Western Carpathians (Czech Republic): exemplified by the Štramberk cliff. 14th Jurassica Conference & Workshop of the ICS Berriasian Working Group, Bratislava. Abstract volume, *Earth Science Institute, Slovak Academy of Sciences & Faculty of Natural Sciences, Comenius University*, ISBN 978-80-85754-41-4, pp. 175-176.

Elbra, T., Košťák, M., Pruner, P., Schnabl, P., Kdýr, Š., Šifnerová, K., **Vaňková, L.,** 2019. Magnetic susceptibility and stable isotope ($\delta^{18}O$) record of shallower and deeper water Jurassic–Cretaceous paleoenvironments in the Outer Western Carpathians, Czech Republic. 14th Jurassica Conference & Workshop of the ICS Berriasian Working Group, Bratislava. Abstract volume, *Earth Science Institute, Slovak Academy of Sciences & Faculty of Natural Sciences, Comenius University*, ISBN 978-80-85754-41-4, pp. 93-94.

1.3 Aims of the thesis and problem definition

As the Lower Cretaceous belemnites of the Outer Western Carpathians were studied only taxonomically decades ago and no further investigations using modern methods have been proven, they hold great potential for additional analysis. The suitability of their use resulting from many studies published in recent years and offering various palaeoenvionmental reconstructions was a fundamental prerequisite for the study of the material.

Main points of the Ph.D. thesis:

- modern taxonomic assessment, based on morphological changes and ontogenetic development of an individual species, describing belemnite assemblages composition
- biostratigraphic evaluation, based on taxonomic revision and geochemical analysis → the age of belemnites and individual stratigraphic levels, definition of the stratigraphical intervals
- palaeogeographic distribution and comparison of studied belemnites with those present in the Tethyan Realm with relation to other realms (Boreal) in order to determine the distribution of taxa in specific areas (provincialism definition)
- bathymetric range obtained on the basis of species diversity and rostrum morphology → subsequent palaeoenvironmental reconstructions
- complex of palaeoecological interpretations summarising several analyses and including stable isotope data of $\delta^{13}C$ and $\delta^{18}O$ from belemnite rostra
- mutual correlation of studied material within other sections within the Tethyan Realm
- in the scope of multidisciplinary research of belemnites, to specify sedimentary characteristics of the environment and to define geological changes in the studied area

2. Geological setting

The Tethys Ocean was situated in the equatorial position during the Lower Cretaceous period and the J/K boundary interval. Its northern part was located between the Eurasian and African (part of Gondwana) continents, where it represented a warm ocean with dynamically changing character due to an initial and progressive phase of the Alpine orogenesis. The emerged land was surrounded by epicontinental seas with shallow-marine areas extending from the shelf zones and the deep basinal parts. Overall, during a warm climate period (greenhouse period), mostly carbonate sediments with marl and claystone beds were deposited. The most complete sequences of sediments can be found along its edge in Africa, the Iberian Peninsula, the rim of the Alpine Ocean, the Carpathian orogenic belt, the Moesian Platform, Cimmeria and further to the East.

The Outer Western Carpathians, represented by the Carpathian Flysch Belt, are situated at the northern part of the Carpathians (Golonka et al., 2006). The sedimentation record begins in the Upper Jurassic and Lower Cretaceous with limestones and/or variation from marls to heterogeneous deposits, with an onset of flysch sedimentation indicating tectonic activity of the area (Picha et al., 2006; Golonka, 2011; Michalík et al., 2016, 2021). Geological development ends in the Miocene by tectonic movements and area relocations (e.g. Csontos and Vörös, 2004; Picha et al., 2006).

2.1 Štramberk locality—Kotouč Quarry

The Kotouč Quarry (49°34.59´ N, 18°6.52´ E) is situated in the northeast part of the Czech Republic in the immediate vicinity of Štramberk town (**Fig. 1**). Complicated geological development of the area with several examples of tectonic thrusting overlap a number of processes which formed rocks around the edge of the Silesian Basin (Silesian Unit/Baška Subunit) (Picha et al., 2006; Golonka et al., 2014).

The oldest deposits are the uppermost Kimmeridgian–lowermost Berriasian biodetritial limestones (Štramberk Limestone). These rocks are extremely rich in macro- and micro-fossils (e.g. calpionellids, foraminifers, calcareous nannofossils, calcareous dinoflagellates, organic-walled dinoflagellate cysts, spores, pollen, corals, crinoids, echinoids, bivalves, brachiopods, gastropods, ammonites, belemnites). It is supposed that these sediments originated close to the carbonate platform with coral-*Diceras* limestone and its slope. Then, it created typical reef slope/talus with material accumulated from the shallow water areas (Picha et al., 2006; **study II.**). Lower Cretaceous sediments are represented by several formations with various lithology (Berriasian–Albian). Their origin is unclear, and several reworking episodes of sea-level changes, sub-aeric exposure phases and tectonic folding caused its mutual mixing. Also, mixing of fauna is evident (Horák, 1988; Houša and Vašíček, 2005; **study IV.**). Ammonites, belemnites, brachiopods, aptychi, echinoids, etc., are often found there (Houša, 1976, 1983a; Houša and Vašíček, 2005, Skupien et al., 2012; **study IV.**). At this locality, several hiatuses and relocations of sediments are observed. Lower Cretaceous sediments are deposited uncontinuously—along tectonic faults, where they are filling gaps, pockets, crevasses, fossil karst and cavities or they are lying directly on the surface of the Štramberk Limestone. The stratigraphically youngest deposits are the Upper Cenomanian sediments with pelitic (i.e. mudstone) character.

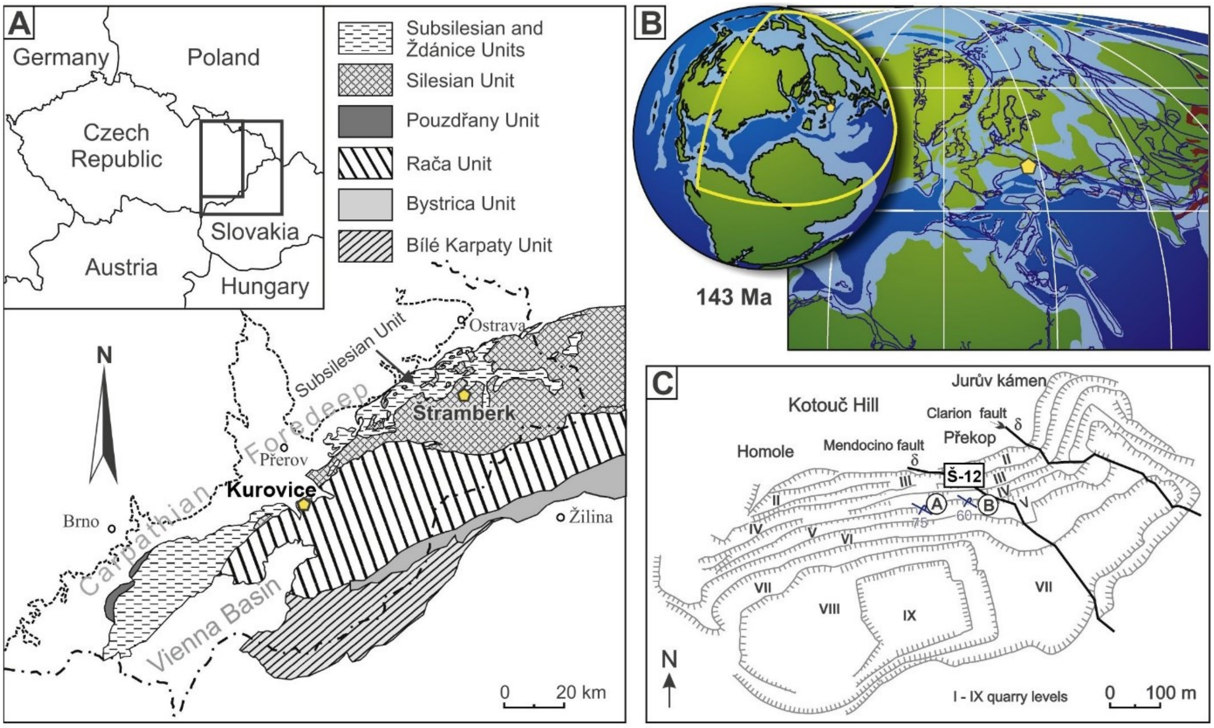

Fig. 1. Geographic position and geological situation of the studied area. A – Štramberk and Kurovice sites in the context of the Outer Western Carpathians (modified after Skupien and Smaržová, 2011); B – Lower Cretaceous period with Štramberk area location (according to Golonka, 2000); C – Kotouč Quarry with the position of A and B sections and the Š-12 pocket (modified after Svobodová et al., 2011; Vaňková et al., 2019, 2021 submitted).

2.2 Kurovice section

The Kurovice Quarry (49°16.40′ N, 17°31.40′ E) is located in the East part of Moravia, near Kurovice and Tlumačov villages (**Fig. 1**). The Kurovice section is situated in the fore of the Magura Unit, at the base of the Rača Unit in tectonically isolated slices (Eliáš et al., 1996; Picha et al., 2006).

It is characterised by pelagic/epipelagic sedimentation of the Tithonian–lowermost Berriasian alodapic micritic limestones (Kurovice Limestone Formation) and tectonically separated from the Lower Berriasian–lower Valanginian marlstones (Tlumačov Marlstone). Deposition of carbonate sediments is presumed as a deep-sea development with slumps, turbidites and gravity flows from the shallower water areas. The basinal sediments of the Kurovice Limestone are alternated by thin layers of marlstones, calcarenites and contourites (Elbra et al., 2018). In well preserved, 77 m thick Kurovice Fm. sequence, the J/K boundary was defined according to microfossil content, magnetostratigraphy and isotopic analyses (Elbra et al., 2018; Svobodová et al., 2019; **study III.**). Besides abundant microfossils (e.g. calcareous nannofossils, caplionellids, calcareous dinocysts, radiolarians, ostracods), also macrofauna (e.g. aptychi, belemnites, rhyncholites, elasmobranchians, crinoids, echinoid spines), which are rarely preserved, are abundant in the slump bodies (Eliáš et al., 1996, Měchová, 2012; **study I.**). According to the characteristics of fossils, a sedimentation regime below ACD is highly probable. The most significant submarine slump—which probably resulted from a tsunami-like event found above the J/K boundary (the lowermost Berriasian part, Bed 105, zone W *sensu* Eliáš et al., 2016) —provided the largest number of macrofossils (**Fig. 2**) (Eliáš et al., 1996; **study I.**). Besides fossils, also volcanic, metamorphic and granitic rocks, probably generated from the Silesian Cordillera were recorded (Eliáš et al., 1996; Košťák et al., 2018).

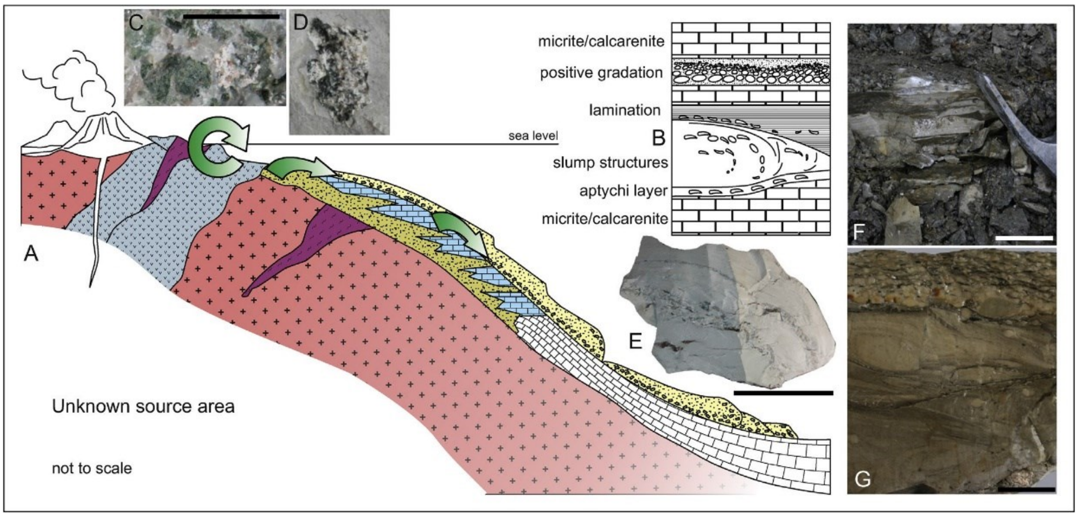

Fig. 2 Schematised genesis of the turbidite structure in the Bed 105 (Košťák et al., 2018).

3. Material

In order to fully describe belemnite fauna and its dependences, a huge number (more than 10,000) of belemnite rostra were studied. All specimens came from the Outer Western Carpathians of the Czech Republic. The vast majority of the studied specimens was collected from the Kotouč Quarry in two studied intervals: A and B sections from the 5th level of the quarry and the Š-12 and Š-11e pockets (exit from the 2nd to the 3rd level and the 3rd level of the quarry) mined in the past (**studies II., IV.**). Only several dozen specimens were collected from the Kurovice Quarry (Bed 105, zone W) (**study I.**). The belemnites from pockets of the Kotouč Quarry were collected by Dr. V. Houša during the 1970s. Belemnite rostra from the Kurovice Quarry were collected by Dr. Z. Vašíček, F. Sedláček and Dr. R. Vodrážka.

Belemnites from the A and B sections recently excavated from the quarry wall (Kotouč Quarry) were further used for geochemical analyses (34 samples) (**study II.**).

Belemnite rostra are deposited in collections of the Chlupáč's Museum of Earth History, Faculty of Science, Charles University, Prague (A and B sections, the Š-12 pocket, samples CHMHZ-LV; Kurovice Quarry, samples CHMZ-kur), the National Museum at Prague (the Š-12 and Š-11e pockets, samples NM-O) and the Ostrava Museum (the Š-12 pocket, samples MOS/002-05-03/127002).

4. Methods

4.1 Belemnites and their general characteristics

Belemnites are extinct cephalopods found in the sedimentary record from the lower Upper Triassic (ca. 240 Mya, *see* Iba et al., 2012) to the Cretaceous/Paleogene boundary (66 Mya) and they represent an important group within the Jurassic and Cretaceous trophic structure. As medium-sized predators, they held a position in the middle to upper parts of the trophic chain. Belemnites were mostly nektobenthic cephalopods and their movement in the water column was provided by a unique buoyancy system (e.g. Ebel, 1987; Monks et al., 1996). It is presumed that belemnites had a great locomotion system with a high level of velocity along the horizontal axis (Klug et al., 2010; Fuchs et al., 2016; Doguzhaeva et al., 2014) and that they tolerated salinity of about 27 to 37 psu (Hoffmann and Stevens, 2020). Their cosmopolitan distribution is clearly documented by migration patterns and endemic forms in high latitudes (e.g. Alsen and Mutterlose, 2009; Mutterlose et al., 2020).

Nevertheless, the comfortable temperature is generally characterised about 10°–30°C (*see* Hoffmann and Stevens, 2020 and references therein). Belemnites occupied the epipelagic zone over the shelves and they did not reach a depth below 200 m (Jeletzky, 1966; Hewitt, 2000; Wierzbowski, 2004; Arkhipkin et al., 2012; Hoving et al., 2014, etc.). Their occurrences are in direct relation to shallowing episodes in some stratigraphical intervals (*see* Mitchell, 2005; Zakharov et al., 2014, etc.). They migrated probably along shores, as deep-sea and sea-bottom conditions could represent an ecological limit/barrier for their spreading (e.g. Zakharov et al., 2014). Life expectancy was probably around 1 to 2 years (Jereb and Roper, 2005; Wierzbowski and Joachimski, 2009; Wierzbowski, 2013, etc.).

Several features of soft tissues of belemnites were investigated in the past (e.g. Naef, 1922). However, only a few findings of nearly complete belemnites with soft parts were reported by Donovan and Fuchs (2016) and by Klug et al. (2010). Besides valid proof of ink sac position, beaks and arms with onychites (arm hooks) have also been preserved. Sexual dimorphism of belemnites was proved by mega-onychites, which characterised the top part of two long arms, probably used for reproduction and/or hunting (Schlegelmilch 1998; Hoffmann et al., 2017), and also by division of bi-modal size classes (Košťák and Pavliš, 1997; Košťák, 2004).

The most studied and the most commonly preserved part of a belemnite is the Mg-low calcite rostrum, which served as a hydrodynamic and balancing organ. Together with proostracum, phragmocone and primordial rostrum, it forms an internal shell of the belemnite. It is presumed that the rostrum recorded original palaeoenvironmental signals during the belemnite ontogeny, as its creation was in equilibrium with the oxygen isotopes (e.g. Urey, 1948; Anderson et al., 1994; Dera et al., 2009; Wierzbowski and Joachimski, 2009; Wierzbowski and Rogov, 2011; Wierzbowski et al., 2017). Generally, this theory is based on the incorporation of conditions from ambient seawater (e.g. Price et al., 2011; Armendáriz et al., 2012; Wierzbowski et al., 2017). Although the rostrum seems to be combined from two alternating types of growth layers, it corresponds to the biomineralisation process composed of two steps (Hoffmann et al., 2016). According to Hoffmann and Stevens (2020) *"during the first step, a belemnite rostrum layer is composed of a filigree network of tetrahedral organic-rich calcite with high amounts of pore space between the tetrahedrals (CP1). This layer formed under strict biological control. During a second mineralisation stage the pore space is occluded by isopachous organic lean calcite crystals (CP2)"*. The horizontal laminae structure intersected a radial crystal structure. Morphologically, the rostrum is highly variable and its shape demonstrates the habitat of an individual genera or species. Beyond the rostrum, an aragonite phragmocone is rarely preserved. As well as in modern sepiids and spirulids (*Spirula spirula*), the phragmocone is composed from thin aragonitic walls and septa (Hoffmann and Stevens, 2020). This buoyancy device (e.g. Spaeth, 1975; Monks et al., 1996; Hewitt, 1999) provided for free swimming in the water column (Naef, 1922; Stevens, 1965; Monks et al., 1996, etc.). The directions of swimming were regulated by a siphon, which was in contact with septal necks on the ventral side (around siphuncle) (Denton, 1974; Combémorel, 1972). Uroliths (hydroxyapatite concrements), as a Ca^{2+} depot for the formation of septa and possibly regulation of the Mg/Ca ratio in the blood during secretion of the shell, are not known in belemnites yet (*see* Hoffmann and Stevens, 2020). As well as the presence of statoliths, alternating structures of carbonate-rich and organic-rich layers were generated during daily cycles (e.g. Clarke and Fitch, 1975; Bettencourt and Guerra, 2000; Klug et al., 2016). This phenomenon, known especially in modern coleoids, has not been confirmed in the fossil coleoids (Hoffmann and Stevens, 2020). Besides phragmocone, primordial rostrum—associated with the protoconch (the initial chamber of the phragmocone) and the proostracum protecting the dorsal part of belemnite body—is also composed of aragonite. Unfortunately, they are preserved very rarely and their taxonomical value is low (e.g. Jeletzky, 1966; Combémorel, 1988; Doguzhaeva et al., 2014 and references therein).

4.2 General preparation

Belemnite rostra stored at museums and collected in the field were cleaned if necessary and detached from the rock clinging to the surface of the rostrum by separating tools. Rostra from A and B sections were collected from the quarry wall by a HILTI DDEC-1 core drill and, if possible, separated from hard limestone. To achieve a good resolution with morphological differences of the specimens, rostra were overlayed by ammonium chloride sublimate and photographed by a Canon700D with Tamron 90 mm Macro objective.

To determine ontogenetic changes during the growth of belemnites, several specimens with clear taxonomic classification were cut by a SRUERS Discoplan saw (Charles University, Prague) in longitudinal (transvers) sections (**study IV.**). Morphology of alveolas (shape, depth and inclination) were studied by X-ray equipment during calibration of the X-ray instrument at the X-ray Department of the General University Hospital in Prague (**study I.**).

4.3 Morphological parameters of rostrum and classification

In general, the following morphological features are used in the rostrum description (see terminology used below): anterior, for the frontal part leading to the head; posterior, for the top part of the rostrum (apex); the alveolus, as the remnant conical part of the preserved phragmocone; rostrum cavum, for the rostrum part with alveolus; rostrum solidum, as the defined part between the protoconch and the top part of the rostrum (**Fig. 3A**).

As the rostrum is an internal shell of belemnite, several parameters connecting with soft-tissue attachment and blood-circulating organs could be observed. The most highly distinguished part is the alveolar groove (also referred to as the furrow), which probably served as a corridor for blood vessels (Stevens, 1965). This groove is often located in the ventral part of the rostrum, but it could also be developed on the dorsal side, and/or more than one groove could be developed (see below) (**Fig. 3**). The length, shape and depth of this groove are variable, generally suggesting an important feature at the genus and species levels (compare the long and deep alveolar groove of the species *Conobelus* Stolley, 1919, or *Berriasibelus* Delattre, 1952 (**studies I., II., IV.**) vs. the weak and short alveolar groove of the species *Hibolites* Auctorum (the correct spelling (i.e. *Hibolithes* vs. *Hibolites*), has still not been clarified based on the ICZN decission (e.g. Janssen, 2020) (**study I.**)). In the posterior part of the rostrum, apical lines are sometimes preserved and the number could vary (e.g., Stevens, 1965; Schumann, 1974). It is presumed that lateral grooves and doppellinien (Stolley, 1919; Stevens, 1965) could be developed for muscle attachment for fins (Schlegelmilch, 1998; Klug et al., 2010). However, its evidence is still lacking. The lateral grooves could lead also to blood vessels or indicate a reduction of the rostrum and its replacement with soft tissue. The rostrum surface is generally smooth; however, in some species, granulation or striation are characteristic features for some taxa (e.g. *Pseudobelus brevis* Paquier, 1990; *see* Thomel-Picolier, 2018).

The first important feature of the rostrum is the shape, which is determined in two view sides: the profile of a rostrum from the lateral view (symmetrical or asymmetrical), and the outline corresponding to the dorso-ventral view (mostly symmetrical). Also, in profile and in outline, terms ‘compression’ is used in the context of the lateral flattening, and ‘depression’ is used for the dorso-ventral flattening, as defined. Several basic shapes, characterised mainly as outline views, are described (conical, cylindrical, hastate), however, mutual combinations are very often found (e.g. conical with significant flattening of the posterior part, compressed duvaliid shape with bulging). In the longitudinal section (**Fig. 3**), it is possible to study the ontogenesis of belemnite, as lamination growth follows individual stages of the rostrum development. In some Jurassic and Cretaceous belemnites, a significant growth line is observed (**Fig. 3A**). From the initial chamber to the top of the rostrum an apical line is observed, which indicates the place where the apex (the apical part of the rostrum) was located during its growth. The apical line is mostly asymmetric, and several types are distinguished: ortholineate, goniolineate and cyrtolineate (Stevens, 1965; Schumann, 1974). Also, the apex region is sorted by its shape into several forms: acute, blunt, mucronate (often with significant mucro structure), etc. The phragmocone is situated in the cavity of the anterior part (alveolus). The top part with maximal diameter is characterised by an alveolar opening and usually is not preserved. For each species and/or genera, the shape of the alveolus is distinguished, including the depth, alveolar angle, bend, protoconch position (if preserved), as well as its inclination to the dorsum or ventrum (**Fig. 3B, C**). The cross-section of the rostrum is a well recognisable parameter and its character is commonly changed along the rostrum. In addition to basic shapes containing circular, quadrate, elliptically compressed, and depressed forms, we also recognise several combinations and peculiarities such as trapezoidal, dorsally or ventrally flattened pyriform, and others.

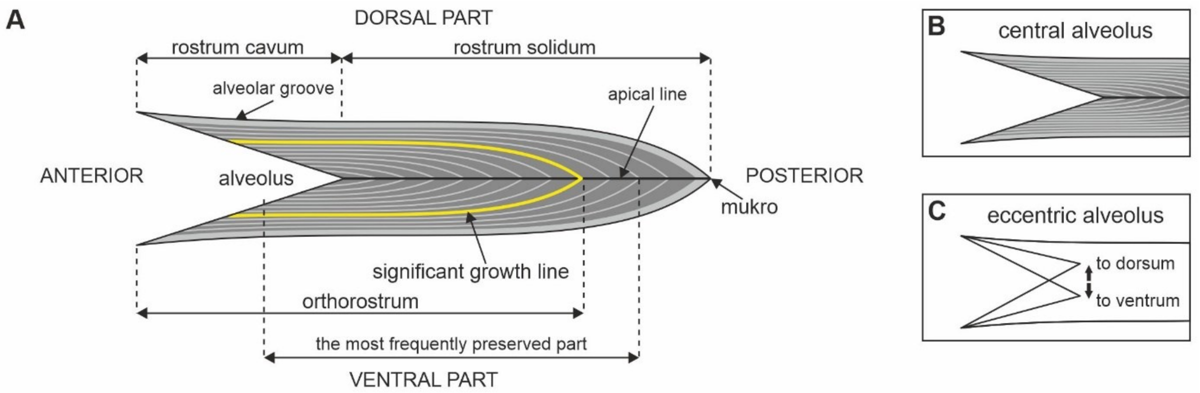

Fig. 3 Idealised longitudinal section of belemnite rostrum of the family Duvaliidae. A – studied parameters; B, C – alveolus position. Not to scale (Vaňková et al., 2021, submitted).

4.3.1 Morphometry

Several measurement indices are introduced for the rostrum characterisation. Parameters of an individual taxa differ (essentially in individual families and genera) and their affiliations could be derived on the basis of size limits. Measured parameters here are consistent with Stoyanova-Vergilova (1970), Doyle and Kelly (1988), Combémorel (1973, 1988), and Vašíček et al. (1994). The morphometry contains the following values (abbreviations in parentheses): total length of preserved rostrum (L), length of the post-alveolar region (l or Pa), dorso-ventral diameter at the alveolar opening (Dv), lateral diameter at the alveolar opening (Dl), maximal dorso-ventral diameter (Dvmax), maximal lateral diameter (Dlmax), and length from apex to Dmax (x). According to the state of rostrum preservation (incomplete rostrum, tectonic deformation, etc.) the measurement was adjusted (*see* Mariotti, 2003). The Pa (l) index determination (length of complete post-alveolar region = rostrum solidum, according to Stoyanova-Vergilova, 1970; Vašíček et al., 1994) could not be implemented for material from the Š-12 pocket (**study IV.**).

4.3.2 Systematics and taxonomy

Taxonomic classification of belemnites is based only on morphological parameters of rostra (e.g. Naef, 1922; Doyle et al., 1994; Riegraf et al., 1998; Lukeneder, 2005). As several combinations and variations of classified parameters were found to exist, the correct assortment to a rightful group is sometimes impossible. Therefore, an exact taxon assignment depends on significant sets of features for the relevant genus or species.

The families Duvaliidae and Belemnopseidae with several genera and species have been studied in the NW Tethys (**studies I., II., IV**.). The taxonomic determination and terminology of belemnite rostra follow Jeletzky (1966), Stoyanova-Vergilova (1970), Combémorel (1973), Janssen and Clément (2002), Janssen (1997, 2003) and Janssen and Főzy (2005).

Class Cephalopoda Cuvier, 1798
Subclass Coleoidea Bather, 1888
Order Belemnitida Zittel, 1895
Suborder Belemnopseina Jeletzky, 1966

Family Duvaliidae Pavlow, 1914

Description. Duvaliid, hastate, conical or cylindrical, and in some species, elongated rostrum. Dorsal alveolar groove is variable in length and extends to the protoconch or to the apex. The cross-section depends on the rostrum shape. The apex could be mucronate; lateral lines are sometimes developed. While the outline is symmetrical, the profile is often asymmetrical.

Genus *Conobelus* Stolley, 1919
Genus *Berriasibelus* Delattre, 1952
Genus *Duvalia* Bayle, 1878
Genus *Pseudobelu*s Blainville, 1827

Family Belemnopseidae Naef, 1922, emend. Jeletzky, 1946

Description. Elongated rostrum with ventral alveolar groove reaches to the protoconch or slightly behind. The shape of the rostrum is hastate or subconical, the dorso-ventral depression could be developed in the rostrum solidum or in the posterior region, the cross-section is circular or depressed. Distinctive lateral lines can be developed. Most often, the apical line is ortholineate.

Genus *Hibolites* Auctorum

Genus *Conohibolites* Janssen and Főzy, 2005

4.4 Palaeoenvironmental and palaeoecological reconstructions

4.4.1 Bathymetric dependence

It is generally assumed that the shape of the rostrum is associated with environmental requirements (e.g. Clément, 2000; Mitchell, 2005; Wiese et al., 2009; Hoffman and Stevens, 2020). Therefore, bathymetric preferences correspond mainly with movement in the water column, and with food requirements. According to thorough studies based on rostrum morphology, lithological specification, and isotopic data, bathymetric preferences of taxa have been determined (e.g. Janssen, 2003; Janssen et al., 2012; Zakharov et al., 2014; Dzyuba et al., 2018). Generally, shorter robust, conical or bulging rostra correspond to shallow near-shore environments and indicate a nektobenthic lifestyle of less active swimmers near the bottom. Rostra with an elongated thin or compressed shape point to fast active swimmers living in the water column near off-shore in the epipelagic-pelagic zone (Mutterlose and Wiedenroth, 2008; Mutterlose et al., 2010; Zakharov et al., 2014; Dera et al., 2016; Dzyuba et al., 2018, etc.).

Numerous studies published from the Tethyan Realm (Janssen and Clément, 2002; Janssen 2003, 2009, 2020; Mutterlose and Wiedenroth 2008; Főzy et al., 2010; Janssen et al. 2012) were used as a tool for bathymetric interpretations (**Fig. 4**). According to a number of specific taxa and belemnite assemblages corresponding to bathymetric dependences, an environmental model was introduced (**study IV.**).

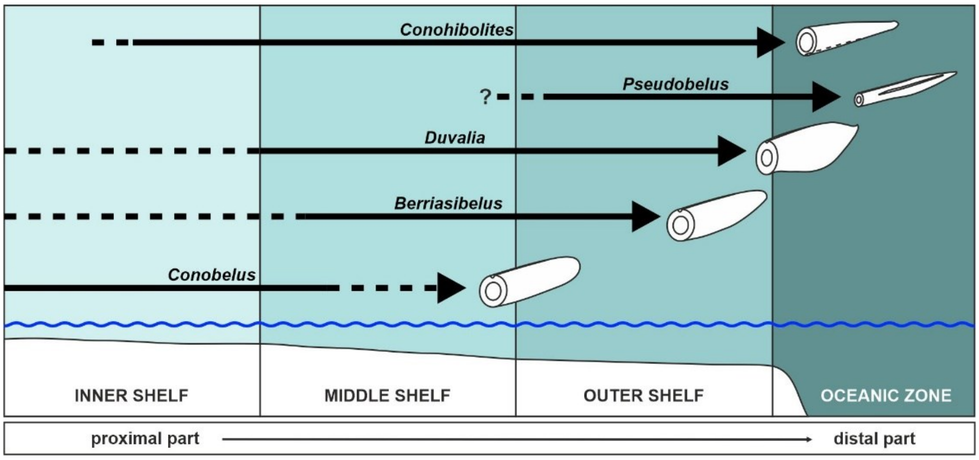

Fig. 4 Bathymetric preferences of belemnites with typical rostrum morphology. Based on a number of studies published by Janssen and Clément (2002), Janssen (2003, 2009, 2020), Mutterlose and Wiedenroth (2008), Főzy et al. (2010), and Janssen et al. (2012) from Tethyan Realm. Not to scale (modified after Vaňková et al., 2021, submitted).

4.4.2 Geochemical analyses

Belemnite rostra are widely used for geochemical analyses resulting in a model of ancient seawater composition (see references below). Since the first use of the isotope method during the 1950s by Urey (1948), geochemical analytical methods have extensively been modernised. Characteristic Mg-low calcite composition of the rostrum should correspond to changes in isotopic composition (and variations) of seawater during belemnite growth. Therefore, according to the research of individual isotopic ratios ($^{18}O/^{16}O$, $^{13}C/^{12}C$, $^{87}Sr/^{86}Sr$), it is possible to interpret palaeoenvironmental conditions and, partly, also stratigraphy. Belemnites are one of the most applicable fossils for the reconstruction of palaeotemperature, palaeobioproductivity, stratigraphy and overall palaeoenvironments (e.g. Jones et al., 1994; McArthur et al., 2004; Price et al., 2016).

It is assumed that oxygen isotopes evidenced in the calcitic rostrum were in equilibrium with ambient seawater (Anderson et al., 1994; Dera et al., 2009; Wierzbowski et al., 2017). As the isotope ratio is dependent on fractionation processes and follows the temperature, the resultant $\delta^{18}O$ values may then signal a cooling or warming event with a long-term trend corresponding to palaeotemperature fluctuations. During recent decades, oxygen isotopes were used for the creation of several palaeotemperature models (e.g. Podlaha et al., 1998; Veizer et al., 1999; Price et al., 2000; van de Schootbrugge et al., 2000; McArthur et al., 2004, 2007a; Bodin et al., 2009, 2015; Mutterlose et al., 2010; Dera et al., 2011; Žák et al., 2011; Price et al., 2016). The obtained values could, however, be influenced by numerous factors, e.g. depth and species-specific habitat, as changing of the belemnites habitat during ontogeny is presumed (Mettam et al., 2014; Dera et al., 2016; Hoffmann and Stevens, 2020). Moreover, oxygen isotope values are affected by salinity variations (e.g. Hoffmann et al., 2016; Stevens et al., 2017). The rostrum composition and precise characterisation of laminae formation, as well as the depth in which the rostrum originated, have not been documented with certainity (e.g. Mutterlose et al., 2010, 2012; Hoffmann et al., 2016; see rostrum structure in Chapter 4.1). On the basis of isotopic composition, the nektobenthic lifestyle is assumed (Anderson et al., 1994; Wierzbowski, 2002; Wierzbowski and Rogov, 2011; Wilmsen and Niebuhr, 2017; Hoffmann and Stevens, 2020), however, the benthic (e.g. Price et al., 2013) bottom-dwellers life-style (e.g. Price and Page, 2008; Mutterlose et al., 2014), as well as the nectonic lifestyle (Rexfort and Mutterlose, 2009) were also discussed.

In contrast to the oxygen isotopes, carbon isotopes are not in equilibrium with ambient seawater (Wierzbowski and Joachimski, 2009). The vital effect influencing belemnite rostrum composition and differences between organic and inorganic carbon and oxygen isotopes were largely discussed by McArthur et al. (2002), Lécuyer et al. (2004), Li et al. (2012), Hoffmann et al. (2016), Stevens et al. (2017) etc. Moreover, the carbon isotope composition could be different depending on taxa (e.g. Wierzbowski and Joachimski, 2009). In direct carbon incorporation into the belemnite rostrum, more negative values resulted (*see* Rexfort and Mutterlose, 2006, 2009). Generally, carbon isotopes are incorporated into the rostrum together with oxygen isotopes, and their ratios are given in the $\delta^{13}C$ values. Thus, these results may reflect changes in the palaeobioproductivity of the oceans, and are correlated with carbon isotopes obtained from the bulk rock. As the $\delta^{13}C$ values follow long-term trends in the ocean development, their fluctuations are used for stratigraphically significant episodes (*see* Price et al., 2011 and references therein). Several events resulting in $\delta^{13}C$ shifts of values are affected by volcanic activity or terrigenous influx (e.g. Podlaha et al., 1998; van de Schootbrugge et al., 2005; Bodin et al., 2009; Mutterlose et al., 2014).

During the Jurassic and Cretaceous periods, several studies dealing with $\delta^{18}O$ and $\delta^{13}C$ were published in order to reconstruct the isotopic signal from belemnite rostra and to understand conditions of ancient seawater (e.g. Podlaha et al., 1998; Veizer et al., 1999; Price et al., 2000, 2011, 2016; van de Schootbrugge et al., 2000, 2005; Price and Gröcke, 2002; McArthur et al., 2004; 2007a; Price and Mutterlose, 2004; Wierzbowski and Joachimski, 2007; Bodin et al., 2009, 2015; Mutterlose et al., 2010, 2014; Dera et al., 2011; Žák et al., 2011).

In contrast to stable isotopes, the strontium isotope ratio is driven by radioactive decay of ^{87}Rb to radiogenic ^{87}Sr. Its quantity is monitored and reported against the stable ^{86}Sr. The strontium isotopic ratio should be worldwide identical in seawater with a long residence-time (4 x 10^6 years). It represents a useful stratigraphical marker for global correlation and it has a great potential for modelling of $^{87}Sr/^{86}Sr$ seawater evolution (e.g. Jones et al., 1994; Podlaha et al., 1998; Bodin et al., 2009; Mutterlose et al., 2014). Belemnite rostra are widely used for obtaining a Sr isotopic signal (e.g. Veizer et al., 1997; Crame et al., 1999; McArthur et al., 2004, 2007a), as biological carbonate is less prone to diagenetic alteration then are sediments at the seafloor (e.g. McArthur et al., 2007b). The global strontium curve follows an increasing trend from a prime value of 0.699 to the recent value of 0.709 (Veizer, 1989) with significant fluctuations (e.g. McArthur et al., 2007a; Bodin et al., 2009; Wierzbowski et al., 2017).

Although the curve of the Sr isotope ratios is relatively well researched in the Late Jurassic (Jones et al., 1994; Podlaha et al., 1998; Wierzbowski et al., 2017) and the Early Cretaceous (van de Schootbrugge et al., 2000; McArthur et al., 2004, 2007a, 2007b; Bodin et al., 2009, 2015; Mutterlose et al., 2014; Frau et al., 2018), in the Tithonian–Berriasian boundary it is only poorly supported by relevant data (Jones et al., 1994; Podlaha et al., 1998; Price and Gröcke, 2002; Price et al., 2016; Kuznetsov et al., 2017; **study III.**).

Probably the most important parameter determining the use of material for geochemical analysis is the detection of rostrum diagenesis. During the diagenetic overprint, minerals and the original isotopic record are both altered (e.g. Podlaha et al., 1998). The affected values then distort the results and cannot be used for palaeoenvironmental reconstructions. Diagenesis in belemnite rostra can be identified by several methods, where limits for the determination of diagenetic overprint are based on studies of the growth layers and geochemical changes. One of the basic methods is cathodoluminescence, in which orange-red luminescent parts signalise diagenesis, and a non-luminescenct dark brown colour indicates an original calcite (e.g. Rosales et al., 2001, 2004a). Another method is represented by trace element analysis for the determination of Fe, Mn, Mg and Sr element concentrations (e.g. Veizer, 1983; Brand, 1989; Veizer and Fritz, 1976; McArthur et al., 2007a). Generally, primary calcite should have more than 1000 ppm of Sr and less than 100 ppm of Mn (e.g. Marshall, 1992; Wierzbowski and Joachimski, 2009). Under reducing diagenetic conditions, Fe and Mn concentrations in belemnite calcite are increased while Sr and Mg are diminished (e.g. Veizer, 1983; Marshall, 1992; McArthur et al., 2007a). The change in values can, therefore, easily be identified by a complete elemental analysis.

In addition to the detection of diagenesis, palaeoenvironmental conditions and changes can also be detected by trace element analysis (Mg/Ca and Sr/Ca ratios) (e.g. McArthur et al., 2004; Rosales et al., 2004a; Ullmann and Pogge von Strandmann, 2017). However, the resulting ratios could be influenced by the lifestyle of an individual taxa and thus reflect species-specific habitat (Wierzbowski, 2013; Wierzbowski et al., 2017, etc.).

The belemnite rostra selected for geochemical analysis were processed by the following methodological procedures (**study II.**).

Only well-preserved calcite rostra were used. The parts of rostra susceptible to diagenetic alteration (last growth laminae, the apical line, alveolus, alveolar groove and apical region) and the surrounded rock on the rostrum surface were removed by separating tools and a micro-drill. All samples were then carefully cleaned in ultra-pure water, crushed into small pieces, and well-preserved calcitic segments were picked up under binocular microscope. Selected pieces were crushed and homogenised in agate mortar to analytical fineness. Subsamples of approximately 50 mg weight were then transferred into a Savillex vial. The 1 ml of 14 M nitric acid was added and the solution was dissolved. The samples were then diluted with deionised water to a volume of 20 ml. For details, *see* Vaňková et al. (2019); (**study II.**).

4.4.2.1 Diagenetic overprint

To determine the diagenetic overprint of samples, analyses of main and trace elements were performed (**study II.**). For complex diagenetic detection, Ba, Ca, Fe, Na, Mg, Mn and Sr elements were analysed by a 5110 VDV Agilent ICP-OES spectrometer. The 20 ml liquid sample (for preparation, see above) was diluted in 2% HNO_3 100× for Ca analysis and 2× for analysis of other elements. For Rb quantity determination, trace elements of Rb were measured by an ICP-MS device (Thermo Scientific XSeries II). These analyses were performed in the Laboratories of the Geological Institutes at the Charles University, Prague. Resulting values were then used to define limits of diagenetic overprint. According to Rosales et al. (2001, 2004b) and McArthur et al. (2004), the limits were set as follows: $Mn < 40$ ppm, $Fe < 150$ ppm, and $Sr > 1000$ ppm.

4.4.2.2 Stable isotopes of carbon and oxygen

The stable isotopes were analysed from 20 mg powder by dual inlet-based mass spectrometry. The subsample was transferred into a double-arm reaction vessel, with carbonate powder in the first arm and 100% phosphoric acid in the second arm. The reaction vessel was evacuated, components were mixed and equilibrated at 25 °C for 24 hours (McCrea, 1950). Isotopic compositions were measured from regenerated CO_2 gas by Delta V

Advantage DI-IRMS (ThermoFisher Scientific) in the laboratories of the Czech Geological Survey in Prague. The accuracy of the measurement was checked by analyses of the international standard (IAEA) NBS 18 ($\delta^{13}C$ = −5.014‰, $\delta^{18}O$ = −23.2‰) and two in-house standards: Carrara marble ($\delta^{13}C$ = +2.29‰, $\delta^{18}O$ = −1.32‰) and CS 2 ($\delta^{13}C$ = +2.93‰, $\delta^{18}O$ = −3.86‰). The long-term reproducibility for all standards (external precision) is better than 0.05‰ for $\delta^{13}C$ and 0.1‰ for $\delta^{18}O$. The resulting values were recorded against the international V-PDB standard in ‰.

4.4.2.3 Strontium isotope analysis

Strontium analysis was carried out by a Neptune Plus instrument MC-ICP-MG (ThermoFisher Scientific) in the static mode at the Stable and Radiogenic Isotope Research Laboratory at the Charles University, Prague. From the calcite matrix, strontium (solution aliquot corresponding to at least 2 μg of Sr) was isolated by exchange chromatography techniques using Triskem's Sr resin (equivalent to Sr. spec) (Pin et al., 1994; Míková and Denková, 2007). Analytical mass bias was corrected to $^{88}Sr/^{86}Sr$ = 8.375209 (defined as $\delta^{88}/^{86}Sr$ = 0 relative to NIST SRM 987; *see* Nier, 1938). External error (overall analytical uncertainty) was given by repeated analyses of the SRM 987 standard, resulting in $^{87}Sr/^{86}Sr$ = 0.710278 ± 0.012 (2 σ; n = 8). To detect possible isobaric interference and correction to radiogenic ^{87}Sr, the Rb concentrations were measured (Laboratories of the Geological Institutes at the Charles University, Prague). For comparison and verification of measurement accuracy, samples were re-measured by a Triton Plus TIMS instrument (ThermoFisher Scientific) in the laboratories of the Czech Geological Survey in Prague.

4.4.3 Stratigraphy and palaeobiogeography

Biostratigraphically, belemnites represent a great potential, especially in those cases where other markers (microfossils, magnetostratigraphy, etc.) are missing. In some regions and ages, belemnite zonation is very well used and in some cases replaces ammonites zones. Due to resistant calcite rostra, belemnites are preserved below ACD (**study I.**). Previously, belemnites were used as index fossils (Oppel, 1856-1858). In the high latitudes of the Boreal Realm and the Arctic Province, belemnite zonation is well calibrated with stratigraphical methods (e.g. Mutterlose, 1990; Baraboshkin and Mutterlose, 2004; Dzyuba, 2004, 2013; Mitchell, 2005; Nikitenko et al., 2013). As belemnite rostra are independent of facies and they are widely distributed (see environmental limits in Chapter 4.1), the investigation of their occurrence provides more detailed information about their biostratigraphy and palaeobiogeographical limits.

Specific occurrences of taxa at individual stratigraphic levels are well researched, notably in recent decades (Janssen and Főzy, 2004, 2005; Janssen et al., 2012; Hoedemaeker et al., 2016; Janssen, 2020, etc.). Therefore, biostratigraphic and palaeogeographic refinement is based herein on numerous Late Jurassic–Early Cretaceous published data within the Circum-Mediterranean Province, Tethyan and Boreal realms and other adjacent areas (e.g. Favre, 1880; Krimholz, 1939; Stoyanova-Vergilova, 1963, 1965a, b, 1970, 1993; Kabanov, 1967; Ali-Zade, 1972; Combémorel, 1972, 1973; Nazarishvili, 1973; Patrulius and Avram, 1976; Vašíček, 1978; Combémorel and Mariotti, 1986a, 1990; Horák, 1988; Doyle and Mariotti, 1991; Weiss, 1991; Barskov and Weiss, 1992; Vašíček et al., 1994; Janssen, 1997, 2003, 2020; Clément, 2000; Janssen and Clément, 2002; Topchishvili et al., 2002; Janssen and Főzy, 2004, 2005; Kvantaliani and Keleptrishvili, 2005; Mutterlose and Wiedenroth, 2008; Alsen and Mutterlose, 2009; Főzy and Janssen, 2009; Janssen, 2009, 2010, 2018; Főzy et al., 2010, 2011; Janssen et al., 2012; Hoedemaeker et al., 2016; Thomel-Picollier, 2018). Several belemnite assemblages, well investigated from the bed-by-bed sampled profiles in France, Bulgarian, Hungary and Spain (e.g. Janssen, 1997, 2020; Clément, 2000; Janssen and Főzy, 2004, 2005; Hoedemaeker et al., 2016), were thoroughly studied and compared with belemnite rostra examined herein (**study IV.**). Affiliation of an individual species/genera was subsequently used as a major marker for the age of lithological units and geological development (**studies I., IV.**).

Recently, many authors studied the conservation of strontium isotopes in rostrum calcite (see references in Chapter 4.4.2) in relation to palaeoecological conditions and changes in time and space. After creating a global strontium isotope curve, the isotopic signal from belemnite rostra started to be widely correlated with the long-term trend. The Sr global curve is continuously complemented (e.g. Jones et al., 1994; Podlaha et al., 1998; McArthur et al., 2007a, b; Bodin et al., 2009, 2015; Frau et al., 2018). As the taxonomic validation is sometimes insufficient, the $^{87}Sr/^{86}Sr$ isotopic signal from rostra offers great potential for age identification **(study III.)**. Stratigraphic determination of belemnites from studied localities were combined by both taxonomic specifications (**studies I., IV.**) and strontium analyses (**study II.**). Resulting ratios of $^{87}Sr/^{86}Sr$ values were then compared with other results obtained from rostra (e.g. Jones et al., 1994; Podlaha et al., 1998; Price and Gröcke, 2002; Price et al., 2016) and from the global strontium trend.

Geographic distribution of belemnites is associated with several factors, such as climatic conditions, sea-level changes and migration patterns (e.g. Christensen, 1997a; Clément, 2000; Alsen and Mutterlose, 2009; Mutterlose et al., 2020). Depending on the belemnites' lifestyle and biological limitation, it is presumed that belemnites migrated along coastlines of the shelves. Temperature was probably the most significant factor for spreading, however, other chemical aspects—including water quality, pH, salinity and oxygenation—played significant roles and encouraged palaeobiogeographical changes (e.g. Doyle, 1987; Mutterlose, 1998; Dera et al., 2016). The causes of faunal turnovers are still not well understood but are assumed to be related to water chemistry and transgression-regression cycles (Christensen, 1997b; Clément, 2000; Janssen and Clément, 2002, etc.). During the studied period, NW Tethys is characterised by the existence of the Mediterranean Province (Stevens, 1973; Mutterlose, 1988). Since the Hauterivian, there are two recognised subprovinces: the Crimean-Caucasian Subprovince with poorly known exact stratigraphical and taxonomical development, and the relatively well-defined French-Bulgarian Subprovince (Stoyanova-Vergilova, 1964; Combémorel and Stoyanova-Vergilova, 1991; Clément, 2000).

5. Results and discussion

All results and discussions of the NW Tethys belemnites study are widely described in the attached articles.

5.1 Belemnite assemblages

The following families were recognised in the studied interval. Duvaliidae Pavlow, 1914 and Belemnopseidae Naef, 1922 (synonymous = Mesohibolitidate Nerodenko, 1983), including six genera with the following species: *Conobelus siciliensis* (Combémorel and Mariotti, 1986), *Conobelus* aff. *siciliensis* (Combémorel and Mariotti, 1986), *Conobelus conophorus* (Oppel, 1865), *Conobelus*? cf. *piradoensis* Janssen, 2003, *Conobelus* sp., *Berriasibelus incertus* (Weiss, 1991), *Berriasibelus* cf. *pseudoheres* (Lukeneder, 2005), *Berriasibelus exstinctorius* (Raspail, 1829), *Berriasibelus conicus* (Blainville, 1827), *Berriasibelus* gr. *conicus* (Blainville, 1827), *Berriasibelus kabanovi* (Weiss, 1991), *Berriasibelus* aff. *triquetrus* (Weiss, 1991), *Berriasibelus* sp. A, *Berriasibelus* sp. B, ? *Berriasibelus* sp. C, *Duvalia ensifer* (Oppel, 1865), *Duvalia tithonia* (Oppel, 1865), *Duvalia* gr. *lata* (de Blainville, 1827), *Duvalia* cf. *miravetesensis* (Janssen, 2003), *Duvalia crassa* Janssen, 2018, *Duvalia superconstricta* Janssen, 2018, *Duvalia emericii* (Raspail, 1829), *Duvalia* cf. *kleini* Janssen, 2018, *Duvalia* sp., *Duvalia* sp. A, *Duvalia* sp. B, *Duvalia* sp. C, *Pseudobelus zeuschneri* (Oppel, 1865), ? *Pseudobelus* aff. *P. zeuschneri* (Oppel, 1865), *Pseudobelus datensis* (Favre, 1880), *Pseudobelus fischeri* (Combémorel and Mariotti, 1990), *Pseudobelus giziltschaensis* (Ali-Zade, 1961), *Pseudobelus* gr. *bipartitus* Blainville, 1829, *Hibolithes semisulcatus* (Münster, 1830), *"Hibolites" minaretoides* (Vetters, 1905), *Conohibolites* aff. *platyurus* (Duval-Jouve, 1841), *Conohibolites* sp. A, *Conohibolites* sp. B, *Conohibolites* sp. C and ? *Conohibolites* sp. D.

Taxonomical, biostratigraphical and palaeobiogeographical results were carefully compared with already published data in numerous papers from the Tethyan and the Boreal Realms (e.g. Azerbaijan (Ali-Zade, 1972), Bulgaria (Stoyanova-Vergilova, 1963, 1965a, b, 1970, 1993), Caucasus (Krimholz, 1939), Crimea (Kabanov, 1967; Weiss, 1991; Barskov and Weiss, 1992), Czech Republic (Vašíček, 1978; Horák, 1988; Vašíček et al., 1994; Eliáš et al., 1996), France (Combémorel, 1972, 1973; Clément, 1999, 2000; Janssen and Clément, 2002; Janssen, 2009, 2010, 2018, 2020; Janssen et al., 2012; Thomel-Picollier, 2018), Georgia (Nazarishvili, 1973; Topchishvili et al., 2002; Kvantaliani and Keleptrishvili, 2005), Hungary (Janssen and Főzy, 2004, 2005; Főzy and Janssen, 2009; Főzy et al., 2010, 2011), Italy (Combémorel and Mariotti, 1986a, b, 1990), Morocco (Mutterlose and Wiedenroth, 2008), North-East Greenland (Alsen and Mutterlose, 2009), Romania (Patrulius and Avram, 1976), Slovakia (Vašíček et al., 1994), Spain (Janssen, 1997, 2003; Hoedemaeker et al., 2016; Janssen, 2018), Switzerland (Favre, 1880), and Turkey (Doyle and Mariotti, 1991)). The biostratigraphical refinement was one of the most significant subjects of whole study, as the belemnite material comes mainly from the accumulation of mixed strata (**studies I., IV.**). In the slump structure of the Kurovice Quarry (Bed 105), the morphologically diverse assemblage was analysed (**study I.**). A majority of the studied species belongs to the family Duvaliidae (except for *Hibolithes semisulcatus*, of family Mesohibolitidae). Stratigraphically, more than a half of classified the taxa are of the Tithonian in age, while other representatives are common in the Berriasian strata (**Fig. 5**). Although all identified taxa are common in the Tethyan Realm, only in recent years has there been evidence that belemnites previously determined as the 'typical Tithonian' continue also to the earliest Cretaceous (*Berriasella Jacobi* Zone) (Hoedemaeker et al., 2016). This fact is also supported by the presence of *Conobelus conophorus*, previously mentioned only for the Jurassic period (described *after* Oppel, 1865, from the Štramberk Limestone). Nevertheless, these taxa could be, according to recent research of the Štramberk Limestone (e.g. Vašíček and Skupien, 2016; Vašíček et al., 2017; **study II.**), also of the earliest Berriasian in age. The only one species, *Berriasibelus* *conicus*, was recognised at both studied localities. Although this taxon has a wide stratigraphical range (*see* **study IV.**), we assume this species to be the most common element in the Upper Jurassic–Lower Cretaceous strata of the studied area. From the lowermost Berriasian sections of the Štramberk Limestone there were also described closely undetermined genera: *Conobelus*, *Duvalia* and *Hibolites* (**study II.**).

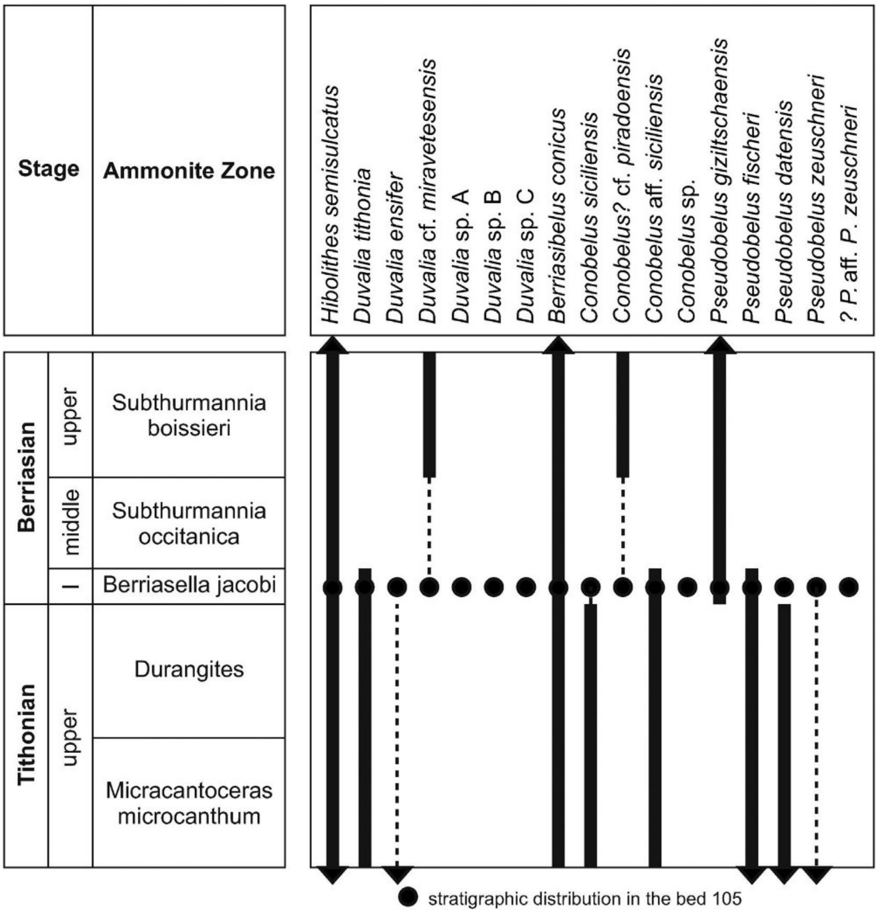

Fig. 5 Stratigraphic distribution of belemnites from the Kurovice Quarry associated with the slump structure (*Calpionella alpina* Subzone)—the Bed No. 105. Dashed lines indicate the expected stratigraphical range based on the belemnites present in the studied interval (Košťák et al., 2018).

Higher stratigraphical intervals are represented only by belemnites from the Š-12 and the Š-11e pockets (**Fig. 6**) (**study IV.**). The Berriasian age is predominantly characterised by the genus *Berriasibelus*. Most of the adult specimens belong to the species *Berriasibelus exstinctorius* with the well recognisable morphological feature of the apical part. Also, many adult rostra of *Duvalia* gr. *lata*, typically used as a marker for the Early Cretaceous, are present in the material. Probably the majority of the studied material originated in the late Berriasian–Early Valanginian. In Early Valanginian, belemnite rostra are highly diversified and are characterised by rather short conical rostra of the genera *Berriasibelus*, as well as by significantly flattened (compressed) rostra of *Duvalia*. Probably the most important taxa are *Duvalia crassa* and *Duvalia superconstricta*, which correspond to Early Valanginian and *Duvalia emericii* known only from the Lower/Upper Valanginian boundary strata (*Karakaschiceras inostranzewi* Zone and the basal *Saynoceras verrucosum* Zone). Although only several specimens of the latter taxon are preserved (mostly adult and subadult rostra), its presence clearly proves the mentioned boundary interval (e.g. Janssen, 1997, 2020; Janssen and Clément, 2002; Főzy et al., 2010). Janssen and Clément (2002), who thoroughly studied belemnite assemblages at French sections, noticed several faunal changes within the Valanginian, including an extinction event at the base of the *Saynoceras verrucosum* Zone. Since the Lower/Upper Valanginian transition, a significant decrease in diversity is recorded. For the Upper Valanginian, only *Duvalia* cf. *kleini* is introduced as a new element. For the Valanginian, they are also typical elongated thin rostra of *Pseudobelus bipartitus*, described in detail by Thomel-Picollier (2018). Within the family Belemnopseidae, the genera *Conohibolites* and *Hibolites* were classified. Whilst tiny rostra of *"Hibolites" minaretoides* represent the only component of ?late Jurassic–earliest Cretaceous age in the Š-12 pocket, the genus *Conohibolites* present the late early/early late Barremian age. Moreover, these belemnites are described for the first time in the Kotouč Quarry and constitute the first macro-faunal evidence of the Barremian age in the Štramberk locality. *Conohibolites* aff. *platyurus* correspond to the so-called 'mid' Barremian belemnite fauna (*sensu* Clément, 2000; Janssen and Főzy, 2005; Janssen et al., 2012).

According to bed-by-bed investigations at numerous Tethyan localities including French and Bulgarian (Clément, 1999, 2000; Janssen, 2009, 2020; Janssen et al., 2012), Spanish (Janssen, 1997, 2003; Hoedemaeker et al., 2016) and Hungarian (Janssen and Főzy, 2004, 2005; Főzy and Janssen, 2009) sections, characteristic belemnite assemblages with typical taxa have been recognised. Within belemnite composition of our studied material, several assemblages were partly determined. In addition to Berriasian belemnites well-defined by Janssen (1997, 2003), Főzy et al., (2010), Hoedemaeker et al. (2016), etc., we can observe these biotic events with faunal turnovers from the Early Valanginian through the 'mid' Barremian (*see* **study IV.**).

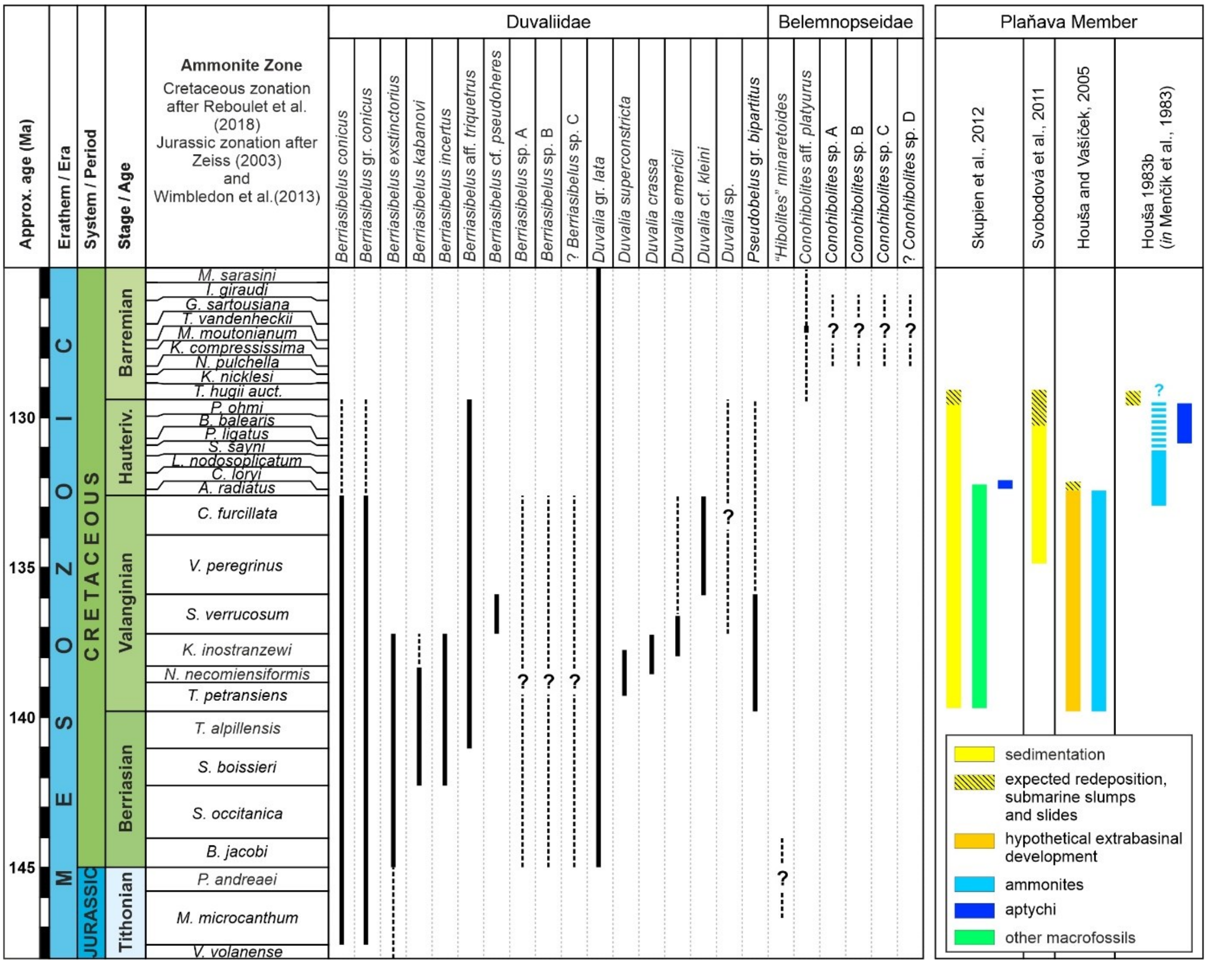

Fig. 6 Stratigraphic distribution of belemnites from the Kotouč Quarry. Stratigraphical ranges of taxa are set on the basis of abundant comparable research from the Tethyan and Boreal Realms (see references in Chapter 5.1). Dashed lines indicate occurrence of the studied species published in older publications with closer undetermined stratigraphy or the suggested range of species in the open nomenclature (marked by a question mark). Results are compared with the Plaňava Member investigations (Houša, 1983b in Menčík et al., 1983; Houša and Vašíček, 2005; Svobodová et al., 2011; Skupien et al., 2012) (Vaňková et al., 2021, submitted).

5.2 Palaeogeographical and palaeoecological evaluation

According to species-specific habitats of belemnites and/or preferences to certain palaeoecological conditions, it is possible to demonstrate bathymetric dependences and palaeobiogeographical distribution for studied taxa (**Fig. 7**). The bathymetric model used herein follows data published mainly in recent years (see references in Chapter 4.4.1 and **Fig. 4**).

In the Kurovice Quarry, belemnite rostra accumulated into one bed (Bed No. 105) were analysed as a flush from a shallower water area, probably by gravitational/turbidite flows (**study I.**). However, later studies provided partial bathymetrical determination of classified taxa. It seems that rostra were accumulated from two different environments and/or from just one common environment (an intermediate zone between shallow and deeper water parts). It is evidenced that the genera *Conobelus*, partly *Berriasibelus* and probably also *Hibolites* (*sensu* Mutterlose and Wiedenroth, 2008), represented shallower environmental elements of the proximal part of the shelf, and *Pseudobelus* and *Duvalia* could signify deeper water conditions. Nevertheless, the belemnite material should only be accumulated together *post mortem* and *via* a turbidite system. The rostra from the Kurovice Quarry show the closest similarity to Italian material, which is well described by Combémorel and Mariotti (1986a, 1990), and to Swiss belemnites, published by Favre (1880). Therefore, similar palaeoenvironmental conditions are presumed. Furthermore, similar belemnite fauna has also been recorded in Spain (Janssen, 1997; Hoedemaeker et al., 2016) and Hungary (Főzy et al., 2011).

The long stratigraphical interval (?latest Tithonian/Berriasian–'mid' Barremian) of preserved belemnites from the Kotouč Quarry, and characterisation of numerous taxa with different morphology belonging to different habitat requirements, also enable the observation of bathymetric demands (**studies II., IV.**). Only for the ?Tithonian–lowermost Berriasian Štramberk Limestone belemnites, rather shallow and stable environmental characteristics for sedimentation around the coral reef are evident. The genera *Conobeus*, *Berriasibelus*, *Hibolites* and *Duvalia* are typical in this facies. From the Valanginian to ?Hauterivian, a change in faunal composition is visible with the onset of the genus *Pseudobelus*. Its presence, together with the genus *Duvalia*, could represent a deeper water environment marking the basin deepening or a transgression event. Moreover, during the Valanginian–Hauterivian interval, the similar faunal changes are recorded in Bulgarian and French sections (*see* Clément, 2000, and references therein). The above mentioned taxa are typical in the Circum-Mediterranean Province of the Tethyan Realm. No Boreal belemnites have been recorded in the studied material. On the other hand, the species *Duvalia lata* and *Pseudobelus bipartitus* are known in the Boreal Realm (Mutterlose, 1979; Alsen and Mutterlose, 2009) and their migration probably happened along the coastline of the NW Tethys edge. According to the elongated and thin shape of the rostrum, the genus *Pseudobelus* is considered to be adapted to the sub-pelagic environment, suggesting migration patterns for long distances. In contrast, the duvaliid type of rostrum of species *Duvalia lata* was presumed to be likely bottom dwellers, with limited ability to move in the water column. However, it is a widespread taxon with well known migration patterns. Therefore, its life style must be subjected to further research.

Since the Hauterivian, the Mediterranean Province was divided into two subprovinces according to belemnite fauna composition (see Chapter 4.4.3) (**Fig. 7**). The belemnite rostra recognised in our studied material fully correspond to the French-Bulgarian Subprovince (Stoyanova-Vergilova, 1964; Combémorel and Stoyanova-Vergilova, 1991; Clément, 2000). Moreover, the presence of the Barremian genus *Conohibolites* confirms the validity of this statement and indicates a re-shallowing of the area during Lower and 'mid' Barremian, as its habitat is considered to lie between inner and outer shelf areas (Janssen et al., 2012).

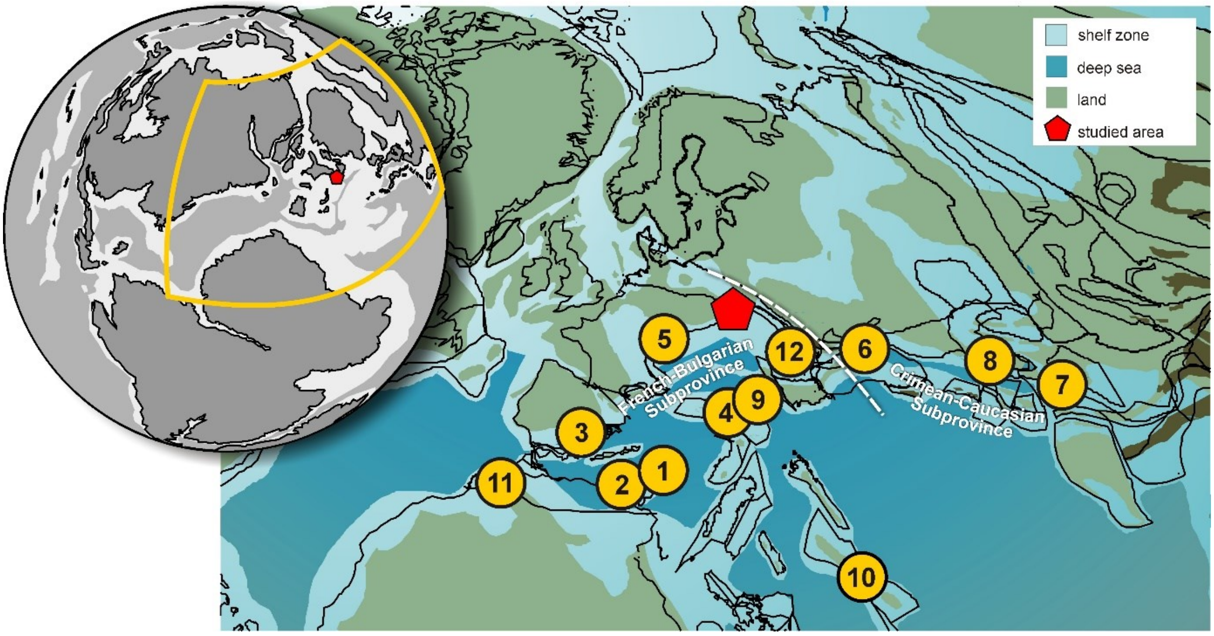

Fig. 7 Belemnite palaeobiogeographic distribution of the Mediterranean Province within the Tethys Ocean during the upper Tithonian–Barremian. Compiled after published data: studied area of the Outer Western Carpathians – Vašíček, 1978; Horák, 1988; Eliáš et al., 1996; Košťák et al., 2018; this study (Tithonian–Barremian); 1 – N Italy: Combémorel and Mariotti, 1986a (Tithonian); 2 – Sicily: Combémorel and Mariotti, 1990 (Tithonian); 3 – SE Spain: Janssen, 1997, 2003, 2018; Hoedemaeker et al., 2016 (Tithonian–Barremian); 4 – Hungary - Bakony Mountains: Főzy et al., 2010, 2011 (Tithonian–Valanginian); 5 – SE France: Combémorel, 1973; Janssen, 2009, 2018; Janssen et al., 2012 (Tithonian–Barremian); 6 – Crimea: Weiss, 1991 (Berriasian–Hauterivian) ; 7 – Azerbaijan: Ali-Zade, 1972 (Berriasian–Barremian); 8 – Georgia: Topchishvili et al., 2002; Kvantaliani and Keleptrishvili, 2005 (Valanginian–Barremian); 9 – Hungary - Gerecse Mountains: Janssen and Főzy, 2004, 2005; Főzy and Janssen, 2009 (Valanginian–Barremian); 10 – Turkey: Doyle and Mariotti, 1991 (Valanginian–Barremian); 11 – SW Morocco: Mutterlose and Wiedenroth, 2008 (Hauterivian–Barremian); 12 – Bulgaria: Stoyanova-Vergilova, 1963, 1965, 1970 (Hauterivian–Barremian). French-Bulgarian and Crimean-Caucasian Subprovinces were established from the Hauterivian to the Barremian. Paleomap modified after Golonka, 2000 (modified after Vaňková et al., 2021, submitted).

5.3 Belemnites as potential indicators of the palaeoenvironment of the Kotouč Quarry

Štramberk area belongs to the most complicated locality with rather unknown geological development. Numerous papers dealing with sedimentary analyses and mainly macro- and micro-fossil contents were published in an effort to decrypt the origin of individual formations, their composition and tectonic history (e.g. Eliáš and Stráník, 1963; Houša, 1976; Houša and Vašíček, 2005; Svobodová et al., 2011; Skupien et al., 2012; Vašíček et al., 2017; **study II.**). The origin of the Plaňava Member infilling the studied pockets is still unclear, as its original position within the Baška elevation (e.g. Skupien et al., 2012). Ammonites and belemnites originating from the Š-12 pocket possess multi-generational sedimentary infills in their chambers and alveolas that clearly demonstrate a reworking from older strata (Houša, 1976; Houša and Vašíček, 2005; **study IV.**). Reworking episodes, generated probably by sea-level changes and tectonic activity, may have happened several times. This is well documented also by the belemnite fauna stratigraphically ranging from the ?latest Tithonian/Berriasian to the Barremian and accumulated together.

According to belemnite taxonomy, stratigraphy and palaeoenvironmental implications allowed for partial reconstruction of the development of the Štramberk area (**study IV.**). During the Tithonian and early Berriasian, a shallow water stable environment surrounding the coral-*Diceras* reef prevailed (**Fig. 8A**). From the late Berriasian, the area was influenced by sea-level changes accompanied by reworking processes (**Fig. 8B**). According to belemnite assemblages (species *Pseudobelus* gr. *bipartitus* and *Duvalia* gr. *lata*), in the Valanginian and partly the ?Hauterivian, deeper water conditions are assumed. After Svobodová et al. (2011) and Skupien et al. (2012), during the Latest Hauterivian to early Barremian, the Lower Cretaceous sediments with the Štramberk Limestone formed a wave-cut cliff that was eroded by wave influence, as result of which, sediments accumulated into the basin. Simultaneously, re-sedimentation of the Plaňava Member is presumed (**Figs 6, 8C**). Finally, in the 'mid' Barremian, the Štramberk Limestone mixed with other Lower Cretaceous sediments were deformed by tectonic activity (**Fig. 8D**). Several cracks and crevasses were opened and infilled by variable material. According to the genus *Conohibolites*, during the early to early late Barremian, a shallower water environment was set again in the area.

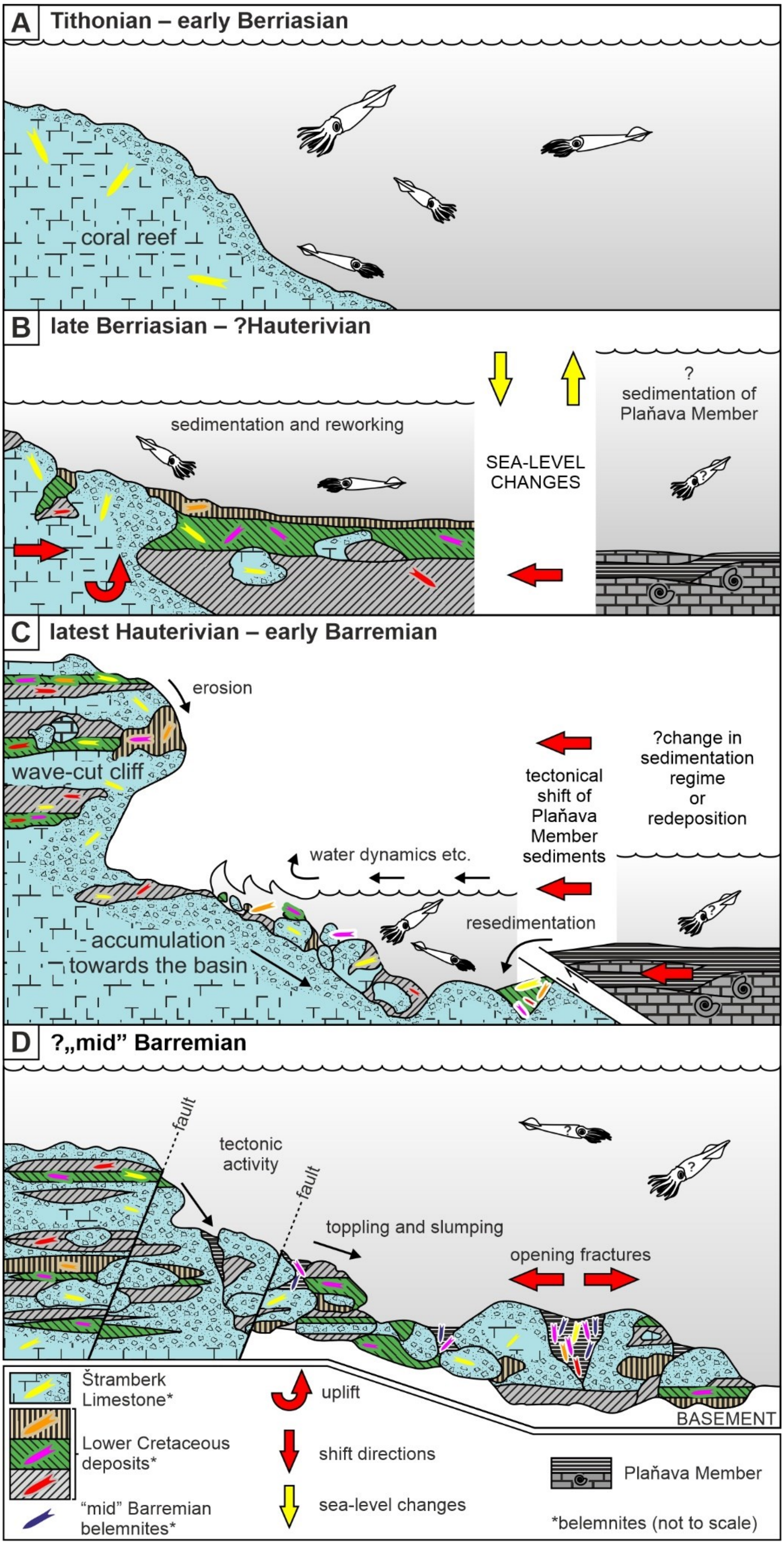
A
Tithonian – early Berriasian
coral reef
B
late Berriasian – ?Hauterivian
sedimentation and reworking
SEA-LEVEL CHANGES
?
sedimentation of Plaňava Member
C
latest Hauterivian – early Barremian
erosion
wave-cut cliff
tectonical shift of Plaňava Member sediments
?change in sedimentation regime or redeposition
water dynamics etc.
resedimentation
accumulation towards the basin
D
?„mid" Barremian
fault
tectonic activity
fault
toppling and slumping
opening fractures
BASEMENT
Štramberk Limestone*
Lower Cretaceous deposits*
"mid" Barremian belemnites*
uplift
shift directions
sea-level changes
Plaňava Member
*belemnites (not to scale)

Fig. 8 Hypothetical development of the Baška elevation (based on depositional distribution and belemnite content). A – coral-*Diceras* reef during the late Tithonian–early Berriasian; B – deposition of the facial of various Lower Cretaceous sediments and their reworking by tectonic and possible sea-level changes in the late Berriasian–Hauterivian. Sedimentation of the Plaňava Member ?outside the studied area; C – emergence of the area and subsequent erosion of a wave-cut cliff with rockfalls and accumulation in the basin. Re-sedimentation and incorporation of the Plaňava Member to depressions, tectonic crevasses and cavities in older deposits, resulting in: D – several pocket infills by heterogeneous, mostly reworked sediment and fossil materials. Not to scale (Vaňková et al., 2021, submitted).

5.4 Palaeoenvironmental geochemistry and isotope stratigraphy

As geochemical analyses are widely used in belemnite rostra during recent decades, the isotopic composition of carbon, oxygen and strontium isotopes are well-researched in the Early Cretaceous. In contrast, the Jurassic–Cretaceous interval is insufficient due to the sporadic occurrence and/or absence of belemnites at the Tithonian–Berriasian boundary in Tethys (Žák et al., 2011; Price et al., 2016) (**study III.**).

Results of oxygen and carbon isotope measurements (**Fig. 9**) show very light fluctuation in both sections (A and B) in the Kotouč Quarry (**Fig. 9**). These values are clearly correlated with isotopic trends observed in other sections within the Tethyan Realm (e.g. Žák et al., 2011; Price et al., 2016). The resultant ratios of the $\delta^{18}O$ values vary in section A from −0.4‰ to −1.0‰ and from −0.1 to −1.1‰ PDB in section B, and for $\delta^{13}C$ from −0.5 to −1.6‰ PDB in section A and from −0.8 to −2.4‰ PDB in section B. The most significant shifts in the $\delta^{13}C$ record were detected in beds A5 and B8. The negative trend of carbon ratios is typical and has also been recorded in other profiles of the Tethys area (*see* Price and Rogov, 2009). Similar results were obtained from belemnite rostra against the bulk rock samples (*see* Bodin et al., 2009). It is presumed that the isotopic signal in the belemnite rostra is more characteristic of a deeper water environment than of the bulk rock with a consequentially lower ^{13}C signal (van de Schootbrugge et al., 2000).

In the $\delta^{18}O$ record, shifts in peaks are observed in beds B8 and B5. Higher values of $\delta^{18}O$ and $\delta^{13}C$ were also measured in bed B21. For oxygen isotopes, negative trends were reported in the Tethyan Realm during the Lower Cretaceous by Bodin et al. (2009), Žák et al. (2011) and Price et al. (2016). No significant isotopic expressions are observed in the studied sections, however, different taxa used for the analyses could signify diverse preferences (e.g. *Hibolithes*, *Duvalia*; Bodin et al., 2009; Mutterlose et al., 2010; etc.). Our obtained data are consistent with $\delta^{18}O$ results of Főzy et al. (2011) and Price et al. (2016), and may suggest similar palaeoenvironmental conditions. The shift to slightly more negative values (*cf.* Žák et al., 2011) may have been caused by warmer (probably shallower) characteracteristics of the environment (surrounding the coral reef) than in the deeper water of the distal, epioceanic environment recorded at Puerto Escaño.

In comparison to stable isotopes obtained from belemnite rostra and bulk rock (van de Schootbrugge et al., 2000; Bodin et al., 2009), our data follow the trends (average 0.7‰ V-PDB for $\delta^{18}O$ and average −1.3‰ V-PDB for $\delta^{13}C$) similar to those published by Žák et al. (2011) and Price et al. (2016). A noticeable decrease of values in section B (Ferasini Subzone) to more negative values is in accordance with carbon-isotope stratigraphy used for the Tethys (e.g. Weissert and Mohr, 1996; Žák et al., 2011) and also for the Boreal areas (Žák et al., 2011; Price and Rogov, 2009; Dzyuba et al., 2013). The declination in values, however, is typical in the Tithonian–Berriasian boundary and during the early Berriasian. In contrast to belemnite isotope data, the bulk rock $\delta^{18}O_{carb}$ values show some variations reflecting temperature changes (supported also by the occurrence of the Sub-boreal ammonite taxa) (Vaňková et al., 2019). In contrast to bulk rock isotope data, belemnites respond to different processes (Hoffmann et al., 2016), therefore, its habitat may correspond with deeper shelf environments (Mitchell, 2005; Price and Page, 2008; Žák et al., 2011).

In the strontium isotope values (**Fig. 9**), a relatively short trend is observed (an average value of 0.707298 and 0.707274). Identified values correspond to early Berriasian age (Jones et al., 1994; Price and Gröcke, 2002) and are in agreement with the global strontium isotope curve (e.g. Price et al., 2016). Obtained strontium isotopes are also well correlated with micro- and macro-fossils and magnetostratigraphy (**study II.**) As a residence time of the strontium is long (see Chapter 4.4.2), the resulting values do not correspond to prominent fluctuations but rather indicate the range of values in the studied sections. In the presented study, the $^{87}Sr/^{86}Sr$ ratios show a minor shift (average ~9×10^{-5}) against data published by McArthur et al. (2007a) and Bodin et al. (2015). According to recently published data, the Sr isotopic values of the Jurassic–Cretaceous interval reach values of 0.70717–0.70722 (Kuznetsov et al., 2017; Ruďko et al., 2017). As the global Sr isotope trend is relatively poorly documented in the Jurassic–Cretaceous interval (**study III.**) and in the early Berriasian, further investigations are necessary.

In well-preserved calcitic rostra, average concentrations of individual elements indicating diagenesis were analysed: Fe (average - section A ~63.5 ppm; section B ~36 ppm), Mn (average - section A ~17 ppm; section B ~7 ppm), Mg (average - section A ~2734 ppm; section B ~2798 ppm), Sr (average - section A ~1115 ppm; section B ~1223 ppm). These results are in accordance with data published by van de Schootbrugge et al. (2000), Rosales et al. (2004a), etc. To determine a degradation of prime calcite and concentration changes (*see* Wierzbowski and Joachimski, 2009) for diagenetic overprint classification, cross-plots of Sr versus Mg and Fe versus Mn were created (**study II.**). Diagenetic alteration was set almost for half of the samples (see diagenetic overprint limits in Chapter 4.4.2.1), which were excluded from interpretations.

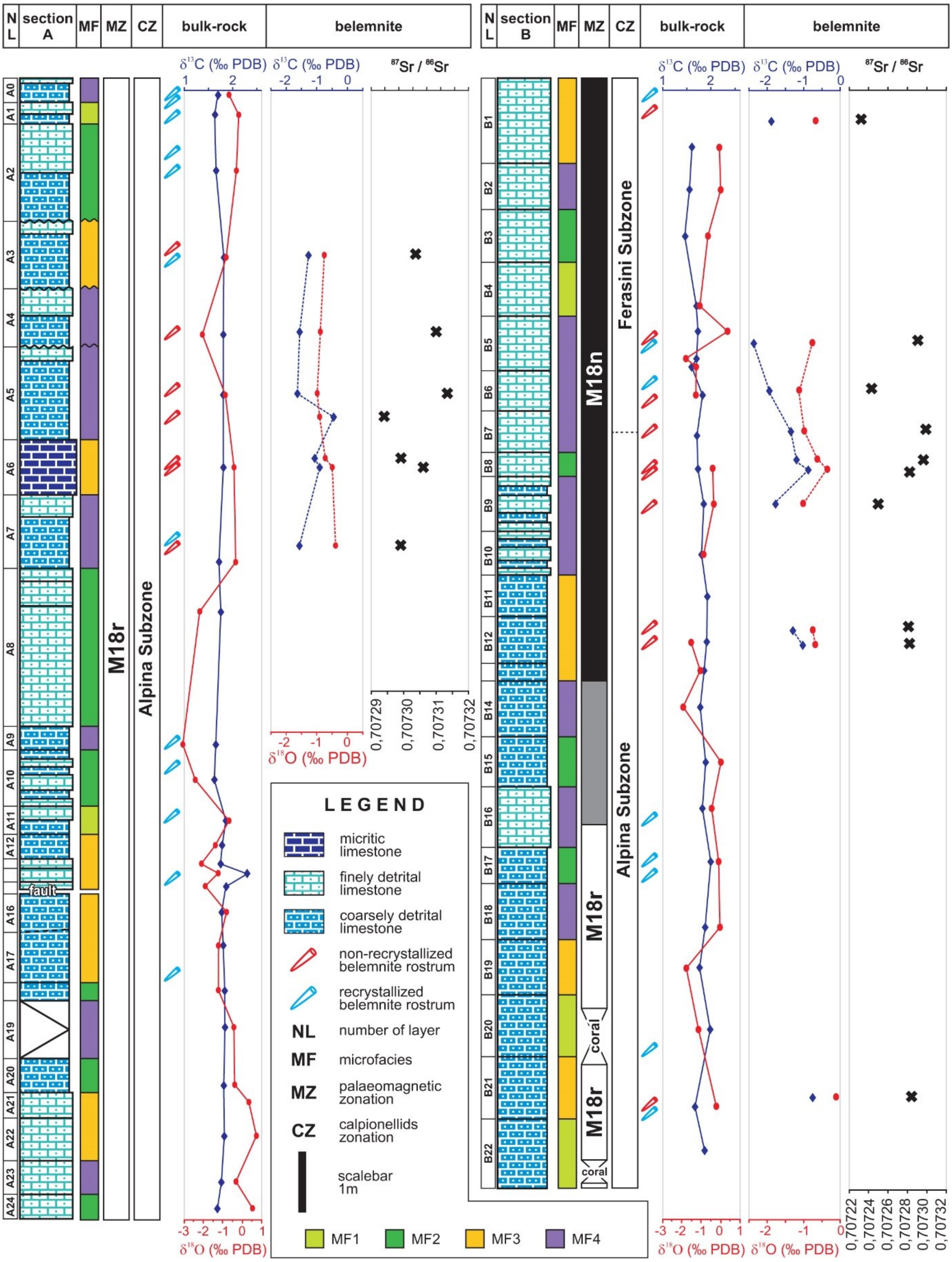

Fig. 9 Section A and B of the Štramberk Limestone with relation to bulk rock and belemnite stable isotope data ($\delta^{13}C$ and $\delta^{18}O$) and belemnite $^{87}Sr/^{86}Sr$ data (Vaňková et al., 2019).

6. Conclusion

In the studied stratigraphical interval, the Tethyan belemnites are abundantly preserved at the investigated localities. The studied material, counting more than 10,000 rostra, provided diversified belemnite assemblages of different ages and palaeoenvironmental requirements. Taxonomically, belemnites of the families Duvaliidae and Belemnopseidae, including genera *Conobelus*, *Berriasibelus*, *Duvalia*, *Pseudobelus*, *Hibolites* and *Conohibolithes*, were determined, counting 28 species and 12 taxa left in the open nomenclature. This is undoubtedly the most diversified belemnite fauna within the Outer Western Carpathians. The unusual diversity is caused by the unique deposition of resistant rostra. Stratigraphically, the oldest belemnite fauna is of the early Tithonian age (Kurovice Quarry), however, it is represented only by a few rostra, which were accumulated together with the Berriasian belemnites *via* probable tsunamite in the lowermost Berriasian. The only ?late Tithonian/early Berriasian belemnite rostra were investigated *in situ* (Štramberk Limestone, Kotouč Quarry) in A and B sections. This material was also analysed by numerous geochemical methods ($\delta^{18}O$, $\delta^{13}C$, $^{87}Sr/^{86}Sr$, main and trace elements) in an effort to create a complex overview of palaeoecological conditions. According to the stable isotope analyses, our obtained data follow a negative trend without significant shifts of values typical for belemnites from the Tethys area. The strontium isotopes from rostra reveal an early Berriasian age for all studied belemnites and clearly provide evidence of the Cretaceous period for both investigated sections. Main and trace element analyses confirmed a diagenetic overprint for almost half of the studied samples. The majority of belemnites come from the upper Berriasian–Valanginian strata (Kotouč Quarry), where also the most massive reworking of rostra is presumed. At this time, the area was affected by sea-level changes and tectonic activity, so reworking processes are highly probable and also explain stratigraphical mixture of recorded fauna. After a shallowing period expressed by taxa that typically preferred the rather proximal part of the inner and middle shelf, during the Valanginian and probably the ?Hauterivian, the deeper water environment of the oceanic zone is expected (sub-pelagic and pelagic zones). The Valanginian extinction event at the base of the *Saynoceras verrucosum* Zone, slightly above the Lower/Upper Valanginian transition, is partly recorded in taxa composition herein, as several identified species became extinct before this interval. Thereafter, a decrease of diversity in the Late Valanginian is observed. For the first time, we have evidence of the late early/early late Barremian belemnites, which represent the first macrofossils known from the

Štramberk locality. These taxa are reported exclusively from the proximal zone and/or the zone between the proximal and distal parts within the NW Tethys. Therefore, we assume a re-shallowing of the area again in the Barremian. Designated taxa fully correspond to the French-Bulgarian Subprovince established during the Hauterivian–Barremian interval. Overall, our studied belemnites belong to the Mediterranean Province. No Boreal (or Sub-boreal) belemnite components have been recorded in the material studied. Palaeobiogeographically, the investigated belemnites show the largest similarity to the material from France, Spain, Hungary, Italy, Morocco and Bulgaria.

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Annex

I. Košťák, M., **Vaňková, L.**, Mazuch, M., Bubík, M., Reháková, D., **2018**. Cephalopods, small vertebrate fauna and stable isotope (δ^{13}C, δ^{18}O) record from the Jurassic-Cretaceous transition (uppermost Crassicollaria through Calpionella Zones) of the Outer Western Carpathians, Kurovice quarry (Czechia). *Cretaceous Research* 92, 43-65.

II. Vaňková, L., Elbra, T., Pruner, P., Vašíček, Z., Skupien, P., Reháková, D., Schnabl, P., Košťák, M., Švábenická, L., Svobodová, A., Bubík, M., Mazuch, M., Čížková, K., Kdýr, Š., **2019**. Integrated stratigraphy and palaeoenvironment of the Berriasian peri-reefal limestones at Štramberk (Outer Western Carpathians, Czech Republic). *Palaeogeography, Palaeoclimatology, Palaeoecology* 532, 109256. https://doi.org/10.1016/j.palaeo.2019.109256

III. Wimbledon, W.A.P., Reháková, D., Svobodová, A., Elbra, T., Schnabl, P., Pruner, P., Šifnerová, K., Kdýr, Š., Dzyuba, O., Schnyder, J., Galbrun, B., Košťák, M., **Vaňková, L.**, Copestake, P., Hunt, C.O., Riccardi, A., Poulton, T.P., Bulot, J.G., Frau, C., De Lena, L., **2020a**. The proposal of a GSSP for the Berriasian Stage (Cretaceous System): Part 1. *Volumina Jurassica* XVIII, 53-106.

IV. Vaňková, L., Košťák, M., Mazuch, M., **2021**. Lower Cretaceous belemnites of Štramberk klippen (Czech Republic): Implications for geological history of the Outer Western Carpathians. *Cretaceous Research*, in review.

Prohlášení školitele o podílu studenta na publikacích, které jsou součástí doktorské práce

Jako školitel studenta Mgr. Lucie Vaňkové prohlašuji, že student se podílel na pracích, které byly předloženy jako součást jeho disertační práce, následujícím podílem:

I. Košťák, M., **Vaňková, L.**, Mazuch, M., Bubík, M., Reháková, D. (**2018**). Cephalopods, small vertebrate fauna and stable isotope ($\delta^{13}C$, $\delta^{18}O$) record from the Jurassic-Cretaceous transition (uppermost Crassicollaria through Calpionella Zones) of the Outer Western Carpathians, Kurovice quarry (Czechia). *Cretaceous Research* 92, 43-65.

30% taxonomické zhodnocení, interpretace stratigrafických, palaeogeografických a paleoekologických dat, podíl na přípravě a finalizaci rukopisu

II. Vaňková, L., Elbra, T., Pruner, P., Vašíček, Z., Skupien, P., Reháková, D., Schnabl, P., Košťák, M., Švábenická, L., Svobodová, A., Bubík, M., Mazuch, M., Čížková, K., Kdýr, Š. (**2019**). Integrated stratigraphy and palaeoenvironment of the Berriasian peri-reefal limestones at Štramberk (Outer Western Carpathians, Czech Republic). *Palaeogeography, Palaeoclimatology, Palaeoecology* 532, 109256. https://doi.org/10.1016/j.palaeo.2019.109256

30% sběr a příprava materiálu, spolupráce při geochemických analýzách, taxonomické zhodnocení, kompilace dat, interpretace výsledků, příprava a finalizace rukopisu

III. Wimbledon, W.A.P., Reháková, D., Svobodová, A., Elbra, T., Schnabl, P., Pruner, P., Šifnerová, K., Kdýr, Š., Dzyuba, O., Schnyder, J., Galbrun, B., Košťák, M., **Vaňková, L.**, Copestake, P., Hunt, C.O., Riccardi, A., Poulton, T.P., Bulot, J.G., Frau, C., De Lena, L. (2020a). The proposal of a GSSP for the Berriasian Stage (Cretaceous System): Part 1. *Volumina Jurassica* XVIII 53-106.

5% interpretace izotopů stroncia z roster belemnitů, podíl na přípravě a finalizaci rukopisu

IV. Vaňková, L., Košťák, M., Mazuch, M. (**2021**). Lower Cretaceous belemnites of Štramberk klippen (Czech Republic): Implications for geological history of the Outer Western Carpathians. *Cretaceous Research*, in review.

85% taxonomické zhodnocení, interpretace stratigrafických, palaeogeografických a paleoekologických dat, tvorba sedimentačního modelu, příprava a finalizace rukopisu

doc. RNDr. Martin Košťák, Ph.D.
školitel

The declaration of the supervisor

As the supervisor of Mgr. Lucie Vaňková I declare her participation in the studies that were submitted as a part of her Ph.D. thesis by the following contribution:

I. Košťák, M., **Vaňková, L.**, Mazuch, M., Bubík, M., Reháková, D. (**2018**). Cephalopods, small vertebrate fauna and stable isotope ($\delta^{13}C$, $\delta^{18}O$) record from the Jurassic-Cretaceous transition (uppermost Crassicollaria through Calpionella Zones) of the Outer Western Carpathians, Kurovice quarry (Czechia). *Cretaceous Research* 92, 43-65.

30% taxonomic classification, stratigraphic, palaeogeographic and palaeoecological interpretations, contribution to the preparation and finalization of the manuscript

II. Vaňková, L., Elbra, T., Pruner, P., Vašíček, Z., Skupien, P., Reháková, D., Schnabl, P., Košťák, M., Švábenická, L., Svobodová, A., Bubík, M., Mazuch, M., Čížková, K., Kdýr, Š. (**2019**). Integrated stratigraphy and palaeoenvironment of the Berriasian peri-reefal limestones at Štramberk (Outer Western Carpathians, Czech Republic). *Palaeogeography, Palaeoclimatology, Palaeoecology* 532, 109256. https://doi.org/10.1016/j.palaeo.2019.109256

30% collection and preparation of the material, collaboration during geochemical analyses, taxonomic classification, data compilation, interpretation of results, preparation, finalization and final editing of the manuscript

III. Wimbledon, W.A.P., Reháková, D., Svobodová, A., Elbra, T., Schnabl, P., Pruner, P., Šifnerová, K., Kdýr, Š., Dzyuba, O., Schnyder, J., Galbrun, B., Košťák, M., **Vaňková, L.**, Copestake, P., Hunt, C.O., Riccardi, A., Poulton, T.P., Bulot, J.G., Frau, C., De Lena, L. (**2020a**). The proposal of a GSSP for the Berriasian Stage (Cretaceous System): Part 1. *Volumina Jurassica* XVIII 53-106.

5% interpretation of strontium isotope analyses from belemnite rostra, contribution to the preparation and finalization of the manuscript

IV. Vaňková, L., Košťák, M., Mazuch, M. (**2021**). Lower Cretaceous belemnites of Štramberk klippen (Czech Republic): Implications for geological history of the Outer Western Carpathians. *Cretaceous Research*, in review.

85% taxonomic classification, interpretation of stratigraphic, palaeogeographic and palaeoecological data, creation of sedimentation model, preparation, finalization and final editing of the manuscript

doc. RNDr. Martin Košťák, Ph.D.
The Ph.D. supervisor