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Jurassic and Lower Cretaceous belemnites like proxy markers of stratigraphy and paleoecology

Belemniti jury a spodní křídy jako proxy markery stratigrafie a paleoekologie

Type of thesis

Doctoral thesis

Supervisor:

prof. RNDr. Martin Košťák, Ph.D.

Prague, 2025

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

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Abstract

This doctoral thesis explores the taxonomy, stratigraphy, and palaeoecological role of almost unknown Jurassic and Lower Cretaceous belemnites in Central Europe, primarily focusing on the Czech Republic. Belemnites, as extinct nektonic/pelagic cephalopods, are valuable tools in palaeontological research due to the robustness of their calcitic internal shells - rostra, which serve as excellent fossil records for systematic, biostratigraphic, and geochemical analyses. The thesis is based on three detailed case studies: (I.) the Jurassic strata of northern Bohemia, (II.) the Jurassic/Cretaceous boundary in the Rettenbacher section (Austria), and (III.) Lower Jurassic deposits from the Lukoveček locality (Outer Western Carpathians).

The study identifies six belemnite families encompassing eleven genera and sixteen species, ten of which are newly recorded from the Czech Republic. Morphometric and taxonomic assessments were combined with stable isotope ($\delta^{13}C$, $\delta^{18}O$) and strontium ($^{87}Sr/^{86}Sr$) analyses to reconstruct palaeoenvironmental conditions and test the applicability of rostra as stratigraphic markers. Although diagenesis limited some geochemical interpretations, valuable data support regional correlations and indicate faunal migrations linked to palaeoceanographic changes.

The results significantly refine the Jurassic stratigraphy of the Bohemian Massif and contribute to the biostratigraphic framework across the Jurassic–Cretaceous boundary. The palaeoecological evaluation of belemnite morphotypes also partly provides insight into habitat preferences and environmental shifts within the Tethyan and Boreal realms. This work thus highlights the potential of belemnites as multi-proxy tools in stratigraphy and palaeoecology, especially in regions where classical index fossils are missing or scarce or poorly preserved.

Key Words: Belemnites; Jurassic; Jurassic/Cretaceous boundary; Biostratigraphy; Paleoecology; Isotope geochemistry

Abstrakt

Tato disertační práce se zabývá taxonomií, stratigrafií a paleoekologií téměř neznámých jurských a spodnokřídových belemnitů ve střední Evropě, se zvláštním zaměřením na území České republiky. Belemniti, vyhynulí nektonní/pelagičtí hlavonožci, představují cenný nástroj paleontologického výzkumu díky pevné vnitřní kalcitové schránce (rostru), která se výborně dochovává a slouží pro systematické, biostratigrafické a geochemické analýzy. Práce je založena na třech případových studiích: (I.) jurské sedimenty severních Čech, II.) hranice jura–křída v profilu Rettenbacher (Rakousko) a (III.) spodnojurské uloženiny lokality Lukoveček (Vnější Západní Karpaty).

Bylo identifikováno šest čeledí belemnitů zahrnujících jedenáct rodů a šestnáct druhů, z nichž deset je na území ČR popsáno vůbec poprvé. Morfometrické a taxonomické studie byly doplněny o analýzy stabilních izotopů ($\delta^{13}C$, $\delta^{18}O$) a stroncia ($^{87}Sr/^{86}Sr$) za účelem rekonstrukce paleoprostředí a ověření využitelnosti rostra jako stratigrafického markeru. I přes vliv diageneze, který omezil některé geochemické interpretace, se podařilo získat cenná data podporující regionální korelace a indikující migrace spojené se změnami paleoceánografie.

Výsledky významně přispívají k upřesnění jurské stratigrafie Českého masivu a biostratigrafického členění jury a hraničního intervalu jura/křída. Paleoekologické vyhodnocení morfotypů belemnitů zároveň částečně přináší poznatky o preferencích prostředí a vývojových změnách v rámci tethydní a boreální oblasti. Tato práce tak ukazuje význam belemnitů jako klíčové skupiny pro stratigrafii a paleoekologii, obzvláště v oblastech, kde chybí jiné spolehlivé indexové fosilie.

Klíčová slova: Belemniti; Jura; Hranice jura/křída; Biostratigrafie; Paleoekologie; Izotopová geochemie

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1. Introduction

Belemnites were carnivorous marine pelagic cephalopods that lived from the Upper Triassic until their extinction at the end of the Cretaceous period. Their predatory lifestyle is also associated with a perfectly developed nervous system, sensory organs, and organs used for movement, hunting, defence, and prey processing (Klug et al. 2010, 2016). According to rare findings of soft body parts, we assume that belemnites resembled some recent representatives of Dibranchiata (e.g., Klug et al. 2016). The stratigraphic importance of belemnites is considerable. They have been important for regional and global biostratigraphy since the Lower Jurassic (e.g., Christensen 1990; Doyle 1991, 1992; Doyle & Benett 1995; Doyle & Howlett 1989; Doyle & Kelly 1988; Dzyuba 2012, 2013; Dzyuba et al. 2016, 2019, 2021).

The shell of belemnites consists of several solid parts - the rostrum (hydrodynamic organ), phragmocone (hydrostatic organ) and proostracum (Arkhipkin et al. 2014). The calcitic rostrum is divided into two basic parts – *rostrum solidum* and *rostrum cavum* (protecting the phragmoconus) (e.g., Fuchs 2012; Klug et al. 2024). In some Jurassic and Lower Cretaceous (with few exceptions of the Cenomanian taxa) belemnites also the epirostrum (mostly aragonitic, prolonging the rostrum solidum) is developed. The phragmocone (starting with the spherical protoconch) is formed by aragonite, yielding various septa and the siphuncle placed exclusively at the ventral side. It is assumed that the part of the phragmocone around the siphonal tube was composed mainly of organic matter (Hoffmann & Stevens 2020). The siphuncle serves to osmotically regulate liquids and gases in the phragmocone, which is therefore a hydrostatic organ. The transformation into calcite or aragonite occurred only secondarily after the individual's death, but it was also possible during life (see Hoffmann & Stevens 2020). The last and largest part of the phragmocone was formed by the living chamber and the proostracum, which reinforced the dorsal part of the body. The phragmocone was then covered by a nacreous-prismatic two-layered conoteca, which subsequently it extended into the proostracum.

While the phragmocone is rarely preserved and the proostracum is almost always missing in the fossil record, the rostra are the most commonly recorded parts of belemnites. They are used for systematics, stratigraphy, palaeoecology and geochemical analyses (see below).

The juvenile belemnite began its life in an egg protecting the protoconch and the embryonal (sometimes primordial in the literature) rostrum that was formed from the earliest ontogenetic phases (e.g., Doguzhaeva et al. 2014; Fuchs 2012; Hoffmann & Stevens 2020). The rostra of juvenile stages are relatively similar and precise determination of species, or even genera, is not possible with certainty on their basis. The way of life of belemnites had a fundamental influence on the shape of the rostrum. Pelagic forms have an elongated rostrum, mainly cylindrical, often forming an organic (or aragonite) epirostrum and sometimes acquiring large dimensions. On the contrary, the bottom-dwelling representatives (e.g., genus *Duvalia* Bayle, 1878) have a significantly laterally compressed rostrum and are thus assumed to be closely related to life on the sea-bottom (see Figure 1).

Belemnites are important index fossils and serve as stratigraphically and palaeogeographically important fossils. Biozonation based on belemnite occurrences is particularly applicable in the

Upper Cretaceous (Cenomanian, Campanian and Maastrichtian mainly) (Christensen 1990; Remin 2015). The possible biostratigraphic use of rostra in other periods is at least debatable (e.g. Doyle & Benett 1995).

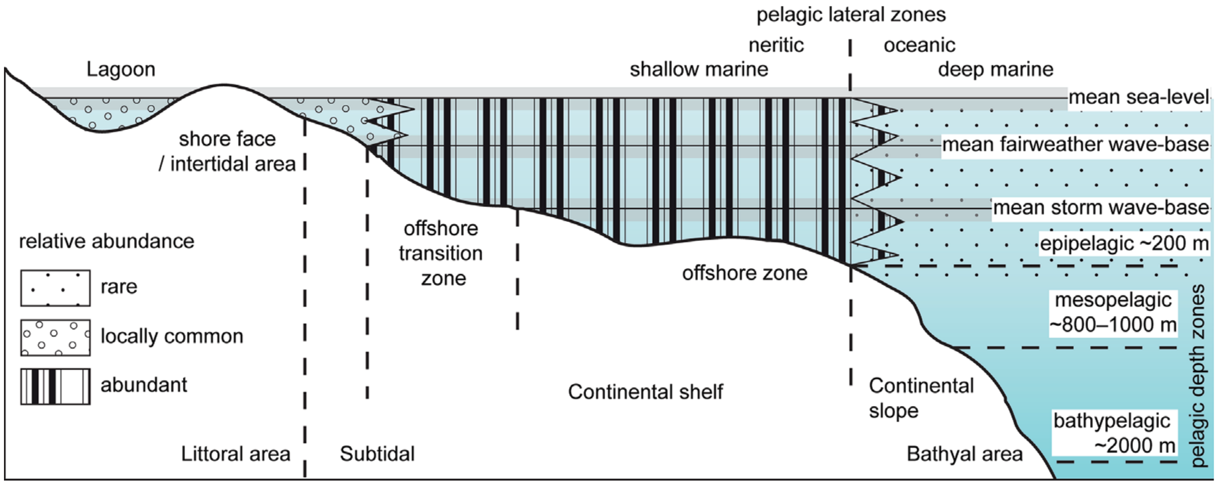

Figure 1: Depth and lateral distribution and relative abundance of belemnites (Hoffmann & Stevens 2020).

Based on data from recent shelf-dwelling, active swimming coleoids, that most belemnites inhabited well-oxygenated water masses at depths between 1 and 200 m, with a salinity between 27‰ and 37‰ and temperatures between 10°C and 30°C (Hoffmann & Stevens 2020).

Belemnites first occurred during the Late Triassic in the north-eastern Tethys (Iba et al. 2012; Zhu & Bian 1984). In the Lower Jurassic (Hettangian), belemnites underwent rapid radiation and a larger number of small forms inhabiting the neritic zone of the then European oceans (Western Tethys) evolved (e.g., the genus *Schwegleria* Riegraf, 1980 or *Nannobelus* Pavlov, 1913). Since at least the Early Jurassic (Toarcian) belemnites were globally distributed with higher diversity towards higher palaeolatitudes during the Jurassic (Dera et al. 2016; Doyle & Pirrie 1999).

Belemnites, like ammonites, diversified into several faunal paleogeographic units during the Mesozoic, Upper Jurassic to Lower Cretaceous, respectively. The development of belemnite biogeographic units within the Boreal and Tethyan realms occurred in the Middle Jurassic and persisted until the Lower Cretaceous (Doyle 1987). The Pacific Realm was introduced by Arkell (1956) and sometimes a fourth realm (Austral) correlated with cooling intervals during the Valanginian to Aptian in the Early Cretaceous (Stevens 1963, 1965; Doyle & Pirrie 1999) is also distinguished. However, the numbers and definitions of individual super/sub-realms are highly variable between individual authors' opinions (e.g. Hallam 1973; Westermann 2000).

It is broadly accepted that the "cosmopolitan" distribution and/or endemism of belemnite groups, e.g. the Belemnitellidae and Dimitobelidae of the Upper Cretaceous, was controlled mainly by temperature and opening of the new migration routes. Other palaeoenvironmental factors (e.g. oxygenation, salinity concentration, pH, water quality, increasing predation, food availability) may have been of the regional importance.

All above mentioned factors causes several faunal turnovers and palaeobiogeographic changes in belemnite distribution during the Jurassic and Cretaceous (Dera et al. 2016; Doyle 1987; Doyle & Bennett 1995; Hoffmann & Stevens 2020).

1.1. Full publication list

Publications included in this thesis:

Study I.

Geist, J., Holcová, K., Vaňková, L., Košťák, M. & Mazuch, M. (2023). Belemnites and calcareous nannoplankton: Proxy tools for recognising of cryptic Jurassic geological history of Central Europe. *Palaeobiodiversity & Palaeoenvironments* 103, 303–325. https://doi.org/10.1007/s12549-022-00538-y

Study II.

Elbra, T., Skupien, P., Bubík, M., Košťák, M., Molčan Matejová, M., Pruner, P., Reháková, D., Švábenická, L., Vaňková, L., Cígler, V., **Geist, J.**, Kdýr, Š., Lukeneder, A., Rybová, P., Mazuch, M., Schnabl, P., Svobodová, A., Trubač, J. & Ucar, H. (2024). Integrated stratigraphy across the Jurassic–Cretaceous boundary in the Rettenbacher section (Northern Calcareous Alps, Salzburg, Austria). *Cretaceous Research* 158, 105854. https://doi.org/10.1016/j.cretres.2024.105854

Study III.

Geist, J., Weis, R., Schlögl, J., Košťák, M. & Mazuch, M. (2025). Olistoliths as overlooked sources of information: An example from Pliensbachian belemnites and ammonites of Lukoveček (Czechia, Western Carpathians). *Swiss Journal of Palaeontology*. accepted https://doi.org/10.1186/s13358-025-00366-5

Publication on related topic but not included in this thesis:

Geist, J. (2024). Jurský svět po Česku. *Živa* 2/2024, 50–53. (Jurassic in the Czech Republic; in Czech)

Focus of included studies:

1.2. Conference contributions

Geist, J. (2020) Belemniti jury severních Čech (Jurassic belemnites of Northern Bohemia). Student geological conference 2020. Conference proceedings, Brno. *Nakladatelství Masarykovy univerzity*. ISBN 978-80-210-9682-0, 30 pp.

Geist, J., Vaňková, L., Košťák, M. (2022). Geochemical characterisation of belemnite rostra from North-West Bohemia (Upper Cenomanian) - A contribution to palaeoenvironmental interpretation of a peri-Tethyan shelf. Abstract Volume of the 11th International Symposium on the Cretaceous System, Warsaw. *The Polish Academy of Sciences*. ISBN 978-83-944813-7-7, 397 pp.

Geist, J., Vaňková, L., Holcová, K., Košťák, M., Mazuch, M. (2022). Belemnites and calcareous nannofossils from the North Bohemia reveal prolonged Jurassic sedimentation in Central Europe. 11th International Congress on the Jurassic System, Budapest. *University of Warsaw, Institute of Geology.* ISBN 978-615-5270-71-0, 154 pp.

Kustmüllerová, L., **Geist, J.**, Kohout, O., Košťák, M., Svobodová, A., Čech, S. (2022). Contribution to the definition of the Lower/Middle Coniacian boundary: A multidisciplinary study from Central Europe (Březno section, Bohemian Cretaceous Basin). The 6th International Palaeontological Congress, Khon Kaen. *Mahasarakham University.* 478 pp.

Geist, J., Schlögl, J., Weis, R. (2023). Lower Jurassic Cephalopod Fauna from the Czech Republic (Lukoveček; Outer Western Carpathians). Jurassica XV, Iłża. *Polish Geological Society & Polish Geological Institute – National Research Institute*. ISBN 978-83-67807-52-4, 86 pp.

Geist, J., Vaňková, L., Košťák, M. (2023). The Plenus Cold Event in NE Bohemia (Bohemian Cretaceous Basin) preliminary results. 22nd Czech – Slovak – Polish Palaeontological Conference, Ostrava.

1.3. Aims of the thesis and problem definition

Belemnite fossils, especially the Jurassic ones, are a relatively neglected group in the Czech Republic. More modern works describing the taxonomy and palaeoecology of Jurassic belemnites from the Czech territory are fully missing. Current research is based on previous works, mainly from the late 19th and early 20th centuries and old museal but also few new records of belemnites. The prospect of using belemnite rostra in current research has significantly increased in the last decades. Proxy isotope data from them can greatly contribute to the completion of unclear biostratigraphic and palaeogeographic facts, however, they are not crucial in this research (see below).

Main points of the Ph.D. thesis:

- clarification of the Jurassic stratigraphy in the Czech Republic using belemnite systematics and taxonomy and (partly) isotopic analyses.
- palaeo(bio)geographical evaluation of the Jurassic strata of the Czech Republic based on modern belemnite taxonomy.
- contribution to the issue of determining the Jurassic/Cretaceous boundary with the possibility of using belemnite rostra.

2. Geological and stratigraphical settings

2.1. Jurassic of the Northern Bohemia

Figure 2: Details of limestone (partly dolomitised) and siltstone alternations at the Doubice (Vápenka) locality, here showing the wall of the gallery (photo by Aleš Novák; length of hammer 30 cm, Geist et al. 2023).

The region of interest is primarily characterised by Jurassic sedimentary units, which are accompanied by Permo-Carboniferous and Cretaceous formations, as well as metamorphic and volcanic rocks dating from the early Palaeozoic to Neoproterozoic and neovolcanites (Opletal & Adamová 2001). The Permo-Carboniferous deposits, identified as the Sudetic basins, are situated along the Lausitian Fault and in various other locations (Holub et al. 1975).

Focusing specifically on the Jurassic period, the sedimentary rocks in Northern Bohemia comprise sandstones, limestones, and dolomites, intercalated by non-carbonate layers (i.e. shales, Chrt 1957; see the Figure 2). These rock formations can exceed 100 metres in thickness, particularly observed at Doubice (Vápenka) and in drill hole D-2 (Chrt 1957). This drill hole is the deepest at 204 metres, revealing a complete stratigraphic sequence that begins with a granitoid basement (0–16 metres), followed by Jurassic sandstones alternating with calcareous dolomite and clay layers (16–70 metres), dolomitised carbonates interlayered with pelitic sediments (70–98 metres), pelitic sediments (98–116 metres), and dolomitic limestones (116–124 metres). The Jurassic strata are overlain by the Upper Cretaceous sandstones, which contain coal seams, marine conglomerates and sandstones with fossils (124–204 metres).

Currently, only mostly non-fossiliferous strata (the absence of fossils is mainly linked to strong dolomitisation) are visible in the area. Consequently, researchers rely on museal materials, such as drill cores and fossils, to study these rocks. Exposed Jurassic sediments are only observable in at the locality of Doubice (Vápenka) and Brtníky (Šternberk).

The Jurassic age of these formations was first proposed by Lenz (1870), based on fossil evidence from Saxony, including a dubious record of *Belemnites giganteus* von Schlotheim, 1820. Bruder (1882, 1885) noted the initiation of sedimentation during this time, suggesting it likely commenced earlier in Saxony, albeit without any relevant evidences. While the sedimentation in Saxony is believed to have concluded during the Kimmeridgian, it appears that this process may have extended later in the Bohemian region (Eliáš 1981). Furthermore, calcareous nannofossils from the Tithonian age were identified by Holcová and Holcová (2016).

Based on our new investigation, the Jurassic sedimentary strata in the northern Bohemian Massif span from the Bajocian to Tithonian ages, as evidenced by records of belemnites and calcareous nannofossils. The belemnite fauna encompasses the lower Bajocian (spanning the *Propinquans* to *Humphriesianum* zones) through the ?Kimmeridgian, with a notable emphasis on the Middle Jurassic belemnite association, particularly the genus *Belemnopsis* (Geist et al. 2023).

Significantly, the presence of megateuthidid belemnites, including *Megateuthis suevica* (Klein, 1773) and *Megateuthis* cf. *M. elliptica* (Miller, 1826), highlights the earliest known faunal components within the Central European Jurassic (Bohemian Massif). The occurrence of *M. suevica* in carbonate rocks suggests the beginning of carbonate sedimentation in the early Middle Jurassic, challenging earlier assumptions that this process started later in the Late Jurassic (Geist et al. 2023).

Moreover, macro- and microfaunal data indicate a trend of a long sedimentation interrupted by frequent gaps, likely triggered by eustatic cycles. As a result, the previously established lithostratigraphic divisions and their definitions (e.g. Brtníky and Doubice formations based on similar lithological characteristics) have to be improved in the future.

In addition, calcareous nannoplankton assemblages suggest fluctuations in fertility conditions in surface waters throughout the Jurassic in Central Europe. Notably, the taxon *Cylindroteuthis* cf. *C. puzosiana* (d'Orbigny, 1842) illustrates the Boreal influence and establishing biotic communication between the studied area and cooler regions during the Upper Jurassic.

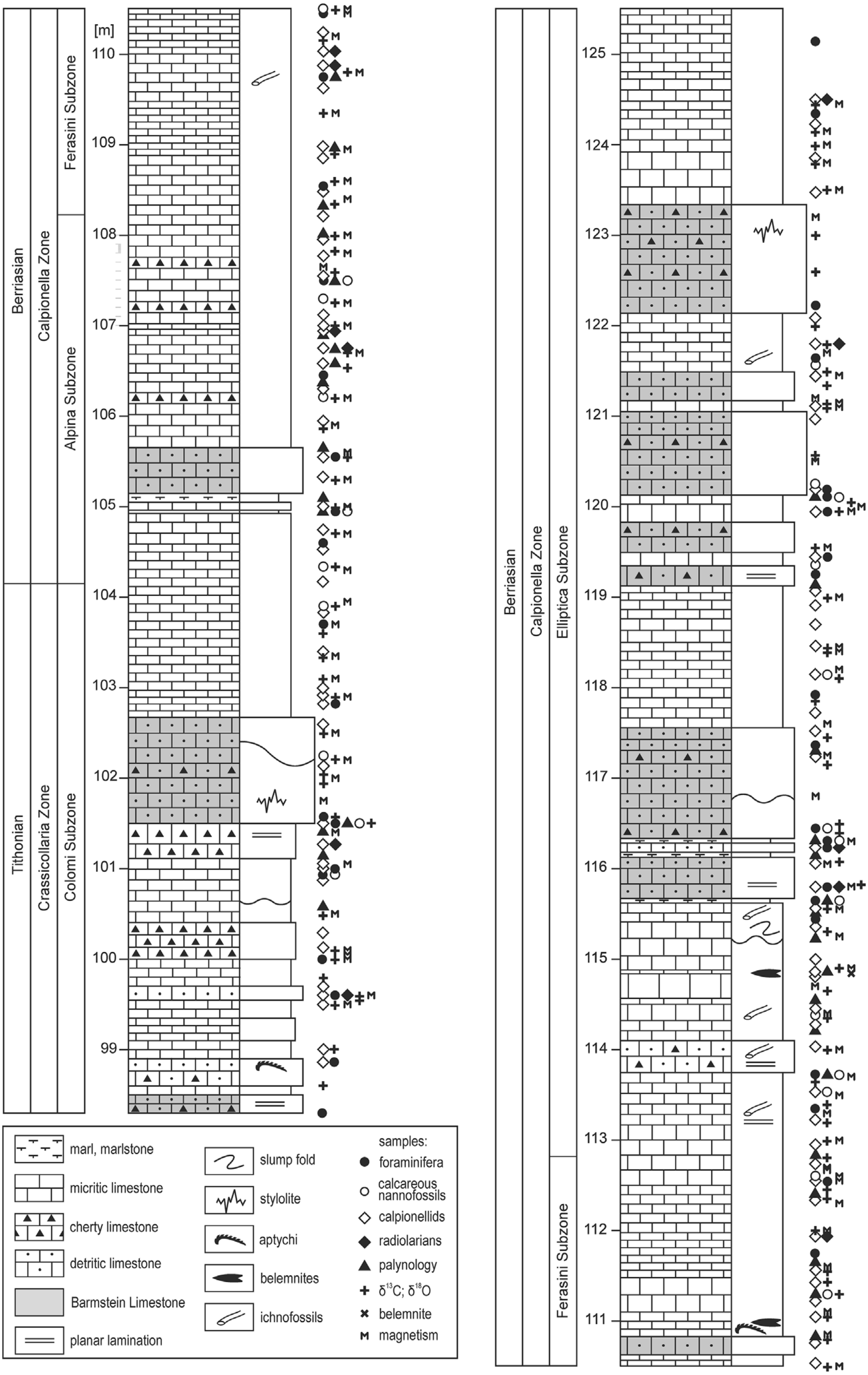

Figure 3: Rettenbacher sequence: lithology, sampling and stratigraphy. Calpionellid zonation after Reháková and Michalík (1997) is applied (Elbra et al. 2024).

2.2. Jurassic/Cretaceous boundary (Rettenbacher, Austria)

The study area is a part of the Lower Tirolic unit in the system of the Northern Calcareous Alps (Elbra et al. 2024). It is situated on the northern Kaltenhausen Block which is bordered by post mid-Cretaceous and Miocene fault systems (Missoni 2003).

The Rettenbacher strata sequence is 27 m thick and is prevailed by varying shades of grey, slab-like-bedded limestones of the Oberalm Formation. In places, grey-brown or grey-black cherts occur in several coarse regular layers, and are usually parallel to the bedding. Often, within the single layer, a change in colour from dark grey to light grey, or light brown-grey emerges (Figure 3; Elbra et al. 2024).

As a characteristic feature of these limestones, a spotting, which in the upper parts of the section fades, in some layers, mostly at the base, signs of lamination can be seen. Only seldom the limestones are shaly, breaking in the upper parts of the section. In the uppermost horizons, rust-brown covers are observed. The limestones are interbedded with dark grey, in the higher horizons grey-green spotted shales, the thickness of which ranges from several mm to 3 cm, sporadically up to 6 cm. In the basal and higher parts of the sequence of strata, conspicuous thick-bedded layers (max. 180 cm) of beige (or pink-brown) the Barmstein Limestone occur. Grey-brown, or black cherts in the form of nodules, lenses and bands that reach the thickness of 6–7 cm and are parallel to the bedding are placed within (Elbra et al. 2024).

Belemnites (genus *Tithonobelus* Janssen, 2022) were recorded only in two horizons of the Berriasian strata (*Ferasini* and the lower part of the *Elliptica* zones). Isotopic data ($^{87}Sr/^{86}Sr$) from rostra of *Tithonobelus* aff. *zeuschneri* (Oppel, 1865) and *Tithonobelus* sp. indet correspond to the lower Berriasian values (Elbra et al. 2024).

2.2. Lower (Middle/Upper) Jurassic of the Outer Western Carpathians

The sediments located near the village of Lukoveček, range from the Lower to Upper Jurassic periods, belong to a geological structure known as the Rača Unit. This unit is a significant component of the Magura Nappe, a complex of geological formations found in Moravia (Kováč & Plašienka 2002). Within this framework, an olistolith—essentially a block of older rock—can be found embedded in the Ráztoky Beds, which are from the Maastrichtian period (Andrusov 1959). This olistolith is situated close to the emerging Ondřejov anticlinal belt, where geological uplift occurs.

Researchers suggest that the presence of these Jurassic sediments does not indicate a tectonic fragment (*klippe*) that has been displaced from lower layers through faulting, as no substantial dislocations have been identified nearby (Rakús 1987).

The understanding of the Jurassic sedimentary history, particularly concerning the marginal Rača Unit, is still evolving. Much of the information available derives from the study of resedimented blocks and clastic materials, especially from Lower and Middle Jurassic strata, which include olistoliths near Lukoveček and Middle Jurassic blocks observed near Koryčany. In contrast, Upper Jurassic deposits are more widely represented and include various types of limestone, such as micritic limestone, red nodular limestone, radiolarian limestone, and marly *Calpionella* limestone. It is noteworthy that, although the late Jurassic was characterised by widespread marine transgression over the Bohemian Massif, some indication of localised transgression along its edge likely occurred as early as the lowermost Jurassic (Kováč & Plašienka 2002).

Within the geological samples from Lukoveček, three main types of limestone were identified. The Upper Pliensbachian grey and dark-grey limestones are classified as organodetritic, featuring numerous fossils such as crinoids, bivalves, sponge spicules, and foraminifers, as well as clastic components like quartz and mica. The Aalenian dark-grey limestones are also organodetritic, predominantly made up of thick-walled bivalve and ammonite fragments and rich in organic matter (Rakús 1987). While Andrusov (1959) described a pseudo-oolitic character for these limestones, this perspective has not been supported by subsequent studies, including those conducted by Rakús and our analyses. Additionally, the light-grey to greenish limestones attributed to the Upper Jurassic have not yet undergone detailed microfacies analysis; however, their overall characteristics suggest similarities with the fauna from Cetechovice, another area in the Kroměříž district known for its olistoliths (Neumann 1907).

The biostratigraphical analysis of the ammonite assemblage indicates that at least two upper Pliensbachian ammonite associations exist among the studied collection, first one of the lower part of the *Margaritatus* Zone and the second one of the middle part of the *Spinatum* Zone (Geist et al. 2025). Based on palaeocurrents analysis and the transported clastic material, the source area of the here studied assemblage as well as other documented olistoliths in this part of the Magura Nappe most probably come from the submarine Hostýn Ridge and represent the cephalopod fauna of the former Magura Basin (Geist et al. 2025).

The stratigraphically oldest ammonite fossil is *Amaltheus stokesi* Sowerby, 1818, the index taxon of the *Stokesi* Subzone of the *Margaritatus* Zone, the lowermost subzone of the late Pliensbachian. *Amaltheus margaritatus* de Montfort, 1808 has a large stratigraphic range, from the *Subnodosus* Subzone of the *Margaritatus* Zone up to the *Apyrenum* Subzone of the *Spinatum* Zone. *Pleuroceras solare* (Phillips, 1829) and *P. quadratum* (Howarth, 1958) indicate the *Apyrenum* Subzone of the *Spinatum* Zone. *P. spinatum* (Bruguière, 1789) shows a similar range but going up to the lower part of the *Hawskerense* Subzone (Geist et al. 2025).

The studied samples are dominated by the genus *Passaloteuthis* Lissajous, 1915, one of the most widespread belemnite genera in pre-T-OAE rocks. A substantial part of the material also consists of *Catateuthis longiforma* (Blake, 1876) *in* Tate & Blake (1876) probably also represented in many unidentifiable fragments of rostra in the collections. The identified taxa show a large stratigraphical extension, from the uppermost Sinemurian to the lowermost Toarcian. The belemnites thus corroborate the (Upper) Pliensbachian age given by the studied accompanying ammonite taxa. It is, however, not possible to distinguish the *Margaritatus* and *Spinatum* zones based only on belemnites alone (Geist et al. 2025).

The belemnites described from this locality originate from the Upper Pliensbachian crinoidal limestone and some cand be referred to Aalenian (Geist et al. 2025).

3. Material

The material described herein consists exclusively from rostra (with only few figured or mentioned exceptions, see below - articles) as the most rigid parts of the belemnite shell.

The studied belemnite rostra of the **Study I.** are deposited in collections of National Museum at Prague (N…); Chlupáč's Museum of the Earth History, Faculty of Science, Charles University (CHMHZ-…); Municipal Museum of Ústí nad Labem (G…); Senckenberg Naturhistorische Sammlungen Dresden (MMG SaJ…) and Geowissenschaftliche Sammlungen der TU Bergakademie Freiberg (RS…). The belemnite material consists of more than 125 mostly fragmentary specimens, including 40 complete and/or determinable rostra. The rostra are mostly dissected from the rock and sometime glued together, with a smaller percentage preserved within the original rock.

Fossil material comes mostly from the 19th century when intensive mining took place in several quarries. A smaller portion of the fossils come from more recent collections, some from research in the last few years. In addition to belemnites, the collections also contain specimens of ammonites, brachiopods, sea urchins, crinoids, corals, bivalves, and chondrichthyes (e.g. Bruder 1881, 1882; Lenz 1870).

The studied belemnite rostra of the **Study II.** are deposited in collections of Chlupáč's Museum of the Earth History, Faculty of Science, Charles University. The belemnite material consists of two determinable specimen and one unspecified Belemnite sp. indet. Single rostrum of *Tithonobelus* was found directly in the section, the other two come from debris (Elbra et al. 2024).

In the past, several investigations were carried out in the studied quarry (Rettenbacher) (e.g., Boorová et al. 2000). During these investigations, a certain amount of macrofossils, especially aptychi, were also found. To a lesser extent, ammonites, belemnites and rhyncholites were found here. However, the locality is not a rich in fossils generally.

The studied belemnite rostra of the **Study III.** are deposited in collections of the Moravian Museum in Brno. The belemnite material consists of approximately 120 rostra fragments and only 24 rostra were identified at the species level. Preserving the phragmocone within and/or outside the alveolus is a relatively common feature. Belemnites and other fossils show *post-mortem* damages of rostra, probably caused by mining. They are broken and, less often, variously deformed and conservated with wax. Some morphological features are almost indistinct, only slightly visible but still valuable for the taxonomic determination.

All samples deposited in the Moravian Museum date from the late 19th and early 20th centuries, when the local bituminous limestone was mined (see the previous chapter for more information). In addition to investigated belemnites and ammonites, the collections also contain specimens of bivalves, echinoids, brachiopods, foraminifers, gastropods and others (e.g., Rzehak 1904).

4. Methods

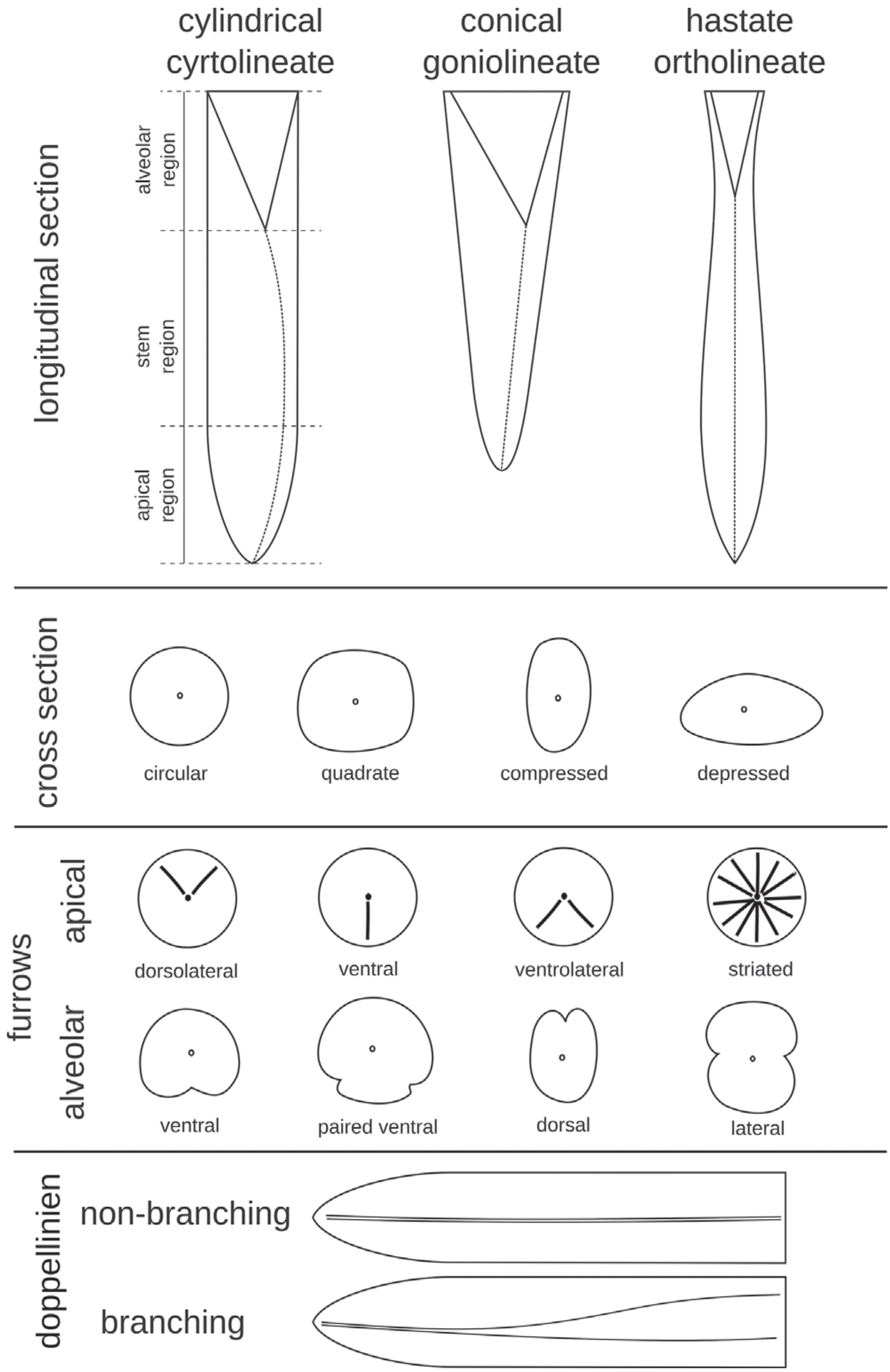

Figure 4: Descriptive terminology of belemnite rostrum morphology. Note that the outline types shown in longitudinal section are not necessarily associated with any particular apical shape, and that all three apical shapes can occur for each longitudinal outline shown (Hoffmann & Stevens 2020).

4.1. Morphometry and taxonomy

Abbreviations and used terminology:

orthorostrum	belemnite hydrodynamic organ; inner shell
rostrum solidum	posterior part of the orthorostrum; posteriorly from the protoconch
rostrum cavum	the phragmocone-bearing part of the orthorostrum; anteriorly from the protoconch

The terminology of belemnite morphology used here follows Pugaczewska (1961) and Hoffmann & Stevens (2020); see Figure 4. The following parameters are used: MLD (maximum lateral diameter), d-s (lateral diameter), d-v (dorsoventral diameter) and total length of rostrum preserved (L). The division of rostra into size categories – small, medium and large – is often a highly subjective definition that depends primarily on the periods studied. During the Mesozoic, the sizes and shapes of belemnite rostra underwent intensive development. Sometimes, significant variations influenced by paleoenvironmental changes are well distinguishable. The term outline is used as a shape in the dorsoventral view of the rostrum and profile as a lateral shape in the lateral view of the rostrum.

The taxonomy of belemnite rostra is based solely on the morphometrics of preserved fossils. However, different authors sometimes do not equally accept the definition of taxa. Modern morphometric works (e.g., Rita et al. 2021) suggest that new taxa can now be defined using different morphometric approaches. For the correct definition of genera or species, it is necessary to use a combination of available parameters of the studied rostra.

4.1.1. Taxonomy: A brief overview and remarks to the belemnite taxonomy related to this thesis

Class Cephalopoda Cuvier, 1798

Subclass Coleoidea Bather, 1888

Order Belemnitida Zittel, 1895

Suborder Belemnopseina Jeletzky, 1966

Rostra of the **Study I.** belong to four families- Belemnopseidae, Duvaliidae, Megateuthididae and Cylindroteuthididae with several genera and species. They mostly belong to cosmopolitan and/or widespread taxa with some taxonomical discrepancies mentioned below. Individual taxa belong to different stratigraphic levels and thus demonstrate a relatively wide preserved age of the rocks.

Family Belemnopseidae Naef, 1922, emended Jeletzky (1946)
Description: Hastate or subconical elongated rostra with ventral alveolar groove. The groove (alveolar furrow) sometimes along the entire length of the (ortho-)rostrum (rostrum solidum and rostrum cavum). The cross-sections are circular, compressed or depressed. *Doppellinien* can be developed. Apical line mostly ortholineate (see Figure 4, longitudinal section).

Genus *Hibolithes* de Montfort, 1808 (non *Hibolites* Mayer-Eymar, 1883)
Remarks: The monotypical genus *Hibolithes* de Montfort, 1808 is currently under revision. Janssen (2022) together with other authors prefer the term *Hibolites* auctorum. The original designation of the type species by de Montfort (1808) from Callovian–Oxfordian black marls located in south-eastern part of Gap (France) is ambiguous (*nomen dubium sensu* Riegraf et al.

1998). A number of morphologically similar rostra with a wide range of occurrence (Middle Jurassic to Lower Cretaceous) have been assigned to the genus *Hibolithes*, and the species *H. hastatus* respectively. The original definition of the taxon, although with a description of the type locality and the age of the source rocks, probably cannot compete with newer and valid taxon definitions. *Belemnites hastatus* de Blainville, 1827, junior objective synonym of *H. hastatus* de Montfort, 1808 seems to be the first validly described definition of this taxon and should be preferred in the future. The taxon *Hiboli<u>tes</u>* probably belongs to the younger period (uppermost Jurassic) and the Cretaceous, while the poorly defined genus *Hiboli<u>thes</u>* is generally assigned to fossils from older periods (Middle Jurassic to lower part of the Upper Jurassic).
Because the new status is not yet fully defined and used in an effort to avoid inconsistencies, we follow the original designation. Future detailed investigation of the validity of this taxa is necessary.

Genus *Belemnopsis* Bayle, 1878 [non *Belemnosis* Edwards, 1849 in Gray, 1849 (incorrect original spelling; see Mitchell 2015 for details); non *Pachybelemnopsis* (Riegraf, 1981)]
Remarks: According to some authors, the validity of the taxon is unclear (e.g. Riegraf 1999). In 1849, Gray introduced the new genus *Belemno(p)sis* Edwards in Gray, 1849, assigned to the tertiary spirulid species *Beloptera anomalus* Sowerby, 1829, first introduced by Edwards. Gray clearly attributes the taxon name to Edwards. Based on the date of acceptance, it can then be determined that Gray's paper, which contained a reference to Edwards's paper, was accepted for publication earlier. This is probably an "incorrect original spelling" or "misprint" of the genus name *Belemnosis*, which was first described by Edwards (Mitchell 2015).
On the other hand, Riegraf preferred an uncompromising view of the taxon's invalidity. He suggests using the generic name *Pachybelemnopsis* Riegraf, 1981 or assigning representatives of the genus *Belemnopsis* Bayle, 1878 to the genus *Holcobelus* Stolley, 1927 or *Lagonibelus* Gustomesov, 1958 (Riegraf 1999).

Family Duvaliidae Pavlow, 1914
Description: Hastate, conical or cylindrical, sometimes elongated rostrum. Alveolar groove placed dorsally and variable in length. Cross-section circular, (highly) compressed or quadrate. The apex should be mucronate and *doppellinien* are visible. The profile can be asymmetrical.

Genus *Rhopaloteuthis* Lissajous, 1915

Family Megateuthididae Sachs and Nal'njaeva, 1967
Description: Conical and highly elongated rostrum. Epi-rostrum in cases developed. Apical grooves (dorsolateral, ventrolateral) commonly present, shorten as part of ontogenetic development. Compressed, circular (ovate) or quadrate cross-section variable through the ontogeny and within the rostrum.

Genus *Megateuthis* Bayle, 1878

Family Cylindroteuthididae Stolley, 1919
Description: Large-sized cylindrical rostra with a common deep alveolus. The apical grooves well developed. The profile often asymmetrical (ventral side is slightly wider). Characteristic compressed cross-section of the rostrum, in some parts (apex) circular. The apical line eccentric and inclined to the ventral side.

Genus *Cylindroteuthis* Bayle, 1878

Rostra of the **Study II.** belong to the family Duvaliidae Pavlow, 1914.

Genus *Tithonobelus* Janssen, 2022
Remarks: Yet poorly defined belemnite family with hastate shape of rostra with characteristically more or less clear constricted alveolar area of rostra. Superficial similarity with the outer morphology of the late Berriasian–Hauterivian genus *Pseudobelus* Blainville, 1827 but from the Tithonian and the early Berriasian. On the other hand, *Pseudobelus* shows an elongated more or less cylindro-conical outline and only very slightly hastate profile. In closely related *Produvalia* the alveolar area is generally more constricted and sometimes much more elongated (see more in Janssen 2022).

Rostra of the **Study III.** belong to two families – Passaloteuthididae and Hastitidae. The described taxa belong to widely distributed in the European shelf and in the Western Tethys. The stratigraphic range is also wider.

Family Passaloteuthididae Naef, 1922
Description: Characteristic cylindrical, cylindroconical or subhastate rostra, often elongated. Profile slightly asymmetrical. Apical groove(s) common, lateral lines (*doppellinien*) sometimes developed. Cross-section (sub)circular to (sub)quadrate. Apical line commonly cyrtolineate and excentric.

Genus *Catateuthis* (Blake, 1876 *in* Tate & Blake, 1876)
Genus *Parapassaloteuthis* Riegraf, 1980
Genus *Passaloteuthis* Lissajous, 1915
Genus *Pseudohastites* Naef, 1922

Family Hastitidae Stolley, 1919
Description: Elongated cylindrical, hastate or subhastate rostra, slightly asymmetrical in the profile. Grooves, lines and *doppellinien* exceptionally well developed. The apex short and often sharply pointed. Cross-section generally circular or (sub)quadrate. Apical line without eccentricity.

Genus *Bairstowius* Jeletzky, 1994 in Doyle et al., 1994

4.2. Geochemical analyses of belemnite rostra

4.2.1. Belemnite rostra as a source of proxy geochemical data

Although the geochemistry is not a major part of this dissertation (rather marginal due to the strong diagenetical degradation, relatively bad preservation and in some cases not clear stratigraphical position), the belemnite rostra provide important information for palaeoecology ($^{13}C/^{12}C$, $^{18}O/^{16}O$ ratios) and chemostratigraphy ($^{87}Sr/^{86}Sr$ ratio). The significance of the belemnite rostra within the geochemistry is prominent. The PDB standard is based on oxygen isotope ratios from the calcite rostrum of the Upper Cretaceous belemnite *Belemnitella americana* (Morton, 1830).

Belemnite rostra are thus widely used for geochemical analyses. Since Urey's first use of the isotope method during the 1940s (Urey 1947), geochemical analytical methods have extensively been modernised. Therefore, according to the research on individual isotopic ratios ($^{13}C/^{12}C$, $^{18}O/^{16}O$, $^{87}Sr/^{86}Sr$), it is possible to partially interpret palaeoenvironmental conditions and chemostratigraphy. Belemnites are one of the most applicable fossils for reconstructing palaeotemperature, palaeobioproductivity and stratigraphy (e.g., Doyle & Benett 1995; Jones et al. 1994; McArthur et al. 2004, 2007a; Vaňková et al. 2019; Wierzbowski et al. 2009a, 2009b and many others).

Generally, carbon isotopes together with oxygen isotopes in carbonate shells show equilibrium with the sea-water. Isotopic ratios obtained from shells may reflect changes in the palaeobioproductivity of the oceans and can be correlated with carbon isotopes obtained from the bulk rock (e.g., Ullmann et al. 2015). As the $\delta^{13}C$ values follow long-term trends in ocean development, their fluctuations are used for stratigraphically significant episodes. Volcanic activity or terrigenous influx may affect marine conditions, resulting in $\delta^{13}C$ shifts of values (e.g., Bodin et al. 2009; Podlaha et al. 1998).

Oxygen isotopes preserved in the calcitic rostrum were in equilibrium with ambient sea-water (e.g., Dera et al. 2009; Wierzbowski et al. 2017). As the isotope ratio depends on fractionation processes and follows the temperature, the resultant $\delta^{18}O$ values may signal a cooling or warming trends/events in the long-term trend (and subsequently it may reflect arid/humid periods as well). Oxygen isotopes are used for the formulation of several palaeotemperature models (e.g. Dera et al. 2011; Dzyuba 2013; Dzyuba et al. 2016; McArthur et al. 2004, 2007a; Podlaha et al. 1998; Price et al. 2011, 2023; Voigt et al. 2003, 2006; Voigt et al. 2021; Žák et al. 2011 and many others).

Unlike stable isotopes, strontium isotope ratios are influenced by the radioactive decay of rubidium-87 (^{87}Rb) into radiogenic strontium-87 (^{87}Sr). This ratio is typically expressed in comparison to the stable strontium isotope ^{86}Sr. Due to its long residence time in seawater (approximately 4 million years), the $^{87}Sr/^{86}Sr$ ratio is expected to be globally uniform, making it a valuable tool for stratigraphic correlation on a worldwide scale. This ratio also plays a significant role in reconstructing the history of seawater evolution, as demonstrated in various studies (e.g., Bodin et al. 2009; Jones et al. 1994; Kuznetsov et al. 2014; McArthur et al. (2004, 2007b; Podlaha et al. 1998; Vonhof et al. 2011; Wierzbowski et al. 2017).

Belemnite rostra, composed of biogenic carbonate, are commonly used to extract the strontium isotopic signal because they are less affected by diagenesis than seafloor sediments. According to various studies, this makes them especially reliable for isotope analysis. The global $^{87}Sr/^{86}Sr$ curve shows a general increase over time—from an initial value around 0.699 to the modern level of about 0.709—punctuated by significant variations (e.g., McArthur et al. 2007a, Bodin et al. 2009, Wierzbowski et al. 2017).

4.2.2. Rostrum investigations

In all studies, rostra were measured using the attached scale or a calliper with millimetre accuracy. The measured dimensions were used as important morphometric data in taxon determination.

For **Study I.**, 10 thin sections of 50 microns thickness were made and used for subsequent cathodoluminescence. This procedure is general for determining the suitability of samples for geochemical analysis. The pilot geochemical analysis proved problematic and of little relevance, mainly due to the diagenesis of the samples in the vicinity of the Lausitian fault.

The sections were analysed at a magnification of 2.5x10 under a specially adapted microscope (CLmk4 cathodoluminescence apparatus (Cambridge) and Avantes spectrometer connected to a Leica microscope at the Institute of Geochemistry, Mineralogy and Mineral Resources, Faculty of Science, Charles University, Prague) equipped with a vacuum pump and a source of electrical voltage and current.

Suitable parts of the non-affected calcite were thoroughly separated by a drilling machine with diamond and/or corundum drills (the apical line and its vicinity and last growing layers were removed). The samples were then washed in an ultrasonic bath, ground to analytical fineness in agate mortar and divided into subsamples.

For **Study II.**, analysed material from two belemnite rostra was sampled from strictly selected part fulfilling the criteria for diagenetically unaltered part of rostrum (for details see Elbra et al. 2024).

4.2.3. Geochemical analyses

Part of the subsamples of **Study I.** was transferred into a Savillex vial, and 1 ml of 14M nitric acid was added. After dissolution, the material was diluted with deionised water (volume of 20 ml). The contents of the main and trace elements of Ca, Mg, Sr, Fe and Mn were analysed by a 5110 VDV Agilent ICP-OES spectrometer at the Laboratory of the Geological Institutes at Charles University in Prague. The 20 ml liquid sample was diluted in 2%HNO_3 100× for a Ca analysis and 2× for analysis of the other elements. The amount of Rb was measured using an ICP-MS (Thermo Scientific XSeries II) (Geist et al. 2023).

Strontium was isolated from the calcite matrix using exchange chromatography techniques with Triskem's Sr resin (Míková & Denková 2007) and analysed by a Neptune Plus high resolution MC-ICP-MS instrument (ThermoFisher Scientific) in static mode at the Stable and Radiogenic Isotope Research Laboratory at Charles University in Prague. The analytical mass bias was corrected to $^{88}Sr/^{86}Sr$=8.375209 [defined as $\delta^{88/86}Sr$=0 relative to NIST SRM 987 (Nier 1938)].

The overall analytical uncertainty (external error) is given by repeated analyses of the SRM 987 standard, resulting in $^{87}Sr/^{86}Sr$=0.710312 ± 0.001 (2 σ; n=6) (see also Geist et al. 2023).

Pilot analyses of oxygen ($^{18}O/^{16}O$) and carbon ($^{13}C/^{12}C$) isotopic ratios were processed from the rest of the subsamples using a GasBench II (ThermoFisher Scientific) machine equipped with a CTC Combi-Pal (PALSYSTEM) autosampler linked with a MAT253 isotope ratio mass spectrometer (ThermoFisher Scientific) in a Continuous Flow IV (ThermoFisher Scientific) system at the Stable and Radiogenic Isotope Research Laboratory at Charles University in Prague. The internal precision (SD) measured over these six peaks is typically 0.02 and 0.08 for raw $\delta^{13}C$ and $\delta^{18}O$ values (n=16), respectively, given a sample size above 50 mg. Calibration of the raw results versus the VPDB scale was achieved using in-house calcite standards (after linearity correction) that were calibrated against NBS-18, L-SVEC and IAEA-603 international reference materials (IAEA, Vienna, Austria) (Geist et al. 2023).

All measurement for **Study II.** were taken from one sampled section. Main and trace elements were measured at the Laboratories of the Geological Institutes, Charles University, Prague, Czech Republic. Stable isotopes ($\delta^{13}C$, $\delta^{18}O$) were analysed at the Earth Science Institute of the Slovak Academy of Science, Banská Bystrica, Slovakia. Strontium isotope analysis was performed at the Institute of Geology of the Czech Academy of Sciences, Prague, Czech Republic (see Elbra et al. 2024 for details).

5. Results and discussion

5.1. Belemnite taxonomy: described taxa and stratigraphic interpretation

The following families including genera and species were recognised in the studied intervals:

Megateuthididae Sachs and Nal’njaeva, 1967 including one genus with two following species: *Megateuthis suevica* (Klein, 1774) and *Megateuthis* cf. *M. elliptica* (Miller, 1826).

Cylindroteuthididae Stolley, 1919 including the taxon *Cylindroteuthis* cf. *C. puzosiana* (d‘Orbigny, 1842).

Passaloteuthididae Naef, 1922 including four genera [*Catateuthis* Nalnyaeva, 1967 in Saks & Nalnyaeva 1967; *Parapassaloteuthis* Riegraf, 1980; *Passaloteuthis* Lissajous, 1915 (= *Holcoteuthis* sensu Stolley, 1919); *Pseudohastites* Naef, 1922] with following species: *Catateuthis longiforma* (Blake, 1876) in Tate & Blake (1876); *Parapassaloteuthis* cf. *P. ferea* (Simpson, 1855); *Passaloteuthis armata* (Dumortier, 1869); *Passaloteuthis bisulcata* (Blainville, 1827); *Passaloteuthis* cf. *P. krimholzi* Činčurová; 1974 and *Passaloteuthis* aff. *tunezicensis* Činčurová, 1989.

Hastitidae Stolley, 1919 including the genus *Bairstowius* Jeletzky, 1994 in Doyle et al., 1994 with the taxon *Bairstowius* sp. indet.

Belemnopseidae Naef, 1922 including two genera (*Hibolithes* de Montfort, 1808 and *Belemnopsis* Bayle, 1878) with following species: *Hibolithes hastatus* de Montfort, 1808; *Belemnopsis canaliculata* (von Schlotheim, 1820); *Belemnopsis latesulcata* (Voltz, 1832) in Thurmann (1832); *Belemnopsis subhastata* (Zieten, 1831) and *Belemnopsis* sp. indet.

Duvaliidae Pavlow, 1914 includes the genera *Rhopaloteuthis* Lissajous, 1915 and *Tithonobelus* Janssen, 2022 with following species: *Rhopaloteuthis sauvanausa* (d’Orbigny, 1842) and *Tithonobelus* cf. *zeuschneri* (Oppel, 1865) (see Figures 5 and 6 for detailes).

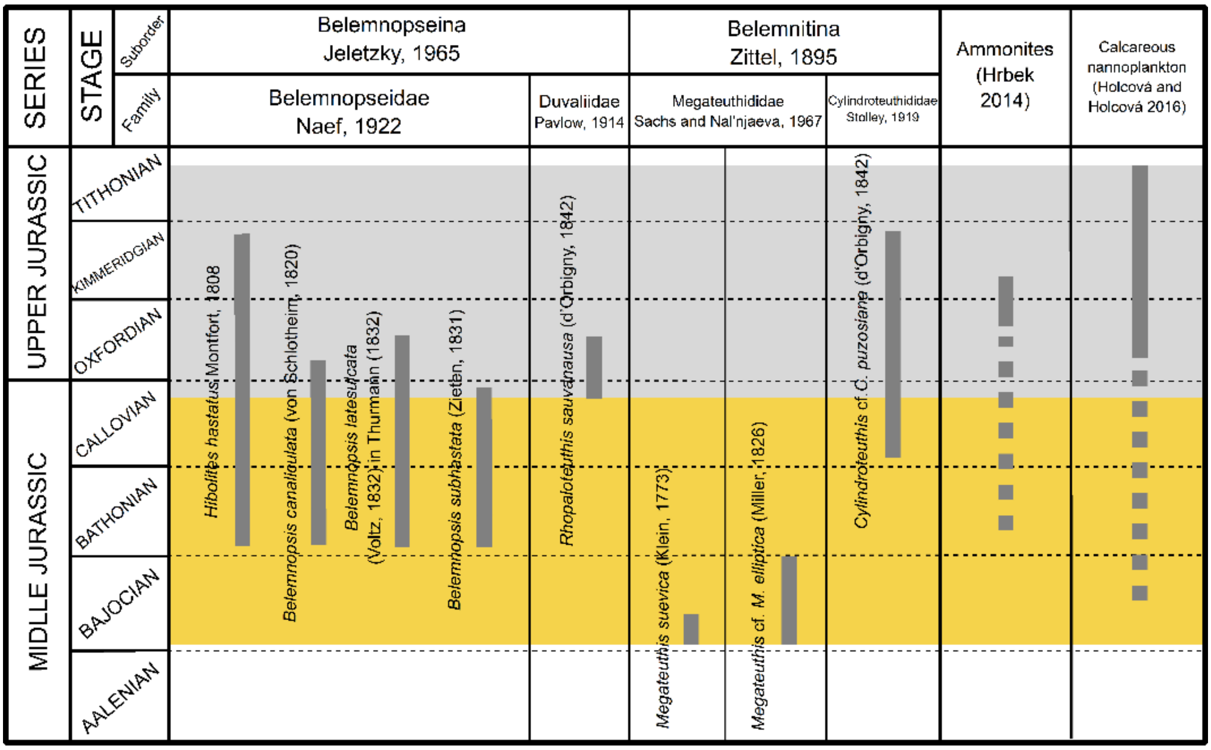

*Figure 5: Total stratigraphical ranges of belemnite taxa (recorded from the northern Bohemian Massif) according to published literature [modified after Pugaczewska (1961), Gustomesov (1964), Mariotti (2002), Dzyuba (2005), Weis and Mariotti (2008) and Mural (2011)] in relation to ammonite (Hrbek 2014) and calcareous nannofossil data (Holcová and Holcová 2016; Geist et al. 2023). Grey and orange background timespan of sedimentation based on summarised biostratigraphic data; orange background: prolonged sedimentary history of studied rocks (**Study I.** Geist et al. 2023).*

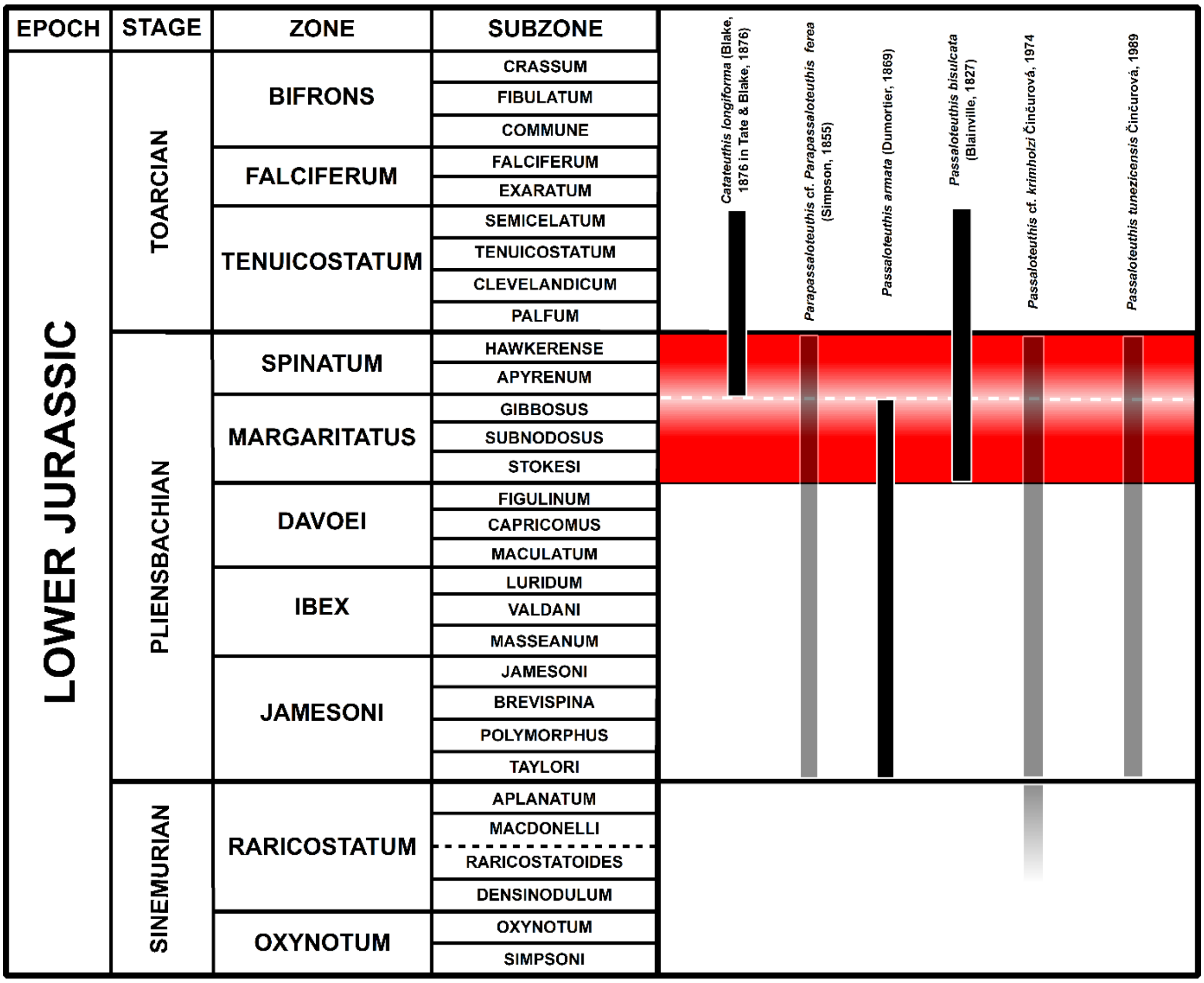

Figure 6: Biostratigraphy: ammonite biostratigraphic zonation in relation to belemnite ranges (black columns: distribution considered certain; grey columns: presumed distribution). The distribution of the ammonite fauna is marked by a red space (adopted after Bristow & Donovan 2015). Ammonite associations can be differentiated into the older Stokesi *Subzone and the slightly younger* Apyrenum *Subzone. Stratigraphic ranges of the belemnite taxa are reported herein based on literature data (Arabas et al. 2017, Činčurová 1974; 1989; 1991, Doyle 2003, Rita et al. 2021, Santantonio et al. 2016, Weis et al. 2018) (**Study III.** Geist et al. 2025).*

All these obtained results were intensively compared with the existing literature comprising the taxonomy, palaeogeography and palaeoecology of belemnites of Tethyan and Boreal realms in the Jurassic and the lowermost Cretaceous:

Bulgaria (Rita et al. 2021; Sanders et al. 2015; Stoyanova-Vergilova 1993), Caucasus (Dzyuba et al. 2021; Gulyaev et al. 2015; Mariotti et al. 2013), England (Bruder 1881; Doyle 1990, 2003; Ippolitov 2018; Mariotti 2002; Mural 2011; Schlegelmilch 1998; Weis & Mariotti 2008), France (Janssen 2022; Weis et al. 2018), Germany (Schlegelmilch 1998; Schumann 1974), India (Mariotti et al. 2013; Pugaczewska 1961), Italy (Mariotti et al. 2007; Santantonio et al. 2016; Weis et al. 2015), Luxemburg (Rita et al. 2021; Weis et al. 2018), Marocco (Mariotti et al. 2013; Sanders et al. 2015), Poland (Mariotti 2002; Pugaczewska 1961), Russia (Dzyuba 2012, 2013; Ippolitov et al. 2017; Janssen 2022; Mural 2011; Paryshev & Nikitin 1981), Slovakia (Činčurová 1964, 1971, 1974, 1989, 1991), Spain (Janssen 2022; Sanders et al. 2015; Rita et al. 2021) and Ukraine (Mural 2011; Paryshev & Nikitin 1981).

5.2. Belemnites like palaeogeographical and palaeoecological indicators

In the later Toarcian stage, following the regeneration of the world's oceans after the Toarcian Oceanic Anoxic Event (T-OAE), the beginnings of differentiation of belemnite faunas into two prominent biogeographical realms can be traced –Tethyan and Boreal realms. However, the (Indo-)Pacific Realm experienced its expansion/emergence significantly later – in the uppermost Middle Jurassic (Doyle 1987; Stevens 1963; Westermann 2000). Since then, with some exceptions, belemnites can be used to reconstruct the relationships between individual realms within the world's oceans.

In the **Study I.,** the belemnite assemblage is strongly associated with the Tethyan Realm. However, the presence of taxon *Cylindroteuthis* cf. *C. puzosiana* clearly documents also Boreal faunal influence. During the Jurassic and Cretaceous, respectively, several belemnite migrations/incursions took place within Europe because of changes in the environmental conditions, such as alternation of warmer and colder periods and sea-level changes (see the discussion in: Geist et al. 2023).

Because belemnites were rather stenothermic organisms, during these temperature fluctuations, they often migrated to refuges – e.g. they followed shifts of warmer and cooler-water masses – for example to the Arctic region during warmer periods and to the Tethyan/Mediterranean Realm during cooler times (Dera et al. 2016; Dzyuba 2013; Sano et al. 2010). In the Oxfordian stage, a considerable cooling event with significant changes in species composition is assumed (Cecca et al. 2005). During this period, species of the Tethyan genus *Belemnopsis* stopped dominating, and the typically Boreal taxa (*C. puzosiana* in our case) occurred also in northern Bohemia.

This assumption is also discussed by Hrbek (2014), who revised and described sub-Boreal ammonites from this area. The majority of accompanied fauna (both benthic and nektonic) in the studied rocks, however, indicates conditions typical for the Peri-Tethyan shelf (Geist et al. 2023). The sub-Boreal ammonite taxa, however, clearly document the connection between the Peri-Tethyan shelf (including Bohemian Massif margins) and the Boreal Realm.

The belemnite rare record described in the **Study II.** contains the Tethyan belemnites of the genus *Tithonobelus*. This recently defined genus (Janssen 2022) is not yet described in great detail. However, its affiliation to the Tethyan Realm is obvious (Janssen 2022). The belemnite material described in the **Study II.** is unfortunately too scarce to be interpreted in more details within the palaeobiogeographical context.

The **Study III**. is an unconventional outcome of the analysis of fossil assemblages from olistolith. Thanks to a detailed taxonomic revision, we are able to determine the original source of these fossiliferous rocks within the Pliensbachian seas of Europe at that time.

In this study, the close taxonomic and palaeogeographic similarity of the locality Lukoveček with Fatricum of Carpathians is obvious. Local Upper Pliensbachian dark crinoid limestones (Trlenská Formation of Manín Unit) consist of species *Passaloteuthis armata*, *P. bisulcata*, *P. milleri* and discussed *P. tunezicensis* and genera *Parapassaloteuthis* and *Pleurobelus* (Margaritatus Zone) (Geist et al. 2025).

Belemnite populations of the Lukoveček locality did not display provincialism in the Lower Jurassic of the Western Tethys, a fact that has been recognised by several earlier authors (Doyle 1987; Neige et al. 2021; Sanders et al. 2015).

The genera recorded in Lukoveček (Western Carpathians) are widely distributed in European shelf environments, and most of them occur from the UK in the West to northwestern Turkey in the East (see the Figure 7).

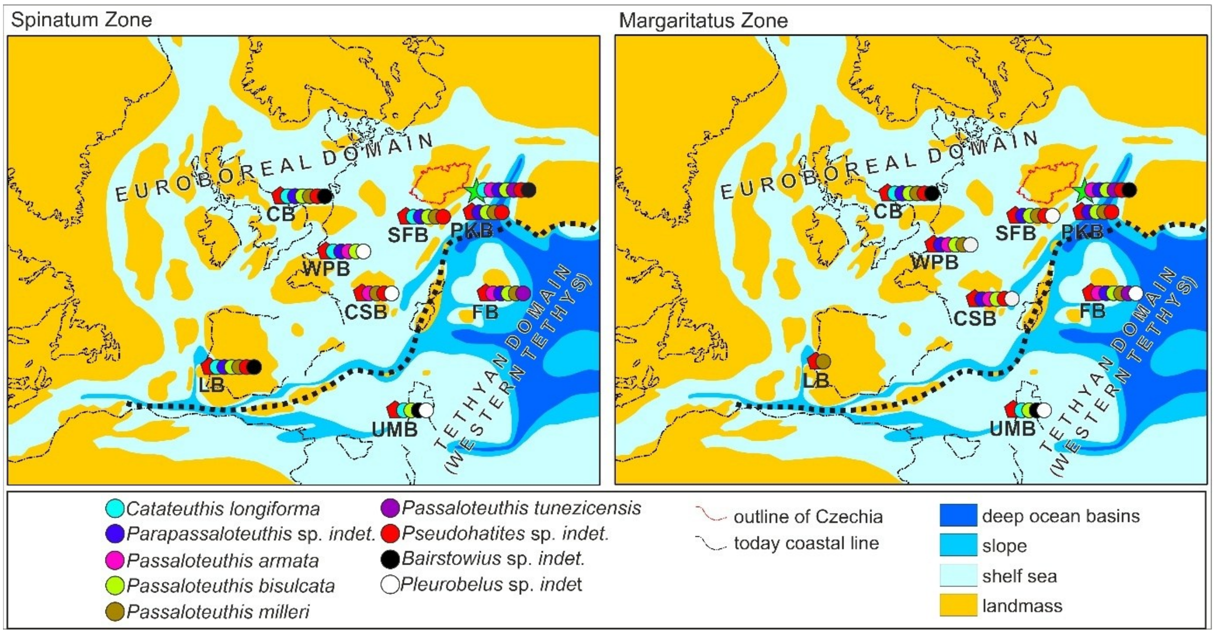

Figure 7: Palaeobiogeographical situation in the uppermost Pliensbachian: palaeobiogeographical maps of Europe and adjacent localities during the Spinatum *and the* Margaritatus *zones. The possible original positions of the most important localities are marked with red pentagons. The locality of Lukoveček is marked with a green star. The dashed black line corresponds with the presumed boundary between the Euroboreal and Mediterranean faunal realms. CB Cleveland Basin (United Kingdom), CSB Causses Basin (France), FB Fatric Basin (Western Carpathians), LB Lusitanian Basin (Portugal), PKP Pieniny Klippen Belt (Oravicum, Carpathians), SFB Swabian-Franconian Basin in Bavaria (Germany), UMB Umbria-Marche Basin (Italy), WPB Western Paris Basin (France) (Geist et al. 2025).*

Individual morphotypes of belemnite rostra can serve well for reconstructing the paleoenvironment of individual taxa (see the Figure 8). The cylindrical shape was probably adapted to life in various environments. Thanks to its shape, this rostrum could serve the belemnite well for migrations over longer distances, as well as for vertical migrations through the water column. The hastate morphotype was found in belemnites that also inhabited relatively deeper waters, in where they could move quickly. It is related to their nekto-benthic lifestyle. This morphotype becomes dominant during the Upper Jurassic. The shape of this rostrum combines excellent hydrodynamic properties with lower energy for its formation and resistance. The conical type is the least variable of these rostrums. The energy required for its formation is higher, and the belemnite with this rostrum could not manoeuvre well in the environment. This type gradually disappears during the Upper Jurassic, when it is replaced mainly by the hastate type (Dera et al. 2016).

In **Study I.**, palaeoenvironmental changes can be traced based on the occurrences of individual morphotypes within the paleontological record.

The oldest preserved rocks (stages Bathonian and Bajocian) serve conical rostra of the family Megateuthididae. These purely pelagic representatives of belemnites dynamically spread in the waters of the oceans of that time at this time. In the Jurassic rocks of Northern Bohemia they indicate rather an open sea. The onset of sedimentation in these locations was likely associated with one of the transgression-regression cycles known and documented within the then-Tethys Ocean (see also Dera et al. 2016).

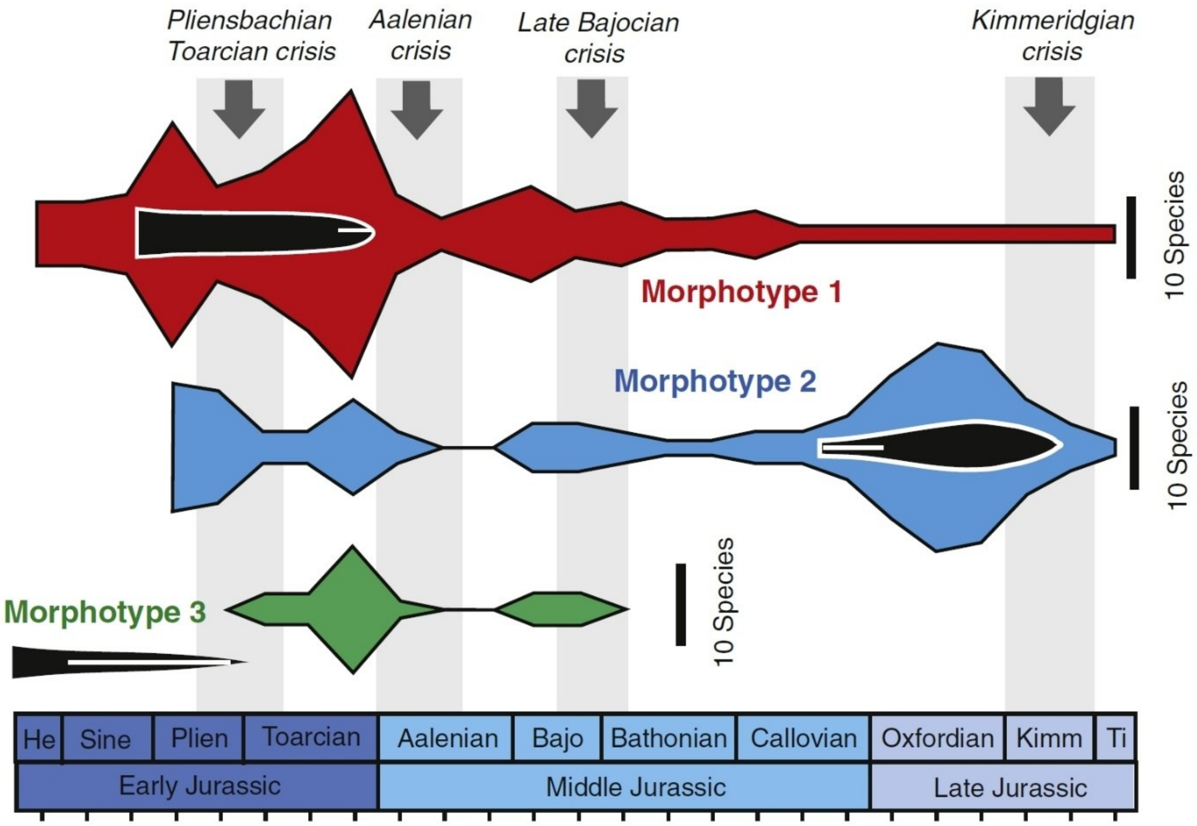

Figure 8: Categorisation and diversity of belemnite morphotypes through time. The main diversity crises are indicated with arrows and grey bands. Representative rostra of each morphotype are represented (see more in Dera et al. 2016).

Rostra of belemnites of the genus *Belemnopsis* are the dominant form in the periods following the disappearance of the family Megateuthididae. Their hastate shape indicates a certain shallowing of the sedimentation space and/or an increase in the nutrient content of the seafloor (Hoffmann & Stevens 2020). A purely pelagic lifestyle is nevertheless possible for this rostral shape. However, it provided belemnites with good manoeuvrability, which is very advantageous within the entire water column (hunting, fleeing from predators; Dera et al. 2016).

The youngest preserved Jurassic rocks of North Bohemia (partially Callovian to Tithonian) then provide rostra of hastate and conical shape. The genus *Rhopaloteuthis* is a morphological link between the typically bottom-dwelling family Duvaliidae and the nekto-benthic Belemnopseidae (e.g., Lissajous 1925; Pugaczewska 1957). This taxon suggests a possible shallowing space and/or a continued increase in the nutrient content of the seafloor.

The hastate genus *Hibolithes* dominates the rocks of Europe and the broader region from the Callovian to the Oxfordian. This taxon foreshadowed the future dominance of the energetically economical, hastate morphotype of belemnites in the world's oceans. The sporadic occurrence of cylindrical rostra in the palaeontological record may be evidence of the influence of taxa from other regions (Boreal genus *Cylindroteuthis*). This morphotype is advantageous for horizontal movements within the seas (Hoffmann & Stevens 2020).

The genus *Tithonobelus* of the **Study II.** characterises the hastate shape of the rostrum. This morphotype is almost identical to the genus *Hibolithes*, which is found at lower stratigraphic levels (Callovian-Oxfordian). This suggests a general preference for a similar rostral shape and poses a problem within the taxonomy of the uppermost Jurassic and Lower Cretaceous belemnites due to the convergency or parallelism.

The morphological diversity of rostra reported in the **Study III.** is relatively low. The samples of this study are dominated by the genus *Passaloteuthis*, one of the most widespread belemnite genus prior the T-OAE (Dera et al. 2016). A significant part of the material also consists of *Catateuthis longiforma*. Rostra of both taxa, with others described included, are typically cylindrical.

Other morphotypes from the Lukoveček locality were found only sporadically. A single representative of the family Hastitidae was recorded in the studied material, possesing the typical hastate shape of the rostrum. However, considering the described benthic taxa, it is possible to assume the relative fertility of the bottom of the sedimentary space, which would provide suitable food and living space sources for nekto-benthic animals.. The relative representation of hastate forms of belemnites in the studied interval (Plinsbachian) is lower than that of cylindrical or conical forms, which is reflected also in our material studied. Moreover, the fossil material does not show signs of longer *post-mortem* transport, and therefore, it is possible to assume a probable syn-sedimentary formation of fossiliferous rocks.

5.3. Geochemistry of belemnite rostra

The use of belemnite rostra for geochemical analyses is limited mainly by frequent diagenetic overprints.

In the **Study I.** only limited material could be studied because the majority of the belemnite rostra belongs to unique institutional collections of the National Museum in Prague. For this study, ten samples were analysed by cathodoluminescence and five from them by elemental components analyses. The results proved extensive diagenetic overprint and/or unsuitability of geochemical analyses. Only one sample was included in the final interpretation (CHMHZ-JG-13b; Figure 9).

Sample No.	Species	$\delta^{13}C$	$\delta^{18}O$	$^{87}Sr/^{86}Sr$	Ca (ppm)	Fe (ppm)	Mg (ppm)	Mn (ppm)	Rb (ppm)	Sr (ppm)
CHMHZ-JG-10/4	B. *incertae sedis*	1.70	-1.97	0.707280	328000	540	2710	40	–	1380
CHMHZ-JG-1/4	*M. suevica*	1.83	-1.84	0.707229	422000	1380	3200	160	–	1670
CHMHZ-JG-13a	*H. hastatus*	1.47	-3.71	0.707255	164000	1740	1100	80	10	190
CHMHZ-JG-13b	*H. hastatus*	1.93	-0.48	0.706886	341000	300	3110	30	–	1380
CHMHZ-JG-13c	*H. hastatus*	0.44	-0.77	0.706868	207000	530	1840	30	–	650

Figure 9: Geochemical analyses of belemnite rostra. Sample CHMHZ-JG-10/4 – locality Peškova stráň (Kyjov); CHMHZ-JG-1/4 – locality Hohnstein; CHMHZ-JG-13a, CHMHZ-JG-13b and CHMHZ-JG-13c – locality Šternberk (Brtníky) (Geist et al. 2023).

The $\delta^{13}C$ and $\delta^{18}O$ isotope values show consistency within the Middle and Upper Jurassic interval, where the lower $\delta^{18}O$ values fit well with the material from a similar strata and environment (sub-Mediterranean) of Middle Europe. The $^{87}Sr/^{86}Sr$ value of 0.706886 corresponds to the Callovian–lower Kimmeridgian data of the global $^{87}Sr/^{86}Sr$ curve (Geist et al. 2023; Jenkyns et al. 2002). This period is characterised by a rather uniform signal with balanced stagnation (Jenkyns et al. 2002).

In the **Study II.** the analysed material shows values -1.63 ‰ for $\delta^{13}C$, -0.08 ‰ for $\delta^{18}O$ VPDB, and 0.7072292 for $^{87}Sr/^{86}Sr$. More negative value of $\delta^{13}C$ from belemnite rostrum, in relation to the values obtained by bulk-rock analysis, was expected, what was also observed in *Hibolites jaculoides* Swinnerton, 1952 with estimated deeper habitat depth and nektic lifestyle with more significant vertical migration (Wang et al. 2023). The oxygen isotopic signal is only slightly negative, which corresponds to data typical for the lower Berriasian stage and to the Jurassic/Cretaceous boundary interval respectively (see Elbra et al. 2024). The isotope $^{87}Sr/^{86}Sr$ ratio recorded from the only one analysed belemnite rostrum of this study (CHMHZ-RE1) clearly corresponds to the lower Berriasian values (see Jenkyns et al. 2002; Price & Gröcke 2002).

6. Conclusions

The studied material provided a new and complex insight to rare Jurassic strata yielding belemnites in the Czech Republic. Six families with eleven genera and sixteen species (some in the open nomenclature) were described. Ten of them were described from the Czech Republic for the first time (see Study I. and Study III.) and they are included into families: Magateuthididae, Cylindroteuthididae, Passaloteuthididae, Hastitidae, Belemnopseidae and Duvaliidae. The following genera were recorded: *Megateuthis* (family Megateuthididae), *Cylindroteuthis* (family Cylindroteuthididae), *Catateuthis*, *Parapassaloteuthis*, *Passaloteuthis*, *Pseudohastites* (family Passaloteuthididae), *Bairstowius* (family Hastitidae), *Hibolites*, *Belemnopsis* (family Belemnopseidae), *Rhopaloteuthis*, *Tithonobelus* (family Duvaliidae) which document belemnite diversity in the Central European space in the Jurassic. Included species are mentioned above, in the Chapter 5.

The belemnites significantly helped with clarification of the stratigraphy and palaeobiogeographical position of fragmentarily preserved Jurassic sediments in the Czech Republic. The stratigraphical range of autochthonous Jurassic strata in Northern Bohemia is newly reported to be the Bajocian to Tithonian (Kimmeridgian based on belemnites, Tithonian based on Ca-nannofossils; Geist et al. 2023). Allochthonous Jurassic strata (olistolith of Lukoveček) yield the typical Pliensbachian belemnite fauna, which for the first time documents the Lower Jurassic belemnites within the Czech Republic.

Palaeobiogeographically, Northern Bohemian Jurassic strata represent the Peri-Tethyan with some Boreal (Sub-Boreal) influences (based on ammonites and belemnites, see above). The majority of the described belemnite fauna shows stronger affinities to the Tethyan Realm. The olistolith in Lukoveček palaeogeographically belongs to the Carpathian system and the original source area was approximately identified. The stratigraphic interval (Upper Pliensbachian) could not serve to specify the paleobiogeographic position of the Lukoveček locality within the faunal Realms, as the division of the Tethys and Boreal realms occurred only after the Toarcian Oceanic Anoxic Event. However, ammonite assemblage already in this stratigraphic interval shows the beginnings of the separation of ammonite fauna into (Eu)Boreal and Tethyan Realms.

Morphological aspects of studied rostra indicated the prevail of hastate-shape-bearing belemnite taxa, suggesting rather pelagical lifestyle. This morphology is commonly associated with fast-swimming, nektonic forms typical of open marine environments (e.g. Stevens 1965). Such shapes further support the interpretation of stronger ties to the Tethyan Realm, where pelagic conditions prevailed during the Early Jurassic (Page et al. 2003).

The belemnite record from Rettenbacher confirms a relatively newly established genus *Tithonobelus*. This small contribution, however, documents low diversity and disparity of the belemnite fauna within the Jurassic/Cretaceous boundary interval in the Northern Tethys.

The geochemical analyses of belemnite rostra only partly provided relevant information. Diagenetic processes relatively strongly affected geochemical signal. Well preserved samples, however, chemostratigraphically confirmed our biostratigraphic presumptions (see above).

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