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ORIGINAL PAPER

Belemnites and calcareous nannoplankton: Proxy tools for recognising of cryptic Jurassic geological history of Central Europe

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Abstract
Belemnites and calcareous nannoplankton (which are both stratigraphically and palaeoecologically important groups of organisms) have been used as crucial evidence for exploring an extended timespan of Jurassic sedimentation in the northern part of the Bohemian Massif. Tectonically and fragmentarily preserved Jurassic strata along the Lausitian Fault have long been considered exclusively as belonging to the Callovian through the Kimmeridgian. Based on a systematic revision of older collections, new sediment sampling and analysing data, the stratigraphic range of Jurassic sedimentation in the northern part of the Bohemian Massif has been extended, at least from the Bajocian until the Tithonian. Belemnite taxa are represented by six species and two taxa identified as *Megateuthis* cf. *M. elliptica* and *Cylindroteuthis* cf. *C. puzosiana* (five genera belonging to four families) document a stratigraphic range from the Bajocian (*Megateuthis suevica* and *Megateuthis* cf. *M. elliptica*) through the Kimmeridgian. Additionally, calcareous nannofossils do not contradict the Bajocian–Kimmeridgian while also proving the Tithonian age. Moreover, belemnites clearly show the prevailing Tethyan (*Belemnopsis* fauna) but also Boreal (*Cylindroteuthis* cf. *C. puzosiana*) provenance. Recorded fossils reveal a longer time span of sedimentation than previously known (starting at least in the Bajocian and terminating in the Tithonian), suggesting the existence of a significantly larger sedimentary basins that had been eroded prior to the Cenomanian transgression event (Upper Cretaceous).

Keywords Bohemian Massif · Middle · Upper Jurassic · biostratigraphy · palaeobiogeography

Introduction

Historically, some of the first studies focused on the Jurassic rocks of North Bohemia were published in the second half of the nineteenth century. Lenz (1870) studied Jurassic strata in great detail as numerous limestone quarries were explored and, thus, became well exposed. He described numerous Jurassic fossils, including ammonites, belemnites, brachiopods, bivalves, echinoids and so forth. Lenz investigated geological and sedimentological contexts, including the descriptions of a periodic alternation of carbonate and non-carbonate strata. Bruder (1881) followed this research; his intense work includes several papers focused mainly on palaeontology. Bruder systematically described additional ammonites, brachiopods, echinoderms, bryozoans, porifera and belemnites (Bruder 1881, 1882, 1885, 1886, 1887, 1888). The Jurassic rocks of N Bohemia were examined also for prospecting silver, copper and zinc from under-represented ores (e.g. Herrmann and Beck 1897; Chrt 1957). In the second half of the twentieth century, five boreholes were drilled in the studied area (Chrt 1957). A microfacial analysis of Jurassic rocks was provided by Eliáš (1981) and most recently by Valečka (2019).

Modern studies have summarised data, especially in stratigraphically important fossil groups, i.e. ammonites (Hrbek 2014) and calcareous nannoplankton (Holcová and Holcová 2016). An analysis of the ammonite assemblage (part) shows a sub-Boreal provenance under considerable sub-Mediterranean

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influence. Ammonites indicate exclusive the Upper Jurassic, that is, in the Kimmeridgian and Oxfordian stages (Hrbek 2014). However, calcareous nannoplankton has proved prolonged sedimentation up to the Tithonian stage (Holcová and Holcová 2016).

Belemnites from N Bohemia were studied at a systematic level and have only partly been used as biostratigraphical markers (Bruder 1882; partly mentioned by Hrbek 2014). However, belemnite rostra are one of the most important sources of proxy data for palaeoecological and stratigraphical interpretations because they are relatively taphonomically resistant and preserve an important geochemical data (i.e. carbon and oxygen stable isotopes, strontium isotopes and the content of other elements) incorporated into the rostrum. The obtained values are significant for the palaeoenvironmental reconstructions and geochronology of sedimentary units (McArthur et al. 2007; Wierzbowski and Joachimski 2009; Hoffmann and Stevens 2020). A similar approach has recently been used for the Jurassic–Lower Cretaceous belemnites from the Outer Western Carpathians (Vaňková et al. 2019, 2021). In contrast, no detailed analyses of the Jurassic belemnites from northern parts of the Bohemian Massif have been performed yet.

The latest research has sought to confirm the connection between the Boreal and Tethyan realms through a seaway *via* the Bohemian Massif. A new finding of pebbles of Jurassic sediments in the Coniacian sandstones of the Bohemian Cretaceous Basin (BCB) in N Bohemia has permitted an analysis of the stratigraphical—and probably also palaeogeographical—extent of Jurassic sedimentation in the NW part of the Bohemian Massif (Valečka 2019). Records of pebbles of Jurassic silicites, deposited in Cretaceous and Tertiary rocks, from the vicinity of Svitavy, Moravský Krumlov, Třebíč, Zittau and other localities may indicate a significantly larger sedimentary space of the Jurassic basin(s) (Eliáš 1981; Valečka 2019).

Geological and stratigraphical settings

The studied area (Fig. 1) is characterised by Permo-Carboniferous, Jurassic and Cretaceous sedimentary units, here accompanied by metamorphic and volcanic rocks dating to the early Palaeozoic to Neoproterozoic (Opletal and Adamová 2001). Permo-Carboniferous deposits are referred to as the Sudetic basins, and they occur along the Lausitian Fault and in some other areas (Holub et al. 1978).

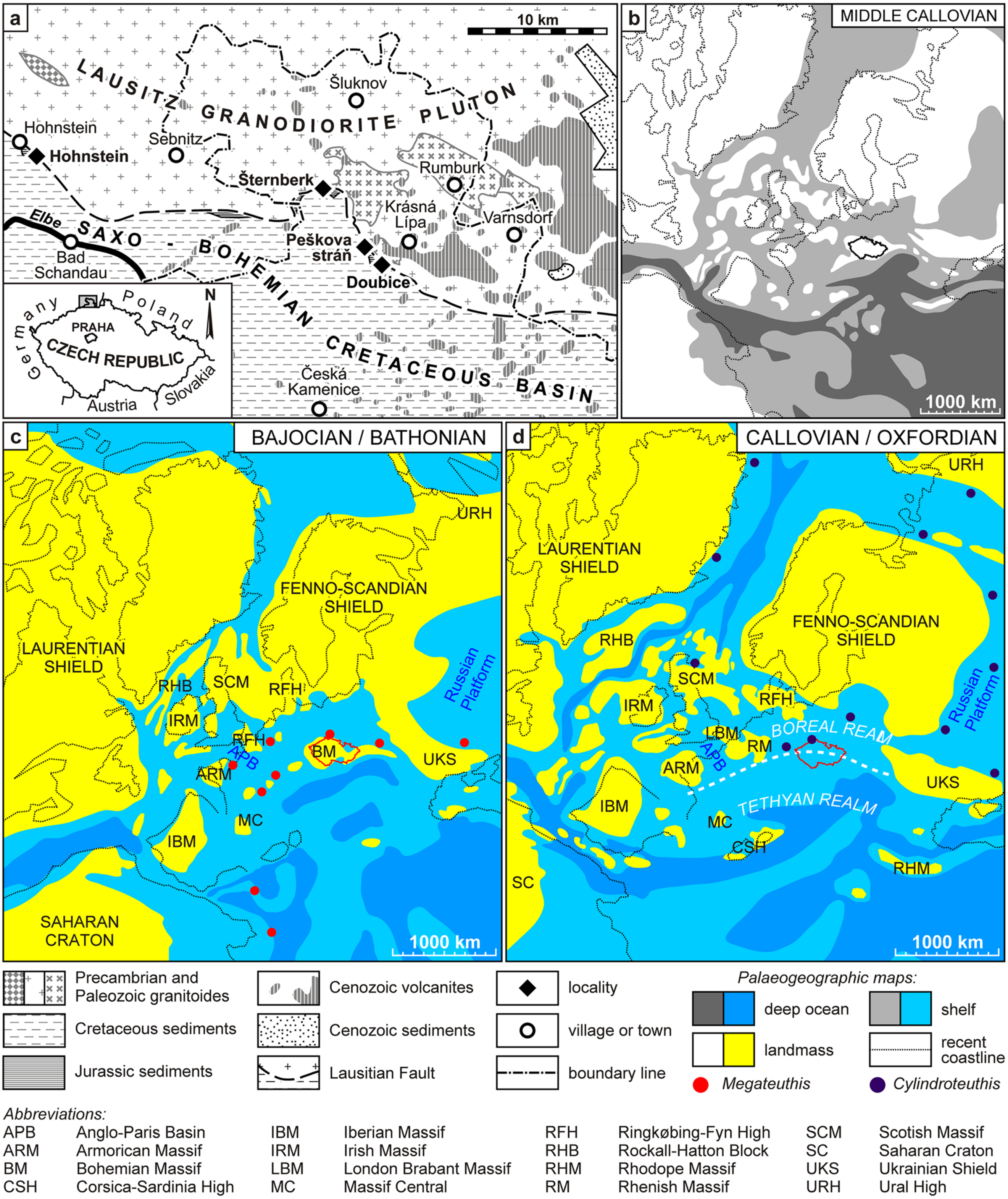
According to a historical point of view, the upper Callovian (Middle Jurassic) is represented by ten-metre-thick sandstones of the Brtníky Formation without significant fossils (Eliáš 1981). The Oxfordian limestones to dolomitic limestones of the Doubice Formation reach a thickness up to several tens of metres. The Kimmeridgian stage is represented by darker limestones with a reduced thickness (Eliáš 1981). These stratigraphic units need to be reconsidered in the future. It is clear from the fossil record that the Jurassic rocks of N Bohemia have a much more comprehensive stratigraphic range than thought initially.

Sandstones, limestones and dolomites represent the Jurassic age of rocks in N Bohemia with alternating layers of non-carbonate composition (Chrt 1957). The thickness of these rocks is sometimes more than 100 metres [locality Doubice (Vápenka); drill hole D-2] (Chrt 1957). This deepest (204 metres) and most complete drill hole consists of the granitoid basement (0–16 metres), Jurassic sandstones with calcareous dolomite and clay alternating layers (16–70 metres), dolomitised carbonates with pelite sediment layers (70–98 metres), pelite sediments (98–116 metres), dolomitic limestones (116–124 metres), overlain by Cretaceous sandstones (with coal seams) and marine conglomerates with fauna (124–204 metres).

Currently, only non-fossiliferous layers are exposed in the area, so museal material (drill cores and fossils) is used to study these rocks. In situ rock layers are now only be seen in part of the former mining gallery at the locality Doubice (Vápenka) (Fig. 2).

First mentioned by Lenz (1870) a Middle Jurassic age is based on fossils from Saxony, including a doubtful record of *Belemnites giganteus* von Schlotheim, 1820. The beginning of sedimentation during this interval was also mentioned by Bruder (1882, 1885). It was generally suggested that sedimentation in Saxony probably began earlier but without relevant evidence. Generally, the end of sedimentation is presumed during the Kimmeridgian in Saxony; however, in the Bohemian part, it is probably ended later (Eliáš 1981). Based on calcareous nannofossils, a Tithonian age has been recognised by Holcová and Holcová (2016).

Fig. 1 **a** Schematic geological map of the studied area with an investigated localities (black rhombs): Doubice (Vápenka) – GPS 50°53'46.5"N 14°28'51.1"E, Peškova stráň (Kyjov) – GPS 50°54'22.6"N 14°28'21.5"E, Šternberk (Brtníky) – GPS 50°56'30.0"N 14°26'44.8"E, Hohnstein – GPS 50°58'17.1"N 14°07'15.7"E; b–d palaeogeographic reconstructions of the Central Europe, modified after Dercourt et al. (2000), Taheri et al. (2009), Golonka (2011), Wierzbowski and Rogov (2011), Leonowicz (2015), Kettle (2016) and Averianov and Zverkov (2020); **b** palaeogeographic map of the middle Callovian prior the major transgression event during the Callovian/Oxfordian transition. Note, Czech Republic (including the Bohemian Massif) is showed like emerged land with only marginal sea influence in the North; **c** Bathonian/Bajocian palaeogeographic situation in Europe. Red dots represent distribution of the belemnite *Megateuthis* in this interval. Czech Republic with Bohemian Massif is highlighted by red contures; **d** palaeogeographic distribution of typical Boreal belemnite *Cylindroteuthis* (dark purple dots) during the Callovian/Oxfordian transition. Based on southern records of cylindroteuthidid belemnites in Central Europe, the hypothetical boundary between Boreal and Tethyan Realms (dashed line) is reconstructed for this area. ▶



At the locality Doubice (Vápenka) near Krásná Lípa, sequences of rocks with rhythmically alternating layers of dolomitised limestones with the intercalation of fine-grained siltstones developed (Fig. 2). The findings of the micritic limestones at the Peškova stráň (Kyjov; Khaa) locality indicate rather hemipelagic to almost pelagic sedimentation, suggesting differentiated depositional area. It is notable that all types of deposits mentioned herein are tectonised fragments of different Jurassic strata that were exposed at different sites along the Lausitian Fault.

Material and methods

Institution abbreviations, terminology and geochemical analyses of belemnite rostra

The studied belemnite rostra are deposited in collections [National Museum at Prague, N, ČK; Chlupáč's Museum of the Earth History, Faculty of Science, Charles University, CHMHZ, CHMHZ-MS (Martin Souček collection), CHMHZ-JG (Jan Geist collection); Municipal Museum of Ústí nad Labem, G; Senckenberg Naturhistorische Sammlungen Dresden, MMG-SaJ; Geowissenschaftliche Sammlungen der TU Bergakademie Freiberg, RS]. Several new samples were collected during the fieldwork (CHMHZ-JG). The belemnite material consists of more than 125 specimens, including 40 complete and/or clearly determinable rostra. Nannoplankton samples come from 15 newly found rocks (CHMHZ-JG, CHMHZ-MS; locality Peškova stráň) and 3 samples from museal collection (N 207/1, N 207/2, N 207/3; locality Šternberk).

The terminology of belemnite morphology follows Pugaczewska (1961) and Hoffmann and Stevens (2020). The following parameters are used: MLD (maximum lateral diameter), d-s (lateral diameter) and d-v (dorsoventral diameter). The length of the rostra is divided as: small (< 50 mm), medium (< 150 mm) and large (> 150 mm). The cross-section of the rostrum was used as a reliable determining feature. In one sample (No. CHMHZ-JG-1/1), a vertical section of the rostrum was used for the correct taxonomical determination. In the taxonomical description, 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. Compression is referred to herein as lateral flattening, while depression reflects dorsoventral narrowing.

For an accurate systematic determination and evaluation of the morphology of the alveolus, one rostrum (No. N 207/1) was studied using micro-CT techniques (Phoenix NANOMEX 180 device) at Czech Technical University, Laboratory for Development and Implementation at the Faculty of Electrical Engineering (Fig. 3).

Diagenetic alterations of the rostra and their suitability for geochemical analyses were verified using the double-checking method. Cross-sections of rostra were analysed in thin sections (max thickness 50 μm) by the cathodoluminescence technique ('Cold-stage' CITL 8200 CLmk4, Cambridge Image Technology Ltd.) with a magnification of 2.5x10 under a modified microscope (Avantes spectrometer connected to a Leica DMLP microscope) equipped with a vacuum pump as well as electrical voltage and current source (U=10–13 kV, I= 300 μA) at the Institute of Geochemistry, Mineralogy and Mineral Resources, Faculty of Science, Charles University (Fig. 4).

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.

Part of the subsamples 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% HNO3 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).

Strontium was isolated from the calcite matrix using exchange chromatography techniques with Triskem's Sr resin (Míková and 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 $^{87}Sr/^{86}Sr=0.710312 \pm 0.001$ (2 σ; n=6).

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 V-PDB 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).

Fig. 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).

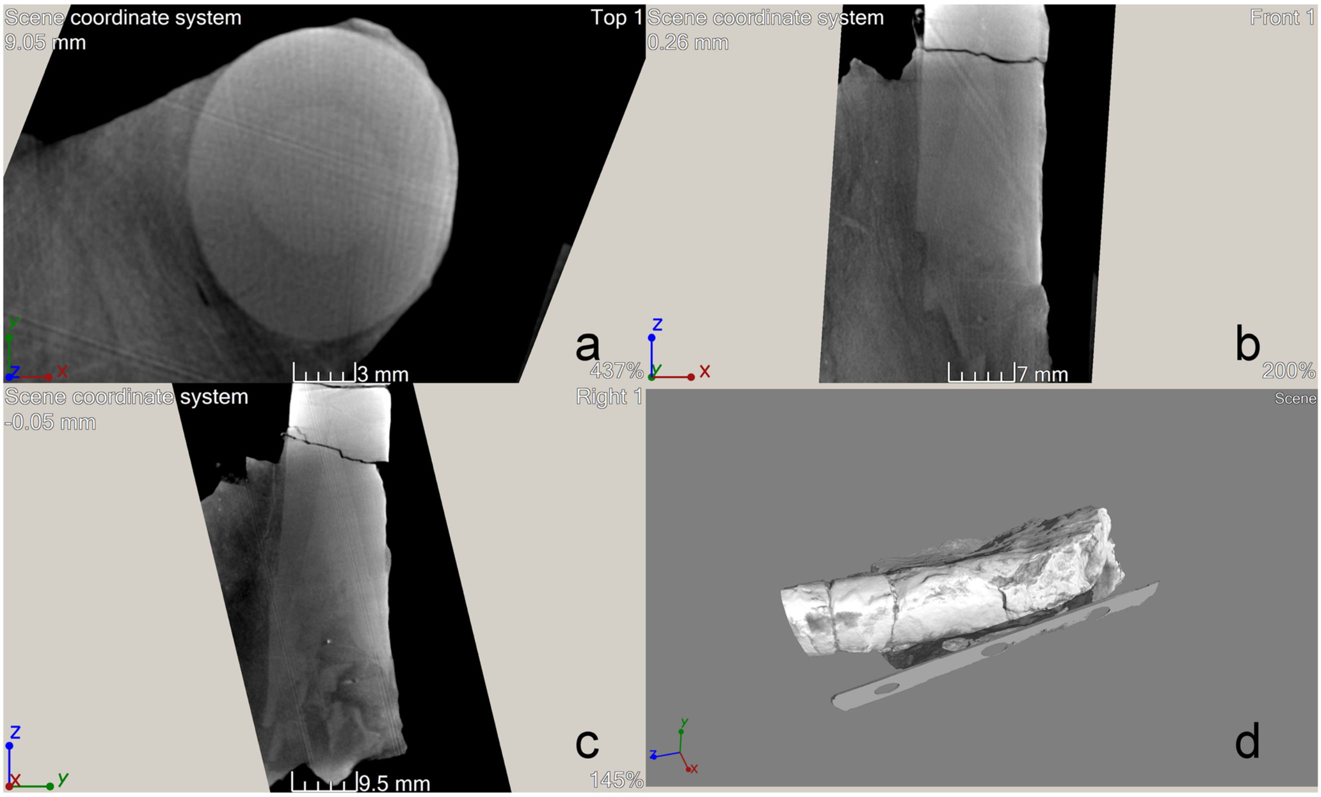


Fig. 3 Micro-CT visualisation with visible alveolus (*Megateuthis suevica*; N 207/1). **a** cross-section, **b** dorsal view, **c** ventral view, **d** sample examined in the machine holder (visualisation by Petr Ježdík, Laboratory for Development and Implementation at the Faculty of Electrical Engineering, Czech Technical University).

Calcareous nannoplankton

For calcareous nannofossils, 13 samples obtained by separating them from the surrounding rocks and alveolus of belemnite rostra were inspected [CHMHZ-JG-9/2 (alveolus), CHMHZ-JG-9/3 (surrounding matrix near alveolus) and CHMHZ-JG-9/4 (surrounding matrix near apex); CHMHZ-JG-10/2 and CHMHZ-JG-10/3 (surrounding matrix); CHMHZ-JG-15 (sample with brachiopod); CHMHZ-JG-1/2 and CHMHZ-JG-1/3 (surrounding matrix); N 207/2, N 207/3 and N 207/4 (surrounding matrix); CHMHZ-MS-5292/2 and CHMHZ-MS-5292/3 (surrounding matrix)]. Ca-nannoplankton was studied from smear slides under an optical microscope (polarised and normal light, magnification 1000x) and in a scanning electron microscope (SEM). Because the samples originated from museal items with unique macrofossils, only a very restricted volume of rock material was available for the nannoplankton study (1–3 mm^3), especially from the belemnite alveolus infill. Therefore, no method for the concentration of nannofossils could be applied. The rock material was suspended in distilled water, and this suspension was dropped to a SEM stub or cover glass to prepare the smear slides. Two smear slides were prepared and inspected from every sample. For the determination of nannoliths, the taxonomical concept presented in the Nannotax database (Young et al. 2021) was applied.

Results

Systematic belemnite palaeontology

Cephalopoda Cuvier, 1797
Coleoidea Bather, 1888
Belemnoidea Gray, 1849
Belemnitida Zittel, 1895
Suborder Belemnopseina Jeletzky, 1965
Family Belemnopseidae Naef, 1922, emend. Jeletzky, 1946

Genus *Hibolithes* Montfort, 1808

Type species: *Hibolithes hastatus* Montfort, 1808; p. 384–385, pl. 47, by monotypy (= *Belemnites sulcatus* v. Münster, 1830 *sensu* Riegraf et al. (1998), *nomen dubium*)
Remarks: The monotypical genus *Hibolithes* Montfort, 1808 described from Callovian-Oxfordian black marls located in south-eastern part of Gap (France) is currently under revision. The type species *H. hastatus* by Montfort (1808) is thus

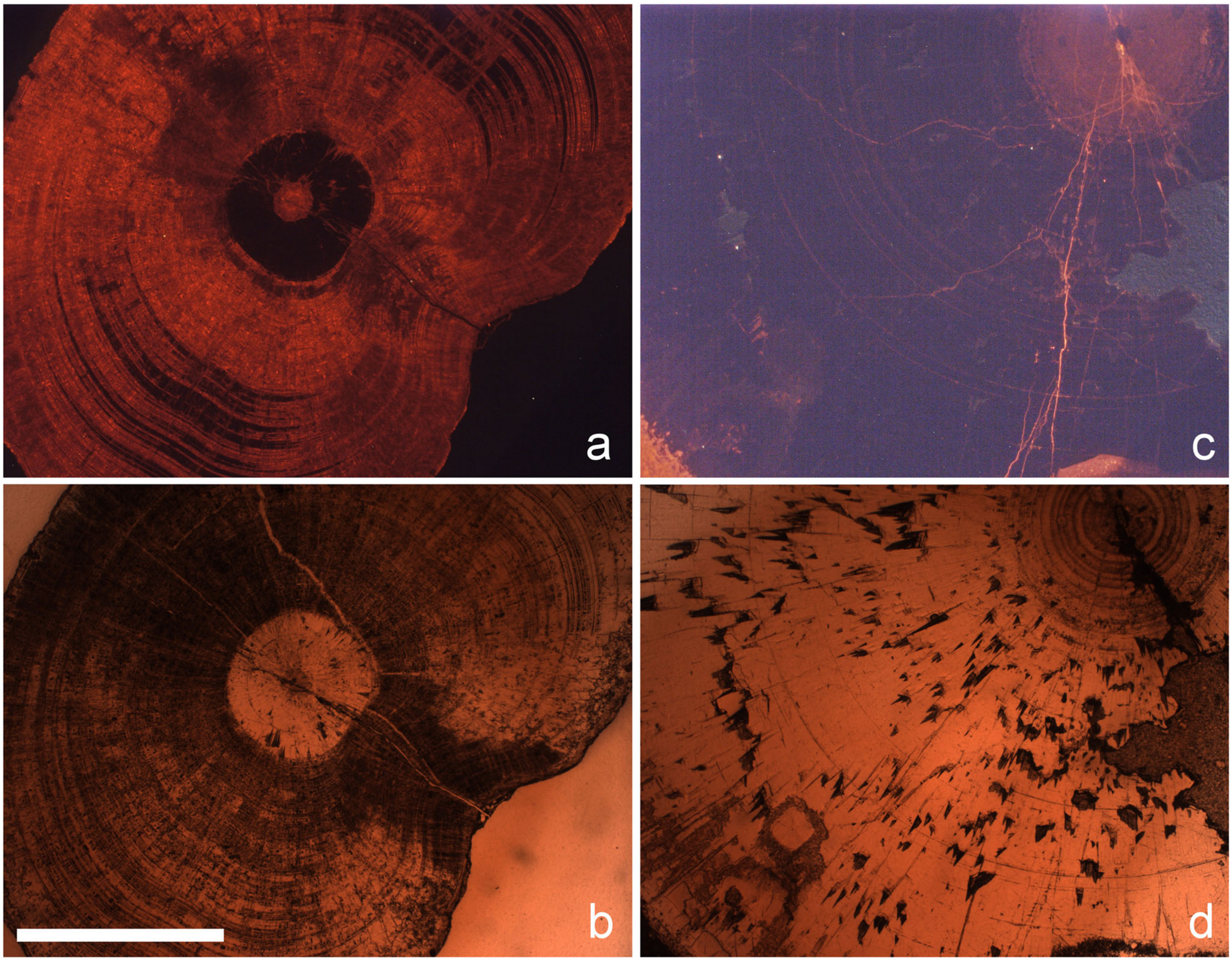


Fig. 4 Cathodoluminiscence of cross-sections of selected rostra. **a**, **b** *Belemnopsis* sp. indet. (CHMHZ-JG-14); **c**, **d** *Hibolithes hastatus* (CHMHZ-JG-13b); **a**, **c** cathodoluminescence images (bright orange colour corresponds to the high Mn content); **b**, **d** normal light.

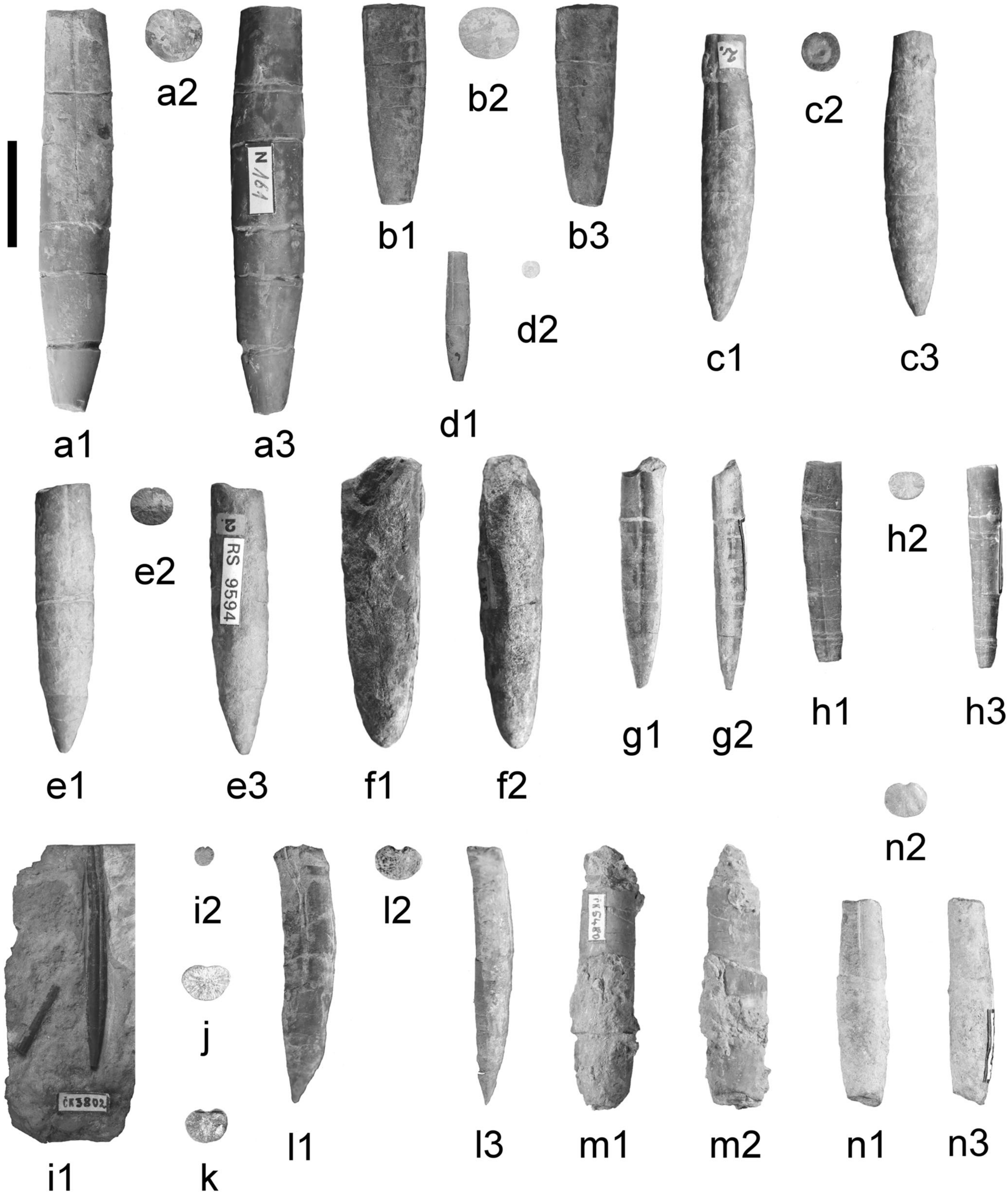
currently without a valid determination but with clear features indicating an Early Cretaceous duvaliid (Janssen 2021). Therefore, the alternative term *Hibolithes* auctorum is preferred. Because the new status is not yet fully defined and used in an effort to avoid inconsistencies, we follow the original designation. Future detailed investigation of the validity of this taxon is necessary.

Hibolithes hastatus Montfort, 1808
(Fig. 5 a–e)

1808 *Hibolithes hastatus* Montfort, p. 384–385, pl. 47
1827 *Belemnites hastatus* de Blainville; p. 71–72, pl. 2, figs. 4–4a
1827 *Belemnites semihastatus* de Blainville; p. 72–74, pl. 2, figs. 5 c–i
1831 *Belemnites semihastatus* von Zieten; p. 29, pl. 22, fig. 4
1849 *Belemnites semihastatus rotundus* Quenstedt; p. 440, pl. 29, figs. 8–11
1870 *Belemnites canaliculatus* (Schlotheim); Lenz, p. 27
1874 *Belemnites hastatus* (de Blainville); Alth, p. 229, pl. 4, figs. 1–3
1922 *Hibolithes hastatus* Blainville; Naef, p. 249, fig. 71, text-figs. 71 k, p, r, 89 f
1981 *Hibolithes* (*Hibolithes*) *hastatus hastatus* Montfort; Riegraf, p. 81–84, 199–201, pl. 6, figs. 45–47
2002 *Hibolithes hastatus* Montfort; Mariotti, p. 17, pl. 1, figs. 1–6

Material and localities: 5 complete juvenile and adult rostra, 18 nearly complete rostra with missing alveolar part or apex (with measurable dimensions); (No. MMG-SaJ 21, N 01–04, N 161, N 163, N 185, N 189–192, N 191–192, N 194, N 196–199, CHMHZ-JG-9, CHMHZ-JG-13a, b, c); and additionally 5 fragments from Hohnstein (Saxony, Germany), Šternberk and Peškova stráň.

Description: The hastate rostrum with an eccentric apical line inclined to the dorsal side. The rostrum of a medium size, the



length of the rostrum reaches a maximum of about 80 mm. The MLD lies approximately at 3/4 of the length of the rostrum where the distinct ventral groove disappears. Doppellinien well developed. The alveolar area is compressed, while the rostrum solidum is depressed. The cross-section of the rostrum is circular and compressed to depressed from the alveolar part towards the apex.

Remarks: *Hibolithes hastatus* belongs to the most widespread Jurassic belemnites. Numerous typical morphological features (e.g. ventral groove ending at place of the MLD,

◀ **Fig. 5** Belemnites of the families Belemnopseidae and Duvaliidae. **a** *Hibolithes hastatus* Montfort, 1808; N 161 (1 – ventral view, 2 – cross-section, 3 – lateral view); locality Šternberk (Brtníky). **b** *Hibolithes hastatus* Montfort, 1808; ČK 5479 (1 – ventral view, 2 – cross-section, 3 – lateral view); locality Šternberk (Brtníky). **c** *Hibolithes hastatus* Montfort, 1808; RS 9595 (1 – ventral view, 2 – cross-section, 3 – lateral view); locality Peškova stráň (Kyjov). **d** *Hibolithes hastatus* Montfort, 1808 (juvenile); N 198 (1 – ventral view, 2 – cross-section); locality Šternberk (Brtníky). **e** *Hibolithes hastatus* Montfort, 1808; RS 9595 (1 – ventral view, 2 – cross-section, 3 – lateral view); locality Peškova stráň (Kyjov). **f** *Belemnopsis* sp. indet (von Schlotheim, 1820); G 17 667 (1 – ventral view, 2 – lateral view); locality Doubice. **g** *Belemnopsis canaliculata* (von Schlotheim, 1820); N 19 (1 – ventral view, 2 – lateral view); locality Šternberk (Brtníky). **h** *Belemnopsis canaliculata* (von Schlotheim, 1820); N 68 (1 – ventral view, 2 – cross-section, 3 – lateral view); locality Šternberk (Brtníky). **i** *Belemnopsis latesulcata* (Voltz, 1832) in Thurmann (1832); N 206 (1 – ventral view, 2 – cross-section); locality Peškova stráň (Kyjov). **j** *Belemnopsis latesulcata* (Voltz, 1832) in Thurmann (1832); N 201 (cross-section); locality Šternberk (Brtníky). **k** *Belemnopsis latesulcata* (Voltz, 1832) in Thurmann (1832); N 202 (cross-section); locality Šternberk (Brtníky). **l** *Belemnopsis subhastata* (Zieten, 1831); CHMHZ-JG-12 (1 – ventral view, 2 – cross-section, 3 – lateral view); locality Šternberk (Brtníky). **m** *Rhopaloteuthis sauvanausa* (d'Orbigny, 1842); N 187 (1 – ventral view, 2 – lateral view); locality Šternberk (Brtníky). **n** *Rhopaloteuthis sauvanausa* (d'Orbigny, 1842); N 20 (1 – ventral view, 2 – cross-section, 3 – lateral view); locality Šternberk (Brtníky). The scale bar equals 2 cm.

characteristic compression and depression at specific parts of rostra) easily determine this species. *H. hastatus* is well distinguishable from *H. semihastatus* (Blainville, 1827) and *H. beyrichi* (Oppel, 1857) because of its distinct ventral groove and different rostra diameters. In addition, the species *H. beyrichi* already occurs in the Bathonian (Mariotti 2002).

Occurrence: Tethyan Realm and adjacent areas, including the sub-Boreal Realm. Upper Callovian–middle Oxfordian strata at Monte Kumeta (Sicily, southern Italy) (Mariotti 2002), Bathonian–Oxfordian in Poland (Pugaczewska 1961); England, Czech Republic (Bruder 1881, this study), Portugal, Algeria, Caucasus, India, Madagascar and other regions (see Mariotti et al. 2013 and references therein).

Genus *Belemnopsis* Bayle, 1878

Type species: *Belemnites apiciconus* Blainville, 1827 [= *Belemnites sulcatus* Miller, 1826 by subsequent designation of Douvillé (1879), depicted as *Belemnopsis sulcata* (Miller, 1826) by Bayle (1878)] (Mitchell 2015).

Remarks: The genus *Belemnopsis* Bayle, 1878 is taxonomically inconsistent. There are many opinions regarding the correct classification of these rostra (e.g. Douvillé 1879; Mitchell 2015). This genus includes many morphologically similar species that have been reduced and reassigned over the years (see Schlegelmilch 1998). According to a large number of rostra from the Šternberk locality, Bruder (1882) defined a new species of the genus *Belemnites* (now *Belemnopsis*): *B. postcanaliculatus* Bruder, 1882. Nevertheless, detailed analyses of the samples have denied the validity of this taxon, and the rostra have been redefined as *Belemnopsis canaliculata* and *Belemnopsis subhastata* (see below).

Belemnopsis canaliculata (von Schlotheim, 1820)
(Fig. 5 g–h)

1820 *Belemnites canaliculatus* von Schlotheim, p. 49
1831 *Belemnites canaliculatus* von Schlotheim; Zieten, p. 27, pl. 21, figs. 3 a–e
1842 *Belemnites canaliculatus* von Schlotheim; d'Orbigny, p. 108–110, pl. 13, figs. 1–5
1882 *Belemnites postcanaliculatus* Bruder, p. 457–458, pl. 1, figs. 5a, 5b
1920 *Belemnopsis canaliculata* (von Schlotheim); Bülow-Trummer, p. 127
1953 *Belemnites canaliculatus* von Schlotheim; Różycki, p. 325
1961 *Belemnopsis canaliculatus* (von Schlotheim); Pugaczewska, p. 143–146, pl. 9, text-fig. 13

Material and localities: 2 almost complete rostra with missing alveolar part and apex (No. N 19, N 68; Šternberk).

Description: Mostly cylindrical to hastate rostra, small– to medium– sized in length. The length of the apical part up to 30 mm. The ventral side is slightly concave. The smallest d-s diameter is in the alveolar region. A significantly wide and deep ventral groove well developed. Indistinct doppellinien are visible only on very well-preserved rostra, continuing along the entire length of the rostrum. In some specimens, a mucro is developed. The cross-section of the rostrum is kidney-shaped, rarely circular in the apical part.

Remarks: A typical morphological feature of this species is a very wide and deep ventral groove that, in many cases, extends to the end of the apex. According to Pugaczewska (1961), the stratigraphical range of this species is from the Bathonian to Oxfordian. However, later authors reported a stratigraphic distribution only from the Bajocian to Bathonian (e.g. van Diggelen 1986). This stratigraphic enigma has not yet been resolved. This problem is also linked to unclear systematic and taxonomic classifications. *Belemnopsis canaliculata* might be misinterpreted with morphologically closely related taxa such as *B. bessina* (d'Orbigny, 1842) or *B. subhastata* (Zieten, 1831). Nevertheless, *B. subhastata* has a longer apex and generally, the ventral groove does not reach the apex.

Occurrence: Bathonian–lower Oxfordian; Tethyan and sub-Boreal realms – Europe, Asia (Caucasus, India), Australia (Pugaczewska 1961), Czech Republic (Lenz 1870, this study).

Belemnopsis latesulcata (Voltz, 1832) in Thurmann (1832)
(Fig. 5 i–k)

1832 *Belemnites latesulcatus* Voltz; Thurmann, p. 27
1893 *Belemnites latesulcatus* Voltz; Riche, p. 327–328, pl. 2, figs. 13–17
non1910 *Belemnites latesulcatus* Voltz; Benecke, p. 129–132, pl. 1, figs. 1–2 = *Belemnopsis canaliculata* (von Schlotheim, 1820)
1920 *Hibolithes latesulcatus* (Voltz); Bülow-Trummer, p. 145
1961 *Belemnopsis latesulcatus* (d'Orbigny); Pugaczewska, p. 150–153, pls. 11–12, fig. 1, text-fig. 14
2002 *Belemnopsis latesulcatus* (Voltz in Thurmann); Mariotti, p. 20, 22, pl. 2, figs. 3–6
2013 *Pachybelemnopsis latesulcatus* (Voltz in Thurmann); Mariotti et al., p. 4, pl. 3, fig. A

Material and localities: 1 complete rostrum (No. N 206; Peškova stráň) and 2 fragments (No. N 201, N 202; Šternberk).
Description: Small, cylindrical to slightly hastate and canaliculated rostrum. The apical part is up to 15 mm long. The MLD approximately at 1/3 (in juveniles) and at 1/2 (adults) of the length of the rostrum. The smallest d-s diameter is positioned in the alveolar part. The wide ventral groove extends almost to the apex, and the rostrum is strongly depressed. The apical part is relatively short, sometimes with mucro. The cross-section of the rostrum is circular to kidney-shaped and depressed.
Remarks: Distinctive keel-shaped lateral walls extending almost along the entire length of the rostrum (with the exception of the rostrum cavum and apex) are the most significant morphological features of this taxon. These walls occur only in the adult stage. *B. latesulcata* can also be distinguished from other related taxa by its relatively smaller size. The dorsal bulging of the rostrum is also the most prominent feature compared to other representatives. The species was originally described as *Belemnites latesulcatus* by Voltz (1830), nevertheless it has taxonomically been established by Thurmann (1832). The first illustration of this species was given by Benecke (1910) (Mariotti 2002), however, the depicted specimen does not correspond to typical representatives of *B. latesulcata*.
Occurrence: Bathonian–lower Oxfordian; Tethyan Realm – England, Poland, Algeria, Italy and other regions (Mariotti 2002, and references therein), Czech Republic (this study).

Belemnopsis subhastata (Zieten, 1831)
(Fig. 5 l)

1831 *Belemnites subhastatus* Zieten, p. 27, pl. 21, figs. 2 a–e
1882 *Belemnites postcanaliculatus* Bruder, p. 457–458, pl. 1, figs. 4a–4b, 5a–5b
1920 *Hibolites subhastatus* (Zieten); Bülow-Trummer, p. 154–155
1953 *Belemnites* (*Hibolites*) *subhastatus* Zieten; Różycki, p. 326
1961 *Belemnopsis subhastatus* (Zieten); Pugaczewska, p. 154–157, pl. 12, fig. 2, pl. 13, figs. 1–7, text-fig. 15
1998 *Belemnopsis subhastata* (Zieten); Schlegelmilch, p. 81, pl. 18, figs. 1–2
2016 *Belemnopsis subhastata* (Zieten); Dzyuba, p. 51–52, pl. 1, figs. 2 A–E

Material and localities: 1 complete and 2 almost complete rostra (No. CHMHZ-JG-12, N 162, RS 9594; Šternberk).
Description: Medium-sized rostra, cylindrical to hastate in shape and considerably elongated. The ventral side is slightly concave. The MLD is located at approximately 1/2 of the rostrum length. The ventral groove is initially pronounced and visibly widened towards the apex, where it gradually disappears. Doppellinien are observed to approximately 1/2 of the rostrum length. In the proximal part, doppellinien are inclined to the ventral side of the rostrum and decline in the distal part. The apex is quite elongated and pointed. The cross-section is slightly compressed in the proximal part and depressed in the distal part, except for the apex, where it is circular.
Remarks: This species shows the closest similarity to *B. bessina*; however, it has a less pronounced ventral groove and it is slightly more elongated. *B. subhastata* may be misinterpreted as *B. canaliculata*, but the latter taxon differs regarding the characteristics of the ventral groove, which is longer and more pronounced than in *B. subhastata*. Moreover, *B. canaliculata* is more dorsoventrally depressed. The relationships of *B. subhastata* to the genus *Hibolithes* have been resolved (e.g. Bülow-Trummer 1920) and the species is firmly entrenched within the genus *Belemnopsis* Bayle, 1878.
Occurrence: Bathonian–Callovian; Tethyan Realm with slight overlap to the sub-Boreal Realm – England, France, Germany, Poland, Serbia, India and other regions (Pugaczewska 1961 and references therein), Czech Republic (Bruder 1882, this study).

Belemnopsis sp. indet.
(Fig. 5 l)

Material and localities: 1 incomplete rostrum (No. G 17 667; Doubice), 8 belemnite fragments (No. N 185–188; ?Šternberk, N 203–205, CHMHZ-JG-14; Šternberk).
Description: Rostra of small to medium size, in many cases with a significant wide and deep ventral groove. The rostrum depression is well visible, cross-sections are characteristically kidney–shaped.
Remarks: Mostly small fragments with some morphological variability, indeterminable features for closer taxonomic classification. Because of taxonomic uncertainties and the wide stratigraphical range of the studied rocks, the samples are not included in the final stratigraphical evaluation.
Occurrence: The genus *Belemnopsis* is known from the Bajocian–lowermost Hauterivian of Europe, Africa, Madagascar, Pakistan, India, Tibet, South East Asia, Australia, New

Zealand, western Antarctica and South America (Mariotti 2002).

Family Duvaliidae Pavlow, 1914
Genus *Rhopaloteuthis* Lissajous, 1915

Type species: *Belemnites sauvanausus* d'Orbigny, 1842, p. 128–130, pl. 21, figs. 1–10 by subsequent diagnosis of Lissajous (1915).

Rhopaloteuthis sauvanausa (d'Orbigny, 1842)
(Fig. 5 m–n)

1842 *Belemnites sauvanausus* d'Orbigny, p. 128–130, pl. 21, figs. 1–10
1878 *Hibolites Sauvaneaui* (d'Orbigny); Bayle, p. 128, pl. 29, figs. 5–7
1882 *Belemnites Sauvanausus* d'Orbigny; Bruder, p. 458, pl. 1, fig. 6
1900 *Hibolites Sauvanaui* (d'Orbigny); Loriol, p. 6, pl. 2, fig. 2
1925 *Belemnites sauvanausus* d'Orbigny; Lissajous, p. 41–43, 131, pl. 23
1961 *Rhopaloteuthis sauvanausus* (d'Orbigny); Pugaczewska, p. 194–195, pl. 6, figs. 7–9
2002 *Rhopaloteuthis sauvanausa* (d'Orbigny); Mariotti, p. 27, pl. 4, figs. 4, 7

Material and localities: 2 almost complete rostra (No. N 20, N 187); Šternberk.
Description: Thick and short club-shaped rostrum with a significantly concave ventral side. The MLD is located at approximately 2/3 of the length of the rostrum. The deeply incised dorsal groove often reaches the place of the MLD. The apical line is eccentric and slightly inclined to the dorsum. The deep alveolus reaches up to 1/3 of the rostrum length. Weak lateral furrows are visible. The apex is short, ending with a mucronate tip. The cross-section of the rostrum is circular in the rostrum cavum and gradually changes to a square in the MLD part.
Remarks: *Rhopaloteuthis sauvanausa* belongs to the most abundant species within the genus *Rhopaloteuthis* in the Oxfordian. It shows the highest similarity to *R. argoviana* (Mayer, 1863); however, *R. sauvanausa* has a shorter and more robust rostrum than the latter species.
Occurrence: Upper Callovian–middle Oxfordian; Tethyan Realm with overlap into the sub-Boreal Realm – Germany, Poland, Czech Republic (Bruder 1882, this study), Italy, Turkey, Algeria, India, Madagascar and other regions (Mariotti 2002).

Suborder Belemnitina Zittel, 1895
Family Megateuthididae Sachs and Nal'njaeva, 1967
Genus *Megateuthis* Bayle, 1878

Type species: *Belemnites giganteus* von Schlotheim, 1820 (younger synonym for *Belemnites suevicus* Klein, 1773) by subsequent designation of Bayle in Douvillé (1879, p. 91).

Megateuthis suevica (Klein, 1773)
(Fig. 6 b, c)

1773 *Belemnites suevicus* Klein, p. 27–28, pl. 7, fig. 2
1820 *Belemnites giganteus* von Schlotheim, p. 45-46
1830 *Belemnites Aalensis* Voltz, p. 60–62, pls. 4, 7, fig. 1
1842 *Belemnites giganteus* von Schlotheim; d'Orbigny, p. 112–117, pls. 14, 15
1882 *Belemnites* conf. *semihastatus* Blainville; Bruder, p. 470–471
1911 *Megateuthis giganteus* (von Schlotheim); Wetzel, p. 219, pl. 19, figs. 7–8; p. 221
1916 *Mucroteuthis giganteus* Abel, p. 126, 140, pl. 49
1925 *Megateuthis giganteus* (von Schlotheim); Lissajous, p. 23–24, 90, pl. 12
1953 *Belemnites* (*Megateuthis*) *giganteus* von Schlotheim; Różycki, p. 326
1961 *Megateuthis giganteus* (von Schlotheim); Pugaczewska; p. 134–142, pls. 7–8
1998 *Megateuthis gigantea* (von Schlotheim); Schlegelmilch, p. 75, pl. 13, figs. 1–2, pl. 14, figs. 3–5
2000 *Megateuthis suevica* (Klein, 1773); Riegraf, p. 289–290, figs. 11–12, 19 (with additional synonymy)
2008 *Megateuthis suevica* (Klein, 1773); Weis and Mariotti, p. 166, pl. 6, figs. 1–3

Material and localities: 1 complete subadult rostrum (No. N 207/1; Šternberk) and 2 fragments (No. CHMHZ-JG-1/(1–4); Hohnstein, No. G 17 674; Šternberk).
Description: Conical rostrum with an obtuse angle of apex termination in the juvenile stage. During ontogeny, the tip of the apex stretches and turns polluted and can grow out into an epirostrum. The rostrum is long and elongated, reaching up to 100 mm. Apical grooves in the juvenile stages reach up to 2/3 of the rostrum length proximal to the apex (not seen in our material). Longer grooves are on the dorsolateral sides and shorter on the ventrolateral sides. In the gerontic stage, this range is shortened to about 1/3 of the rostrum length proximal to the apex. Characteristic of geronts are wrinkles (furrows) placed around the apical grooves. In the juvenile stage, the alveolus reaches up to approximately 1/3 of the rostrum length. During ontogeny, it shrinks to 1/5 of the length of the rostrum. The apex is long, compressed in the cross-section, circular to ovate and quadrate in adulthood.
Remarks: The taxonomic status of *M. suevica* is rather complicated. According to a priority, the taxon should be described as *M. suevica* (Klein, 1773). However, Klein's (1773) figured specimen has been lost. Von Schlotheim

(1820) established the new species *Belemnites giganteus* based on 20 specimens, but the holotype was not designated. Thereafter, the lectotype of *B. giganteus* was designated by Riegraf et al. (1998, p. 219–220). For detailed and thorough discussion, see Riegraf (2000). In the current study, we prefer the concept of the taxonomic name *M. suevica*, because it has been used steadily for last 20 years (Riegraf 2000; Weis 2006; Arkadiev and Dzyuba 2021). Moreover, Riegraf (2000, p. 290) noted that *B. giganteus* von Schlotheim, 1820 is a so often misunderstood species, which lacks any type figure thus far that it could be supposed to be a *nomen dubium*. In *M. gigantea*, *M. suevica* respectively, a possible sexual dimorphism has been described (e.g. d'Orbigny 1842; Hoffmann and Stevens 2020) expressed by the epirostrum, the apical grooves, furrows characteristics or connection with the bulging of the ventral side of the rostrum surface (Pugaczewska 1961). The presence of the epirostrum may, however, represent an adaptation to a purely pelagic way of life (e.g. Hoffmann and Stevens 2020). Possible sexual dimorphism was discussed many times; for example, the species *Megateuthis elliptica* (Miller, 1826) or *M. acuminata* (Simpson, 1855) were considered males and *M. gigantea, M. aalensis* (Voltz, 1830) or *M. longa* (Voltz, 1830) as females (d'Orbigny 1842). These hypotheses were discussed mainly based on the synchronous (or almost synchronous) occurrences of these taxa. With the exception of *M. elliptica*, however, some of these taxa may represent only intraspecific varieties. The concept of sexual dimorphism is still not completely resolved. *M. gigantea* differs from *M. elliptica* by having an obtuse apex and more conical profile and outline, with a cross-section that is more rounded across the entire rostrum length in *M. suevica* (Fig. 6c2). The stratigraphic range is similar. Both taxa are known from the *Propinquans* to *Parkinsoni* zones (doubtful in *M. suevica* = *M. gigantea*; Weis and Mariotti 2008). *M. elliptica* seems to have a wider range (see below). These taxa are common especially in the *Humphriesianum* Zone. Bruder (1882) considered some fragments from the N Bohemia as *B. giganteus* but did so without comparative evidence. After micro-CT investigation (Fig. 3) and detailed analyses of the cross-sections, we have recognised *M. suevica* and probably also *M. elliptica* (see below) in the studied material.

Occurrence: Lower Bajocian (*Propinquans–Humphriesianum* zones) (Schlegelmilch 1998; Weis and Mariotti 2008; Ippolitov 2018); France, Great Britain, Germany, Luxembourg (Weis and Mariotti 2008), *Humphriesianum* Zone of the Northern Caucasus (Gulyaev et al. 2015); Czech Republic (Bruder 1882; this study).

Megateuthis cf. *M. elliptica* (Miller, 1826)
(Fig. 6f)

? 2006 *Megateuthis elliptica* (Miller, 1826); Weis, p. 157, figs. 9–10 (with additional synonymy)
? 2008 *Megateuthis elliptica* (Miller, 1826); Weis and Mariotti, pl. 7, fig. 1

Material and localities: A single fragment (No. MMG-SaJ 10) from the Saxonian part of the Lausitian Fault; Hohnstein.

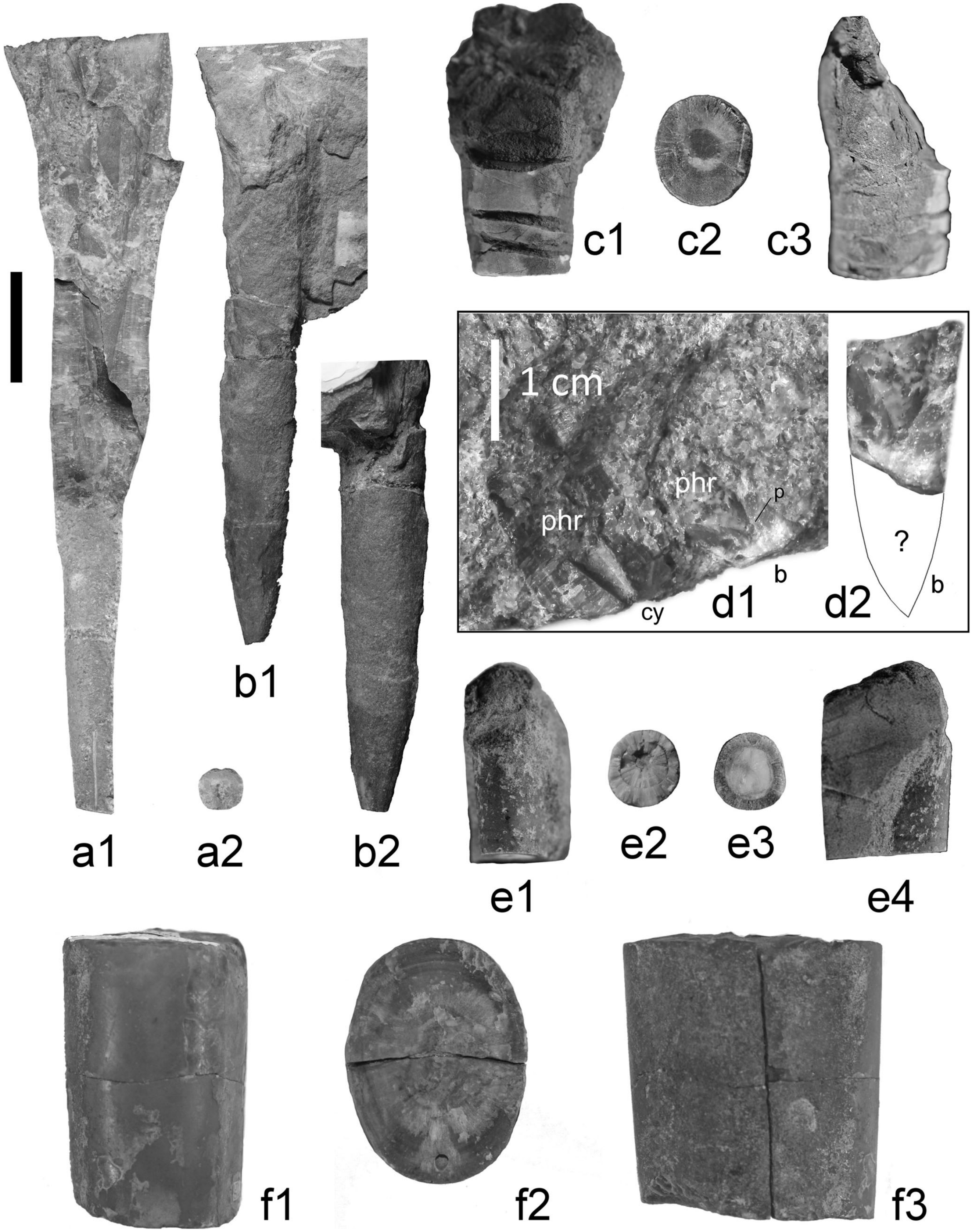
Description: The cross-section is typically ovate. The ventral flattening is lacking. The fragment represents the middle part of the rostrum solidum.

Remarks: According to Riegraf (2000) and Weis and Mariotti (2008), the important difference between *M. suevica* and *M. elliptica* can be observed in the cross-section: *M. suevica* is more rounded while *M. elliptica* is more ovate within the entire rostrum. Moreover, in *M. elliptica* the rostrum lacks the ventral flattening and/or depression. Therefore, we assume that the incomplete specimen from Hohnstein belongs to *M. elliptica*. Generally, specimens of *M. elliptica* differ in size in various stratigraphical intervals. Although smaller rostra (reaching up to 250 mm) are observed in the *Laeviuscula* and *Propinquans* zones, huge specimens (600–700 mm long; corresponding to the specimen MMG-SaJ 10) are known from the *Humphriesianum* Zone (Weis and Mariotti 2008). Bajocian and Bathonian megateuthidid taxa are considered to be a typical sub-Boreal elements (e.g. Doyle 1987), but they occasionally occur in the northern Tethyan areas (Fig. 1) (e.g. Calabria and others; Mariotti et al. 2007).

Occurrence: *M. elliptica* ranges from the *Laeviuscula*/*Propinquans* zones (lower Bajocian) to *Parkinsoni* Zone (uppermost Bajocian). France, Germany (also Saxony in this study), Great Britain, Luxembourg (Weis and Mariotti 2008), Switzerland, Poland (Pugaczewska 1961), ?Italy (Mariotti et al. 2007), upper Bajocian of the Northern Caucasus (Dzyuba et al. 2021), Bajocian of Donets Basin and Crimea (Paryshev and Nikitin 1981).

Family Cylindroteuthididae Stolley, 1919
Subfamily Cylindroteuthidinae Stolley, 1919
Genus *Cylindroteuthis* Bayle, 1878

Fig. 6 Belemnites of the families Cylindroteuthididae and Megateuthididae. **a** *Cylindroteuthis* cf. *C. puzosiana* (d'Orbigny, 1842); N 99/1 (1 – ventral view, 2 – cross-section); locality Peškova stráň (Kyjov). **b** *Megateuthis suevica* (Klein, 1773); N 207/1 (1 – ventral view, 2 – lateral view); locality Šternberk (Brtníky). **c** *Megateuthis suevica* (Klein, 1773); CHMHZ-JG-1/1 (1 – ventral view, 2 – cross-section, 3 – lateral view); locality Hohnstein. **d1** (cy – N 99/2 *Cylindroteuthis* cf. *C. puzosiana* (d'Orbigny, 1842); b – N 99/3 Belemnitina indet., phr – phragmocone, p – protoconch); **d2** detail of N 99/3 Belemnitina indet. with possible shape of rostrum; locality Peškova stráň (Kyjov). **e** Belemnitida *incertae sedis*; CHMHZ-JG-10/1 (1 – ventral view, 2 – cross-section of *rostrum solidum*, 3 – cross-section in alveolar part , 4 – lateral view); locality Peškova stráň (Kyjov). **f** *Megateuthis* cf. *M. elliptica* (Miller, 1826); MMG-SaJ 10 (1 – ventral view, 2 – cross-section, 3 – lateral view); locality Hohnstein. The scale bar equals 2 cm, with exception of figs **d1**, **d2** (the scale bar = 1 cm).


c1
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Type species: *Belemnites puzosianus* d'Orbigny, 1842 (p. 117–118, pl. 16) by monotypy.

Cylindroteuthis cf. *C. puzosiana* (d'Orbigny, 1842)
(Fig. 6a, d1(cy))

Material and localities: Rock sample (No. N 99) including one fragment (No. N 99/2) and 1 nearly complete rostrum (No. N 99/1; apicalmost part missing); Peškova stráň.
Description: Large-sized cylindrical rostrum with a deep alveolus, occupying up to 1/2 of the length of the preserved rostrum. The ventral apical or medioventral groove is distinct. The ventral side is slightly wider, rounded and more convex than the dorsum. The apical part is relatively short, with a circular cross-section. The apical line is eccentric and inclined to the ventral side. The rostrum, except for the apex, is compressed. During ontogeny, flattening becomes more pronounced.
Remarks: Possible occurrence of cylindroteuthidid belemnite should be also supported by occurrence of aulacostephanid (Boreal and sub-Boreal) ammonites. The appearance of typical lower Kimmeridgian Boreal and Sub-Boreal assemblages in northern Bohemia, represented by *Prorasenia* Schindewolf, 1925, *Rasenioides* Schindewolf, 1925 or *Eurasenia* Geyer, 1961, marks the Oxfordian/Kimmeridgian boundary (Hrbek 2014). The family Cylindroteuthididae is widespread in the Boreal Realm (e.g. Sachs and Nal'njaeva 1964; Doyle 1987; Dzyuba 2011). All cylindroteuthidids are relatively easily determinable from other related taxa within the family because of its typical ventral apical groove. Weakly eccentric apical line is typical for most species within the genera *Cylindroteuthis* and *Arctoteuthis* Sachs and Nal'njaeva, 1964. This sample belongs possibly to the genus *Cylindroteuthis*, which is morphologically distinguishable from the genus *Arctoteuthis*. The genus *Arctoteuthis* differs from the genus *Cylindroteuthis* by more flattened venter and uncompressed (circular to depressed) cross-section. The relative elongation of genera *Arctoteuthis* and *Cylindroteuthis* varies within close limits. The affinity of the sample for the species *C. puzosiana* is the largest due to the expected age of the rocks and unclear visibility of morphological parameters of the rostrum.
Occurrence: *Cylindroteuthis puzosiana* ranges Callovian–Kimmeridgian; Boreal belemnite – Russia, France, England, Ukraine (Mural 2011), Czech Republic (this study).

Belemnitina indet.
(Fig. 6d1(b), d2)

Material and localities: A single incomplete rostrum (No. N 99/3 sample); Peškova stráň.
Description: A 20 mm long fragment possessing a phragmocone/alveolar part with an eccentric apical line in longitudinal dorsoventral section. The alveolus is characteristic of one convex wall. The protoconch is well visible. The cross-section is compressed, circular to ovate.
Remarks: This rostrum is preserved within the N 99 sample (a piece of carbonate rock). Based on presence of *Cylindroteuthis* species in the same sample, we conclude a Late Jurassic age. Only one specimen with this type of alveolus was found in the studied material, however, the alveolar angle fits well with cylindroteuthidids. Nevertheless, we attribute this alveolus to a megateuthidid [possibly also genera *Arcobelus* Sachs and Nal'njaeva, 1967 and *Brevibelus* Doyle, 1992, however, both are of the Early (Toarcian, Aalenian), respectively the Middle Jurassic age (until Bajocian/Bathonian)]. Unfortunately, more detailed taxonomical classification is not possible due to the incomplete preservation of this studied fragmentary individual.

Belemnitida incertae sedis
(Fig. 6 e)

Material and localities: A single incomplete rostrum [No. CHMHZ-JG-10/(1–4)]; Peškova stráň.
Description: Small-sized, compressed rostrum (length of about 50 mm) without an apical part. The apical line is eccentric. No lateral, apical or alveolar fissures are present. The alveolus is relatively short, and the cross-section of the rostrum is subpyriform to subquadratic. In the alveolar part, the pyriform shape is more pronounced.
Remarks: The pyriform and subpyriform shape of the rostrum is characteristic for the Cylindroteuthididae, Megateuthididae and Hastitidae Naef, 1922 families. However, the overall shape may correspond to the genus *Eocylindroteuthis* Riegraf, 1980 (family Megateuthididae; e.g. *sensu* Dzyuba et al. 2015), which is known from the lower Bajocian, or to the genus *Brevibelus*, ranging from the upper Toarcian to the upper Bajocian (Schlegelmilch 1998). This assumption is supported by the absence of grooves and by the characteristic cross-section of the rostrum.

Belemnite rostra geochemistry

Only limited material could be studied because most of the belemnite rostra belong to unique institutional collections. Analyses of cathodoluminescence and elemental components (Tab. 1) proved extensive diagenetic overprint and/or unsuitability of almost all samples for further analyses. Therefore, only one sample (*Hibolithes hastatus*; CHMHZ-JG-13b) is included in final interpretation. The $\delta^{13}C$ and $\delta^{18}O$ isotope values show consistency for the Middle and Upper Jurassic interval, where lower $\delta^{18}O$ values fit well with the material from a similar environment (sub-Mediterranean) and the period around the Middle and Upper Jurassic boundary (e.g. Wierzbowski 2004; Wierzbowski et al. 2009). The $^{87}Sr/^{86}Sr$

Table 1 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); orange line: utilisable sample

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

value of 0.706886 corresponds to the Callovian–lower Kimmeridgian data of the global $^{87}Sr/^{86}Sr$ curve. This period is characterised by a rather uniform signal with balanced stagnation (Jenkyns et al. 2002).

Often, complete recrystallisation of the primary calcite of the rostra is present. Mostly, diagenetic processes significantly affected belemnite rostra and isotopic signals; therefore, the resulting values do not correspond with the original data. The amounts of Fe and Mn are higher than are generally considered to be applicable for relevant results of strontium analyses. Commonly, the amount of Mn should be <100 ppm, preferably <40 ppm (Vaňková et al. 2019) or <50 ppm (Jones et al. 1994), and ideally, the amount of Fe should not exceed 150 ppm (Wierzbowski 2004; McArthur et al. 2007). The amount of iron plays a much larger role in the analysed material and final evaluation than the amount of manganese (Jones et al. 1994). In addition, the concentration of Sr in the samples should be higher than 1000 ppm. Acceptable concentrations of the elements and isotope ratios vary between the authors and studied material (e.g. Jenkyns 1987; Jones 1994; Rosales et al. 2001, 2004; Jenkyns et al. 2002; McArthur et al. 2007). The Rb analysis was used to confirm the applicability of the samples for the strontium analyses. With a larger amount of rubidium, the final results are questionable. Moreover, ^{87}Rb decays to ^{87}Sr and higher concentrations of Rb isotopes can greatly affect the analysed amount of ^{87}Sr.

Diagenetic overprint is relatively common in the studied area and characteristic also for other fossils and rocks. Isotopic data from most of the Jurassic strata in the northern Bohemian Massif and in Saxony (Hohnstein) are not relevant due to significant tectonic activity of Lausitian Fault during the Tertiary. At that time, the fault re-activating led to the strong diagenesis and dolomitisation of older lithological units. Moreover, some of them were strongly tectonically affected, influenced by later contact metamorphism (basaltic intrusions) linked to dolomitisation (Doubice).

Calcareous nannoplankton

Although calcareous nannoplankton were recorded in every sample, the preservation in most of the samples was poor to extremely poor, which often did not allow taxonomical determination. Analysis of the nannoliths under SEM showed dissolution of coccoliths in these cases and common strong overgrowth (Fig. 7bb–gg).

The abundance of nannoplakton varies between 0.1 and 1 nannolith/field of view in the optical microscope for the samples CHMHZ-JG-9/3, CHMHZ-JG-9/4, CHMHZ-JG-1/2, CHMHZ-JG-1/3, N 207/2, N 207/3, N 207/4, CHMHZ-MS-5292/2 and CHMHZ-MS-5292/3. A higher abundance of nannoliths, reaching 2–5 nannoliths/field of view, is recorded in the samples CHMHZ-JG-9/2, CHMHZ-JG-9/3 and CHMHZ-JG-9/4. However, the assemblages in these samples are composed only of the dissolution-resistant genus *Watznaueria* Reinhardt, 1964, and the preservation of coccoliths is poor (Fig. 7t–aa).

Well preserved, relatively abundant and diversified assemblages have been recorded in sample CHMHZ-JG-10/2. Besides *Watznaueria barnesiae*, also *Zeugrhabdotus noeliae* (common), *Ethmorhabdus gallicus* (rare), *Axopodorhabdus cylindratus* (very rare) and *Crepidolithus crassus* (very rare; Fig. 7a–q, s) were also observed. In the case of this sample, the abundance varies between 5 and 10 nannoliths/field of view in the microscope. For detailed calcareous nannoplankton data from this area see also Holcová and Holcová (2016).

Palaeoenvironmental and stratigraphical evaluations

All the discovered calcareous nannoplankton taxa are of a broad stratigraphical range. Representatives of the genus *Watzenauria* appeared within the Bajocian and survived to the end of the Cretaceous. Only sample CHMHZ-JG-13 (*H. hastatus*) can be correlated to the interval from the base of the Oxfordian (FO of *Zeugrhabdotus noeliae*; Young et al. 2021) to the middle Tithonian (LOs of *Axopodorhabdus cylindratus*, *Ethmorhabdus gallicus* and *Crepidolithus crassus*; Young et al. 2021). However, stratigraphical correlation based on belemnites is more accurate here.

Unfortunately, the calcareous nannoplankton species *Helenea chiastia* Worsley, 1971, which appeared first at the base of the NJT16a subzone (middle Tithonian; Young et al. 2021) has not been found in the new sample set. However, this

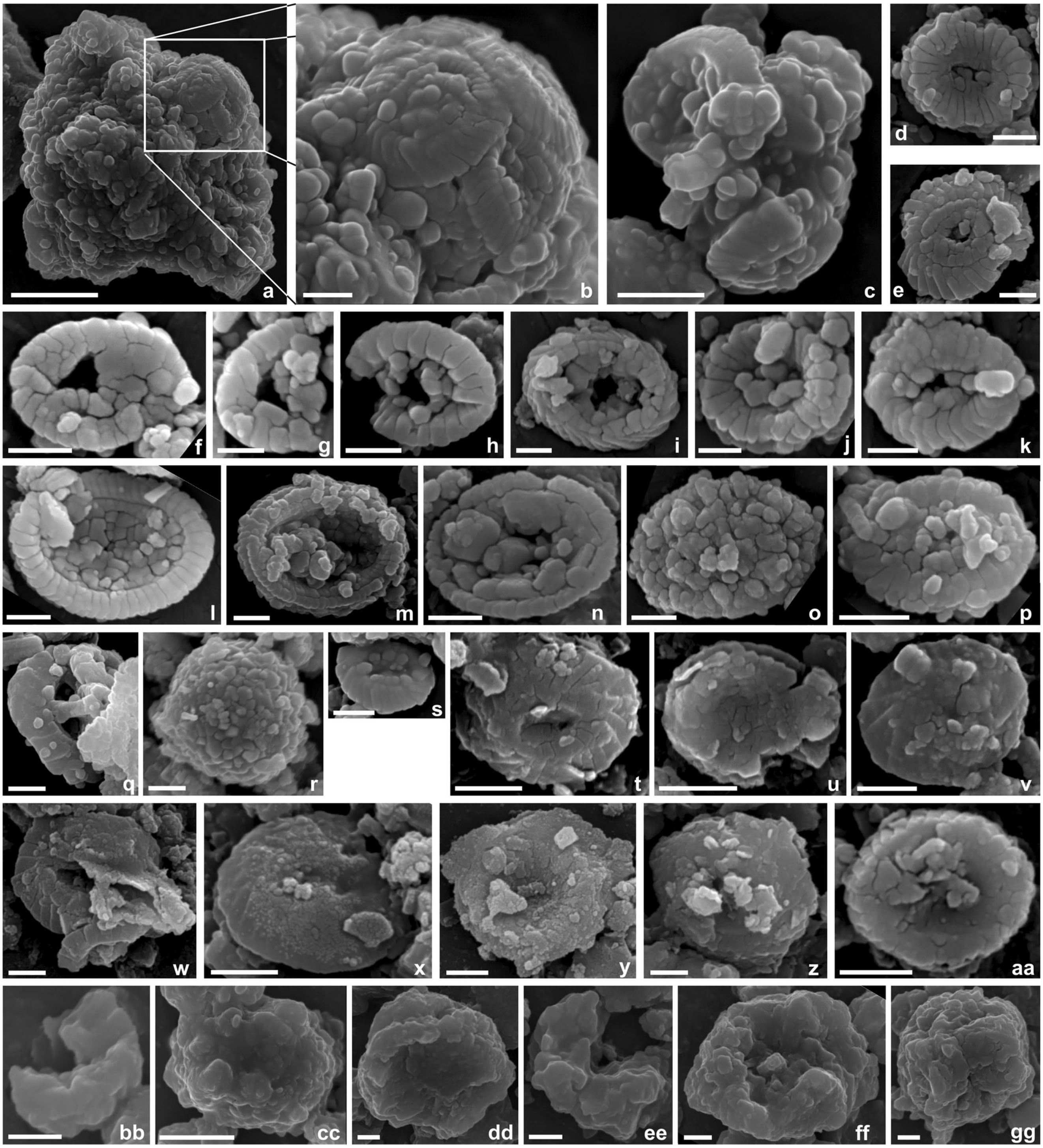

Fig. 7 Calcareous nannoplankton (SEM view). **a–e**, **j–k** *Watznaueria barnesiae* (Black in Black and Barnes, 1959), Perch-Nielsen, 1968; CHMHZ-JG-10/2, a–b cocosphaera in (?) faecal pellet; locality Peškova stráň (Kyjov). **f–i** *Zeugrhabdotus noeliae* Rood et al., 1971; CHMHZ-JG-10/2; locality Peškova stráň (Kyjov). **l–p** *Ethmorhabdus gallicus* Noël, 1965; CHMHZ-JG-10/2; locality Peškova stráň (Kyjov). **q** *Axopodorhabdus cylindratus* (Noël, 1965) Wind and Wise in Wise and Wind, 1977; CHMHZ-JG-10/2; locality Peškova stráň (Kyjov). **r** Calcisphaera; CHMHZ-JG-10/2; locality Peškova stráň (Kyjov). **s** *Crepidolithus crassus* (Deflandre in Deflandre and Fert, 1954) Noël, 1965; CHMHZ-JG-10/2; locality Peškova stráň (Kyjov). **t–w**, **y–aa** *Watznaueria barnesiae* (Black in Black and Barnes, 1959) Perch-Nielsen, 1968; **t-w** CHMHZ-JG-9/3; locality Peškova stráň (Kyjov). **w–y** CHMHZ-JG-9/2, z–aa CHMHZ-JG-9/4; locality Peškova stráň (Kyjov). **t–aa** corroded and overgrowthed specimens; locality Peškova stráň (Kyjov). **x** *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964; CHMHZ-JG-9/2; locality Peškova stráň (Kyjov). **bb–gg** strongly corroded and overgrown undeterminable coccoliths; CHMHZ-JG-1/2, CHMHZ-JG-1/3; locality Šternberk. The scale bar equals 2 μm, with exception of figs **a** and **c** (scale bars = 10 μm).

species was recorded in the studied area earlier and it extending the stratigraphical range of the sedimentation history in N Bohemia (Holcová and Holcová 2016).

Palaeoecological interpretation is restricted herein because dissolution and recrystallisation of coccoliths evoke taphonomical bias. The prevailing genus *Watznaueria* represents dissolution-resistant taxa (Hill 1975); therefore, their dominance could be increased secondary to the dissolution of other taxa from the original assemblages. This assumption could be supported by the low diversity of the assemblages in our samples. Typically, 15–30 species of calcareous nannoplankton occur in the assemblages during the Callovian–Oxfordian interval (Giraud 2009 and reference herein). In any case, watznaueriaceans represent an eurytopic life strategy with wide palaeoecological tolerance and could live in unstable environments (Lees et al. 2004, 2006; Colombié et al. 2014). Similar assemblages significantly dominated by watznauerias were also recorded in a previous study from this area (Holcová and Holcová 2016).

In the sample CHMHZ-JG-10/2, higher abundances of the genus *Zeugrhabdotus* Reinhardt, 1965 might be considered as indicating enhanced fertility conditions of the surface waters and colder surface waters (e.g. Roth and Krumbach 1986; Erba 1987, 1989). However, Eleson and Bralower (2005) doubted this interpretation and interpreted a rather oligotrophic habitat for this species. This discrepancy suggests an eurytopic life strategy for *Zeugrhabdotus*, one that is similar to watznauerias. Generally, the dominating taxa points to unstable conditions in the surface water. Very rare *Crepidolithus crassus* is interpreted as a deep dweller within the photic zone (Mattioli et al. 2008; Reggiani et al. 2010; Suchéras-Mar et al. 2010). Its rarity might indicate a rather shallow water environment (outer shelf).

It is worth noting that coccoliths were extraordinarily well preserved in components resembling faecal pellets (Fig. 7a–c). Because of the size of these pellets, among phytoplankton consumers, copepods could be considered the most likely producers of pellets (Kiørboe 2011). The monospecific composition of coccoliths in faecal pellets (*Watznaueria barnesiae*) supports the hypothesis that there might have been a seasonal blooms of this species. This assumption agrees with the well-known seasonality of herbivorous copepods—as potential producers of faecal pellets—which, in the recent oceans, feed during phytoplankton blooms and, during the rest of the year, store up energy from their seasonal food as oil droplets (Kiørboe 2011).

Discussion

Belemnites

Six species and two taxa identified as *Megateuthis* cf. *M. elliptica* and *Cylindroteuthis* cf. *C. puzosiana* (plus two additional indeterminable taxa) belonging to four families (Belemnopseidae, Duvaliidae, Megateuthididae and Cylindroteuthididae) are described from Jurassic deposits of the North Bohemia and Saxony. They mostly belong to cosmopolitan and/or widespread taxa with a well-known morphology. Stratigraphically, the most significant taxa are represented by megateuthidids— *M. suevica* and *M.* cf. *M. elliptica*, which characterise the Lower and possibly upper Bajocian (Fig. 8). Based on these records, we assume the beginning of sedimentation in the early Bajocian (*Propinquans* to *Humphriesianum* zones). Most of the studied belemnite faunas, however, are represented by the genera *Hibolithes* and *Belemnopsis*, which are typical for the late Middle Jurassic period. The genera *Rhopaloteuthis* and *Cylindroteuthis*, which are represented only by a few individuals, could potentially indicate a stratigraphically younger time (Fig. 8).

Palaeobiogeographical assessment

Palaeobiogeographically, most of the belemnite faunas can be linked to the Tethyan Realm (Fig. 1). This is clearly visible in the species composition here with the taxa of the genus *Belemnopsis*. On the other hand, typical Boreal elements—for example *Cylindroteuthis* cf. *C. puzosiana* has also been recorded. During the Jurassic, several belemnite migrations took place within Europe because of changes in the environmental conditions, such as alternation of warmer and colder periods and sea-level changes (e.g. Dera et al. 2011, 2016) (Fig. 1). Because belemnites were stenothermic organisms, during these temperature fluctuations, they often migrated to refuges—that is, to the Arctic region during warmer periods and to the Tethyan/Mediterranean Realm during cooler times (Dera et al. 2016). In the Oxfordian age a considerable cooling event with significant changes in species composition is assumed (Cecca et al. 2005). During this period, species of the genus *Belemnopsis* stopped dominating, and the species *Cylindroteuthis puzosiana* occurred in northern Bohemia (Fig. 1). *C. puzosiana* is an exotic Boreal species and his occurrence clearly demonstrates the Boreal influence in the studied area, which was located at the border of the Boreal and Tethyan palaeobiogeographical provinces (Fig. 6). This assumption is also discussed by Hrbek (2014, see below), who revised and described sub-Boreal ammonites from this area. The majority of fauna (both benthic and nektic) in the studied rocks, however, indicates conditions typical of the Peri-Tethyan shelf. Interestingly, this phenomenon in Central Europe occurred repeatedly much later, during the Upper Cretaceous, when the Tethyan faunal influence/dominance (Košťák et al. 2020) was interrupted by short-termed Boreal immigrations. Short-termed influxes of Boreal faunas, including belemnites, repeatedly occurred at least three times in the Cenomanian through Coniacian (Košťák et al. 2004), when

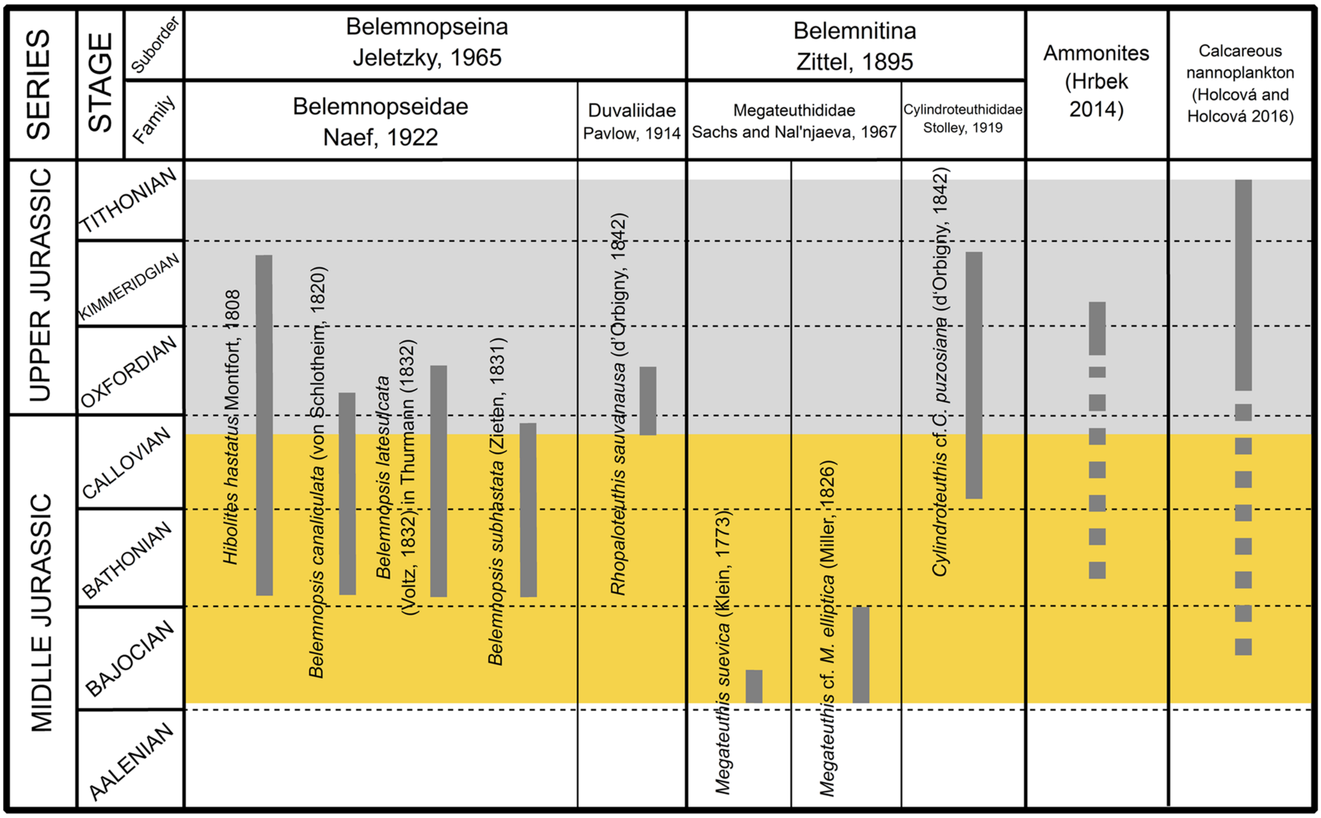

Fig. 8 Total stratigraphical ranges of belemnite taxa (recorded from the northern Bohemian Massif) according to published literature [modified after Pugaczewska (1961), Gustomesov (1964), Mariotti (2002), Dzyuba (2005), Weis and Mariotti (2008) and Mural (2011)] in relation to ammonite (Hrbek 2014) and calcareous nannofossil data (Holcová and Holcová 2016; this study). Grey and orange background: extended timespan of sedimentation (this study) based on summarised biostratigraphic data; orange background: prolonged sedimentary history of studied rocks (this study).

the Peri-Tethyan shelves with typical warm-water fauna prevailed in Central Europe. According to our new data presented herein, this area played an important role in faunal exchanges between the Tethyan and Boreal realms already in the Jurassic; this evokes the possibility of the existence of a significantly older 'Gateway to Tethys' (*sensu* Wiese et al. 2004) over the Bohemian Massif area than has previously been suggested (Table 1).

The considerable influence of the sub-Boreal Realm and sub-Tethyan Realm has been recognised based on Oxfordian and Kimmeridgian ammonites (Hrbek 2014). Unfortunately, no direct evidence of the connection of this area with the Tethys through a biotic communication channel *via* the Bohemian Massif has yet been proven. However, some indirect evidence based on analyses of calcareous nannoplankton (Holcová and Holcová 2016) and ammonite fauna (Hrbek 2014) may support this hypothesis. In the past, another possible communication channel connecting this area with the Polish Jurassic basins has also been suggested (e.g. Bruder 1886; Pienkowski et al. 2008).

According to the lithology of the strata, it is probable that the area was located in the open shelf sea and/or formed a bay with the occasional input of clastic material from the source area (e.g. Hykš and Kumpan 2019). The lithological diversity of limestones and other Jurassic rocks in this area is quite considerable and further research is needed.

Conclusion

We provide a novel and unusual combination using belemnites and calcareous nannofossil to obtain new data acquisition. Based on this approach, we were able to distinguish the geological history and stratigraphy of sedimentary relics in tectonically complicated areas (around the Lausitian Fault).

– Both groups show high potential for preservation in highly tectonised and partly dolomitised strata. Moreover, belemnites may provide primary geochemical data ($^{13}C/^{12}C$, $^{18}O/^{16}O$, $^{87}Sr/^{86}Sr$) from this Jurassic strata.
– Based on belemnite and calcareous nannofossil records, the Jurassic sedimentary strata in the northern Bohemian Massif range from the Bajocian to Tithonian ages. The belemnite fauna ranges from the lower Bajocian (*Propinquans* to *Humphriesianum* zones) through the ?Kimmeridgian, with the most significant group being

the Middle Jurassic belemnite association (especially the genus *Belemnopsis*). We confirmed the stratigraphic distribution by calcareous nannoplankton, including in the Tithonian age.
- Megateuthidid belemnites (*Megateuthis suevica* and *Megateuthis* cf. *M. elliptica*) indicate the earliest known faunal components within the Central European Jurassic (Bohemian Massif).
- The presence of *M. suevica* in carbonate rocks clearly indicate the beginning of carbonate sedimentation in the early Middle Jurassic, not in the Late Jurassic as assumed earlier.
- Macro- and microfaunal data point to possible continuous sedimentation with frequent gaps (linked probably to eustatic cycles). Therefore, the historical lithostratigraphic regional division (Brtníky and Doubice formations based on a similar lithological character) is most likely not relevant.
- Calcareous nannoplankton assemblages may indicate changes in fertility conditions in surface waters during the Jurassic in Central Europe.
- The taxon *Cylindroteuthis* cf. *C. puzosiana* represents Boreal element and have proven the biotic communication of the studied area with colder regions during the Upper Jurassic.
- Scarce, yet, a very important record of belemnites (completed by calcareous nannofossils) document Jurassic sedimentary history in an important part of the Central Europe. In the light of these faunas, we assume that the sedimentary area was significantly larger in this region. This Jurassic basin preceded by dozens of million years of Late Cretaceous transgression and subsequent Cretaceous marine sedimentation.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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