Occurrence and significance of Cenomanian belemnites in the lower Danubian Cretaceous Group (Bavaria, southern Germany)

MARKUS WILMSEN [1], BIRGIT NIEBUHR [1] AND PATRICK CHELLOUCHE [2]

[1]*Senckenberg Naturhistorische Sammlungen Dresden, Museum für Mineralogie und Geologie, Sektion Paläozoologie, Königsbrücker Landstr. 159, D – 01109 Dresden, Germany.*
E-mail: markus.wilmsen@senckenberg.de; niebuhr.birgit@googlemail.com
[2]*GeoZentrum Nordbayern, Fachgruppe PaläoUmwelt, Loewenichstr. 28, D – 91054 Erlangen, Germany.*
E-mail: patrick.chellouche@gzn.uni-erlangen.de

ABSTRACT:

Wilmsen, M., Niebuhr, B. and Chellouche, P. 2010. Occurrence and significance of Cenomanian belemnites in the lower Danubian Cretaceous Group (Bavaria, southern Germany). *Acta Geologica Polonica*, **60** (2), 231–241. Warszawa.

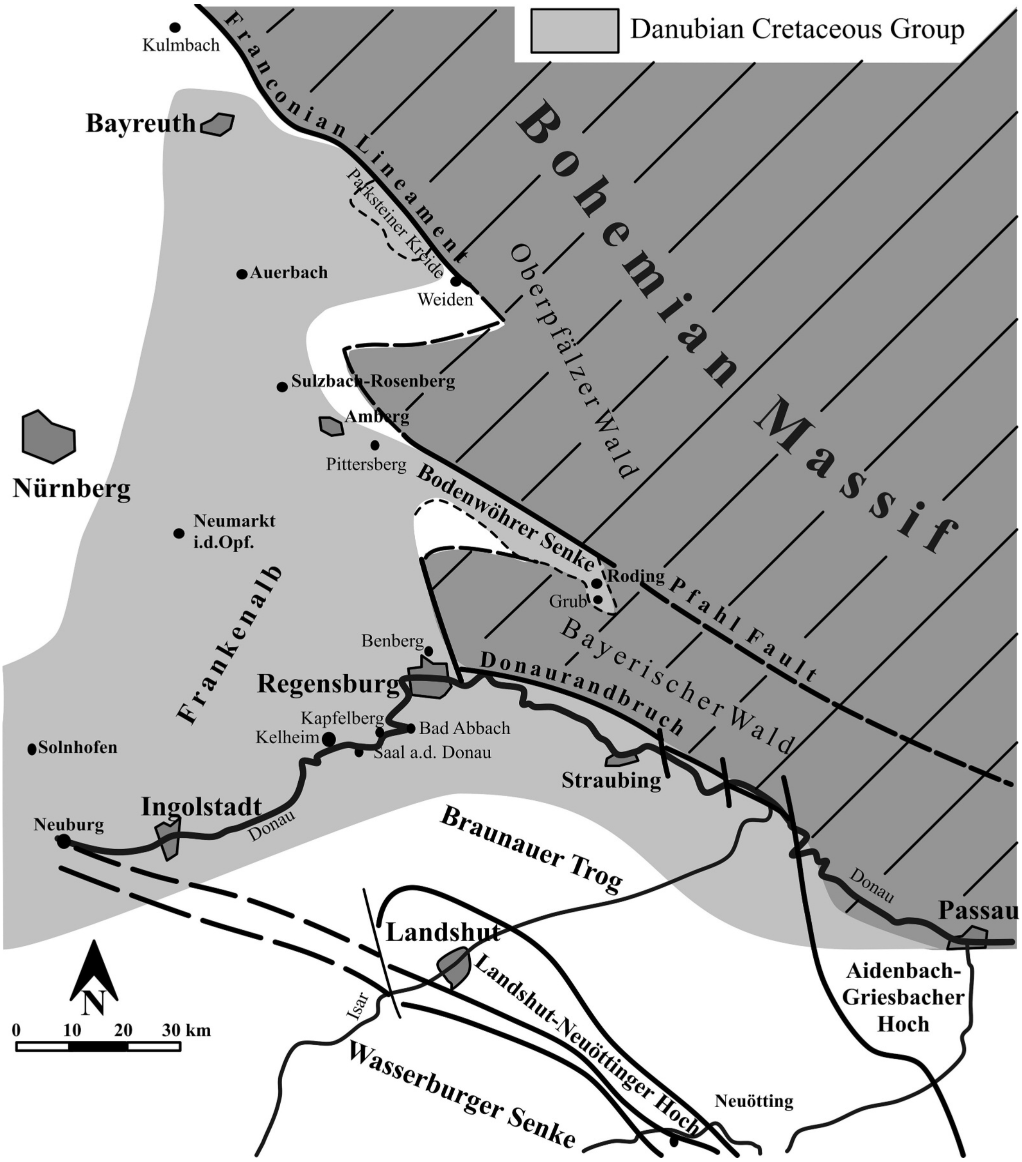
The belemnite records of the lower Danubian Cretaceous Group (DCG, northeastern Bavaria, southern Germany) are compiled, taxonomically described and placed within the new integrated stratigraphic framework of the group. Three specimens from the lower Regensburg Formation (Saal Member) south of Regensburg can be assigned to *Neohibolites* cf. *ultimus* (d'Orbigny) and are dated as late Early Cenomanian (*Mantelliceras dixoni* Zone). Eight specimens represent *Praeactinocamax plenus* (Blainville) and occur in an event (*plenus* Event) in the lower Eibrunn Formation (Regensburg area) or basal Regensburg Formation (Roding area in the Bodenwöhrer Senke). Biostratigraphy and carbon stable isotopes suggest that the belemnite horizon with *P. plenus* in the DCG has strictly the same chronostratigraphic position (mid-Late Cenomanian, middle *Metoicoceras geslinianum* Zone) as elsewhere in Central and NW Europe. The lithostratigraphic units of the lower Danubian Cretaceous Group (i.e., the Regensburg and Eibrunn formations), however, are characterized by a pronounced diachronism based on their time-transgressive (i.e., onlapping) deposition during the Cenomanian–Early Turonian transgression. The distribution of *P. plenus* around the Mid-European Island can be easily explained by migration around the positive area without the necessity of a marine strait across the Bohemian Massif.

Key words: Upper Cretaceous; Belemnitida; Taxonomy; Integrated stratigraphy; Palaeogeography.

INTRODUCTION

The Cretaceous of northeastern Bavaria (formerly often termed "Regensburger", "Oberpfälzer" or "Fränkische albüberdeckende Kreide", now formalized within the Danubian Cretaceous Group by Niebuhr *et al.* 2009) is one of the classic regions for early geological investigations in Germany (e.g., Gümbel 1854, 1868a, b, 1891). However, despite its key position between the well studied Boreal successions in the north and the Tethyan Alpine Cretaceous in the south, knowledge concerning the stratigraphy, macrofossil palaeontology and depositional environments of the Danubian Cretaceous Group remained in a somewhat undeveloped state throughout the 20th century. The few detailed macro-palaeontological monographs date back to Lehner (1937a, b) and Dacqué (1939), followed by short taxonomic accounts on the Upper Cenomanian cephalopod fauna of the Eibrunn Formation from the Regensburg area (Förster *et al.* 1983; Röper and Rothgaenger 1995) or Middle Cenomanian siliceous sponges (Kauffman *et al.* 2000). Cenomanian belemnites were recorded in some of the aforementioned works but never discussed in taxonomic and stratigraphic detail. This is surprising and a waste of important information, as the occurrence of belemnites in the Cenomanian of NW Europe has a considerable stratigraphic and palaeo-ecologic significance (e.g., Christensen 1990a; Gale and Christensen 1996; Košťák *et al.* 2004; Mitchell 2005; Wilmsen *et al.* 2007; Wilmsen and Rabe 2008; Wiese *et al.* 2009).

Thus, the scope of the present paper is a compilation of the belemnite records of the lower Danubian Cretaceous Group based on the examination of collection material of the Bayerische Staatssammlung für Paläontologie in Munich (BSP), new finds (PrNW) from the successions around Regensburg and Roding (Bodenwöhrer Senke), and a re-logging and chronostratigraphic re-interpretation of classic sections of the Danubian Cretaceous Group such as the Mühlberg section near Bad Abbach. Apart from the short taxonomic treatment, the significance of the belemnite occurrences is discussed within an integrated stratigraphic framework. Furthermore, the occurrence of one taxon (i.e., *Praeactinocamax plenus*) around the Mid-European Island is used to evaluate controversial palaeogeographic reconstructions.



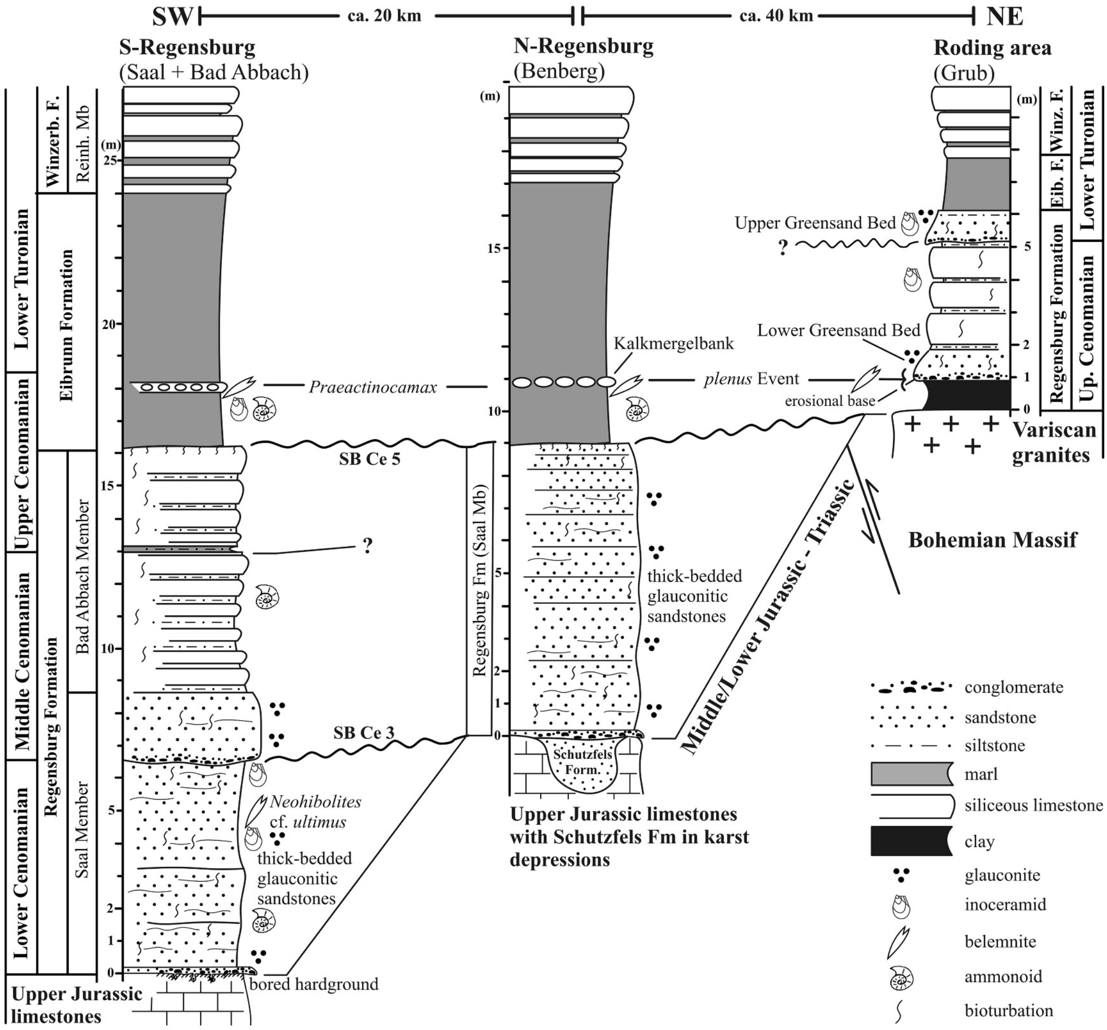
Text-fig. 1. Map showing the regional framework of the study area with main structures and distribution of the Danubian Cretaceous Group (light-grey shading). The sections of Text-fig. 2 and localities mentioned in the text are indicated

GEOLOGICAL SETTING AND LITHOSTRATIGRAPHY

The study area is located in northeastern Bavaria (southern Germany), specifically around Regensburg and Roding in the Bodenwöhrer Senke (Text-fig. 1). Lithostratigraphically, the investigated successions are part of the Danubian Cretaceous Group (DCG) of Niebuhr *et al.* (2009). The DCG represents non-marine to neritic environments of a peri-continental shelf system at the northern margin of the Neotethys, south of the Mid-European Island (MEI), developing in response to the transgression of the early Late Cretaceous. The litho- and biostratigraphic revision of the DCG was carried out recently by Niebuhr *et al.* (2009), Tröger *et al.* (2009), Wilmsen *el al.* (2009) and Wilmsen and Niebuhr (2010).

The DCG comprises conglomerates, sands and sandstones, clays, marls and marlstones, calcarenites, siliceous opoka and limestones, with a maximum thickness of a few hundred metres. Marine deposition started in the Early Cenomanian and persisted into the Coniacian, comprising a nearly symmetrical trans-/regressive mega-cycle with a maximum flooding interval during the late Middle to early Late Turonian (Niebuhr *et al.* 2009; Wilmsen and Niebuhr 2010).

The marine lithostratigraphic units of the lower DCG are the Regensburg, Eibrunn and Winzerberg formations (Text-fig. 2). The Regensburg Formation (Cenomanian–lowermost Turonian) unconformably overlies various older rock units, mainly Upper Jurassic limestones of the Franconian Alb (Frankenalb) or the terrestrial Lower Cretaceous Schutzfels Formation (preserved only in



Text-fig. 2. Correlation of sections from the lower Danubian Cretaceous Group in a SW–NE transect from south of Regensburg to Grub (Bodenwöhrer Senke; intermediate Benberg section modified after Förster *et al*. 1983). Belemnite occurrences are indicated. Note diachronism of lithostratigraphic units and facies-breaking stratigraphic pattern of the *Praeactinocamax plenus* Event (Eib. F. = Eibrunn Formation; Winz./Winzerb. F. = Winzerberg Formation; Reinh. Mb = Reinhausen Member) karst depressions). Towards the northeast, the Regensburg Formation transgresses onto older Mesozoic strata or the Variscan basement of the Bohemian Massif (Text-fig. 2). The Regensburg Formation consists of mixed, more-or-less glauconitic siliciclastic-calcareous sediments. It is subdivided into a lower Saal Member consisting of thickly bedded glauconitic sandstones with a shallow-water fauna of bivalves, brachiopods, echinoids and siliceous sponges, and an upper Bad Abbach Member of interbedded sandy-silty marls and siliceous limestones (see Trusheim 1935; Kauffman *et al.* 2000; Niebuhr *et al.* 2009). The uppermost Cenomanian–lower Lower Turonian silty marls of the Eibrunn Formation document a first maximum flooding interval during the early Late Cretaceous transgression. Their faunal content (cephalopods, inoceramid bivalves and planktonic foraminifera) was the subject of papers by Förster *et al.* (1983), Hilbrecht (1986), Röper and Rothgaenger (1995) and Hilbrecht *et al.* (1996). The Eibrunn Formation is overlain by the spiculitic, calcareous silt- to marlstones (Reinhausen Member) and sandstones (Knollensand Member) of the Lower Turonian Winzerberg Formation. A conspicuous sequence boundary in the Lower–Middle Turonian boundary interval terminates this first (i.e., Cenomanian–Early Turonian) trans-/regressive cycle of the Danubian Cretaceous Group (Niebuhr *et al.* 2009). The Regensburg and Eibrunn formations are characterized by pronounced diachronism from southwest towards the northeast due to the transgressive onlap onto the Bohemian Massif (Wilmsen *et al.* subm.).

In the DCG, belemnites occur in the upper Lower Cenomanian of the Saal Member of the Regensburg Formation south of Regensburg, in the Upper Cenomanian of the lower Eibrunn Formation both south and north of Regensburg, and in the Upper Cenomanian of the lower Regensburg Formation near Roding in the Bodenwöhrer Senke (Text-fig. 2). These occurrences are taxonomically briefly described below, followed by a discussion of their stratigraphic and palaeogeographic significance.

SHORT SYSTEMATIC ACCOUNT

Descriptive terminology of the belemnite rostrum follows Košťák (2004).

Family Belemnopseidae Naef, 1922
Genus *Neohibolites* Stolley, 1911

TYPE SPECIES: *Belemnites ultimus* d'Orbigny, 1845, pl. 75, figs 9–13.

Neohibolites cf. *ultimus* (d'Orbigny, 1845)
(Text-fig. 3A)

cf. 1845. *Belemnites ultimus* d'Orbigny, pl. 75, figs 9–13.
cf. 1971. *Neohibolites ultimus* (d'Orbigny 1845); Spaeth, p. 72, pl. 9, figs 7–12 (see for synonymy).
cf. 1999. *Neohibolites ultimus* (d'Orbigny); Wilmsen, p. 301, figs 4a–c, 5a, b (see for synonymy).
cf. 2005. *Neohibolites ultimus* (d'Orbigny); Mitchell, p. 364.

MATERIAL: 3 incomplete specimens (BSP 1887 VI, BSP 1887 VI 10; PrNW), including the original of Dacqué (1939, p. 69, pl. 4, fig. 14), described and figured as "*Actinocamax* cfr. *plenus* Blainville", from the "Cenomaner Grünsandstein, Brandlerberg bei Kelheim".

DESCRIPTION: The shape of the relatively small, slender rostra is conical, subspherical in the area of maximum diameter, with stronger lateral compression in the (alveolar) area of minimum diameter. Thus, the rostrum is slightly claviform in ventrodorsal view. Due to the incomplete preservation, the ventral furrow is only weakly visible. The alveolus is relatively deep and the alveolar end show the typical concentric defoliation described by Spaeth (1971, p. 73).

REMARKS: Even in this incomplete preservation, the specimens from the Regensburg Formation do not differ significantly from *Neohibolites ultimus* (d´Orbigny) as described and figured in the literature (e.g., Spaeth 1991; Wilmsen 1999). However, due to the incomplete preservation, they are kept in open nomenclature. Representatives of the Cenomanian to Lower Santonian belemnite genus *Praeactinocamax* Naidin (one of the few other belemnite genera present in the Cenomanian of Europe) are clearly differentiated from the present specimens by different shapes of their guards (which are subcylindrical to lanceolate) and the morphology of the alveolar parts of the rostra (Christensen 1990b; Košťák 2004; Wilmsen *et al.* 2007; Košťák and Wiese 2008; Wilmsen and Rabe 2008; Wiese *et al.* 2009). The very rare, small Cenomanian belemnite *Belemnocamax* Crick has short and ventrally strongly flattened rostrum with a distinct ventral groove and a heart-shaped anterior end (Christensen 1993; Wilmsen and Rabe 2008).

Family Belemnitellidae Pavlow, 1914

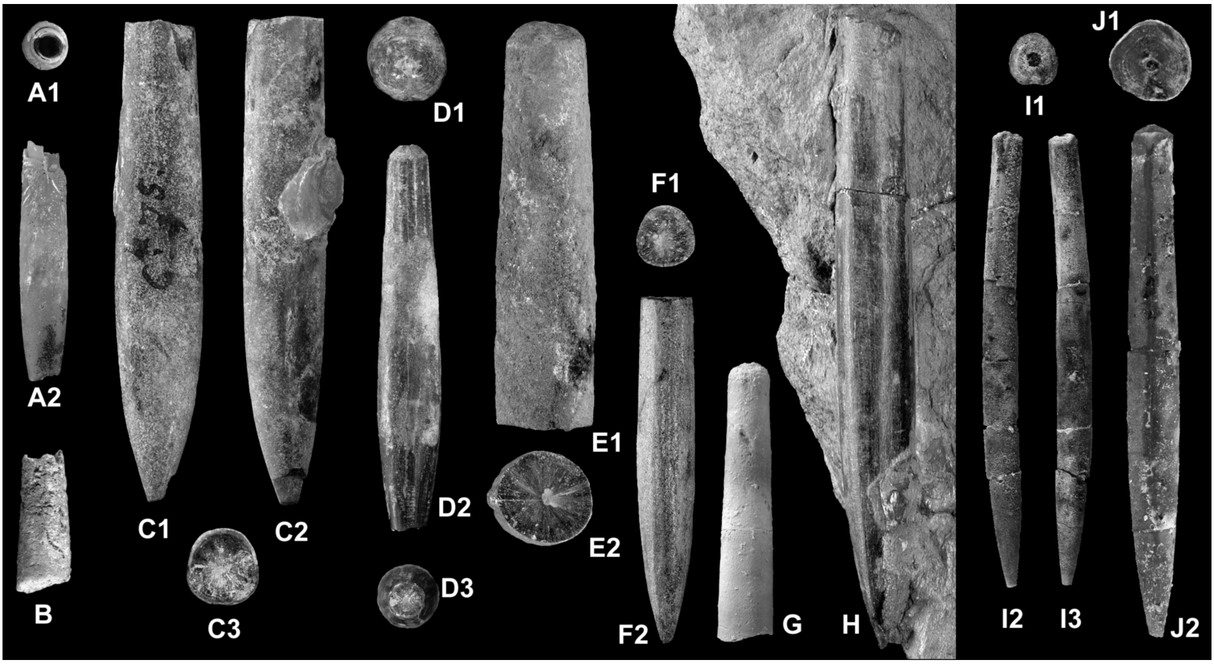
Taxonomy, palaeobiogeography and migration of the Late Cretaceous belemnite family Belemnitellidae were intensively discussed by Christensen (1997a, b), Košťák (2004) and Košťák *et al.* (2004).

Genus *Praeactinocamax* Naidin, 1964

TYPE SPECIES: *Belemnites plenus* Blainville, 1825-1827, p. 376 (1825), pl. 11, fig. 3 (1827).

Praeactinocamax plenus (Blainville, 1825)
(Text-fig. 3C–J)

1825. *Belemnites plenus* Blainville, p. 376.
1974. *Actinocamax plenus* (Blainville); Christensen, p. 4–12, pl. 1, figs 1–3, pl. 2, figs 1–5, pl. 3, figs 1–6, pl. 4, figs 1–5 (see for older synonymies).
1995. *Actinocamax plenus* (Blainville); Röper and Rothgaenger, p. 182.
1997. *Praeactinocamax plenus* (Blainville); Košťák and Pavliš, p. 2, text-figs 3, 4, pl. 1, figs 1–4, pl. 2, figs 1–6 (see for synonymy).
2005. *Praeactinocamax plenus* (Blainville); Mitchell, p. 367, fig. 1.14, 1.15.
2006. *Praeactinocamax plenus* (Blainville); Svoboda, p. 170, fig. 3b.
2009. *Praeactinocamax plenus* (Blainville, 1827); Wiese *et al.*, p. 314, fig. 6a–c (see for some recent synonymies).



Text-fig. 3. Belemnites from the lower Danubian Cretaceous Group. All figures in natural size except B, D1, I1 and J1. – **A1, A2** – *Neohibolites* cf. *ultimus* (d'Orbigny). BSP 1887 VI 10, original of Dacqué (1939, p. 69, pl. IV, fig. 14), from the "Cenomaner Grünsandstein, Brandlerberg bei Kelheim" (= Lower Cenomanian Saal Member of the Regensburg Formation). A1, alveolar view. A2, ventral view. – **B** – *Neohibolites* sp. (× 2). PrNW, lateral view of alveolar fragment from ca. 4.5 m above the base the Saal Member of the Regensburg Formation, Fels-Werke, Kalkwerk Saal an der Donau. **C-J** – *Praeactinocamax plenus* (Blainville) showing different growth stages. C1-3, adult specimen BSP AS XVII 6, original of Dacqué (1939, p. 90, pl. 1, fig. 21), from the "Plenuszone, Eybrunner Mergel, Hainsacker bei Regensburg" (= Upper Cenomanian Eibrunn Formation). C1, ventral view; C2, dorsal view; C3, broken alveolar end. D1-3, adolescent specimen BSP AS XVII 7, original of Dacqué (1939, p. 90, pl. 1, fig. 22), from the "Plenuszone, Eybrunner Mergel, Hainsacker bei Regensburg" (= Upper Cenomanian Eibrunn Formation). D1, alveolar view (× 2); D2, dorsal view; D3, apical view (apex missing). E, alveolar fragment of an adult specimen from sample BSP 1982 XIX 96 from the Upper Cenomanian Eibrunn Formation of the Benberg motorway roadcut 6 km north of Regensburg. E1, dorsal view; E2, mid-guard cross-section at terminal end of rostrum. F, apical fragment of an adolescent specimen from sample BSP 1982 XIX 96 from the Upper Cenomanian Eibrunn Formation of the Benberg motorway roadcut 6 km north of Regensburg. F1, mid-guard cross-section at terminal end of rostrum; F2, dorsal view. G, alveolar fragment (ventral view) of adolescent specimen PrNW-1 from the lower Regensburg Formation (lower part of the Lower Greensand Bed) at Haimerl quarry near Grub (Bodenwöhrer Senke). H, left-lateral view of the complete adult specimen from sample BSP 1982 XIX 96 from the Upper Cenomanian Eibrunn Formation of the Benberg motorway roadcut 6 km north of Regensburg. I, juvenile specimen PrNW-2 from the lower Regensburg Formation (top of the basal black clay) at Haimerl quarry near Grub (Bodenwöhrer Senke). I1, alveolar view (× 2); I2, ventral view; I3, dorsal view. J, adolescent specimen PrNW-3 from the lower Regensburg Formation (top of the basal black clay) at Haimerl quarry near Grub (Bodenwöhrer Senke). J1, alveolar view (× 2); I2, lateral view

MATERIAL: Five complete or nearly complete specimens (BSP AS XVII 6, BSP AS XVII 7, BSP 1982 XIX 96, and PrNW-2 and -3), including the two originals of Dacqué (1939, p. 90, pl. 1, figs 21, 22), described and figured as "*Actinocamax plenus* Blainville", from the "Eybrunner Mergel" (= Eibrunn Formation) at the Winzerberg in Regensburg as well as three fragmentary specimens (alveolar and apical fragments from sample BSP 1982 XIX 96, alveolar fragment PrNW-1).

DESCRIPTION: The complete or nearly-complete guards are medium-sized and between 65–85 mm long with maximum lateral diameters (MLD) of 7–12 mm. MLD is situated approximately one third of the length of the guard from the apical end. The dimensions of the alveolar end of the fragmentary specimen BSP 1982 XIX 96 (Text-fig. 3E) with a length of 55 mm and a lateral diameter of 13.5 mm (without reaching the point of MLD) suggest a length of the complete rostrum of well above 100 mm. The general shape of the rostra is lanceolate in dorsoventral to subcylindrical in lateral view, caused by lateral compression of the alveolar end. Smaller specimens tend to have subcylindrical to only slightly lanceolate shapes (e.g., Text-fig. 3I, J) of their rostra due to allometric growth. Dorsolateral compressions / furrows are well developed in some rostra (Text-fig. 3D, J) at the alveolar end, resulting in somewhat triangular cross-sections. Alveolar ends (when fully preserved) show a cone-shaped alveolar fracture. The apex is placed centrally; however, in most cases the expected mucro is not preserved. The apical angle varies between 20° in juvenile (i.e., subcylindrical) and 35° in adult (i.e., lanceolate) specimens.

REMARKS: The present specimens do not differ from *P. plenus* as described and figured extensively in the literature (e.g., Christensen 1974; Košťák and Pavliš 1997; Košťák 2004; Wiese *et al.* 2009) and can, thus, be securely assigned to Blainville's (1825) species, without any need for further taxonomic comments. The fauna from the Danubian Cretaceous Group shows the typical range of morphological variation in *P. plenus* as for example demonstrated by Gale and Christensen (1996, p. 73, fig. 5) for a fauna from les Lattes (Alpes de Haute-Provence, southeastern France): juveniles, adolescent and adult specimens are present (Text-fig. 3). Košťák (2004) gives a length range from 55–92 mm, but adult rostra can be well above 100 mm (Christensen 1974).

DISCUSSION

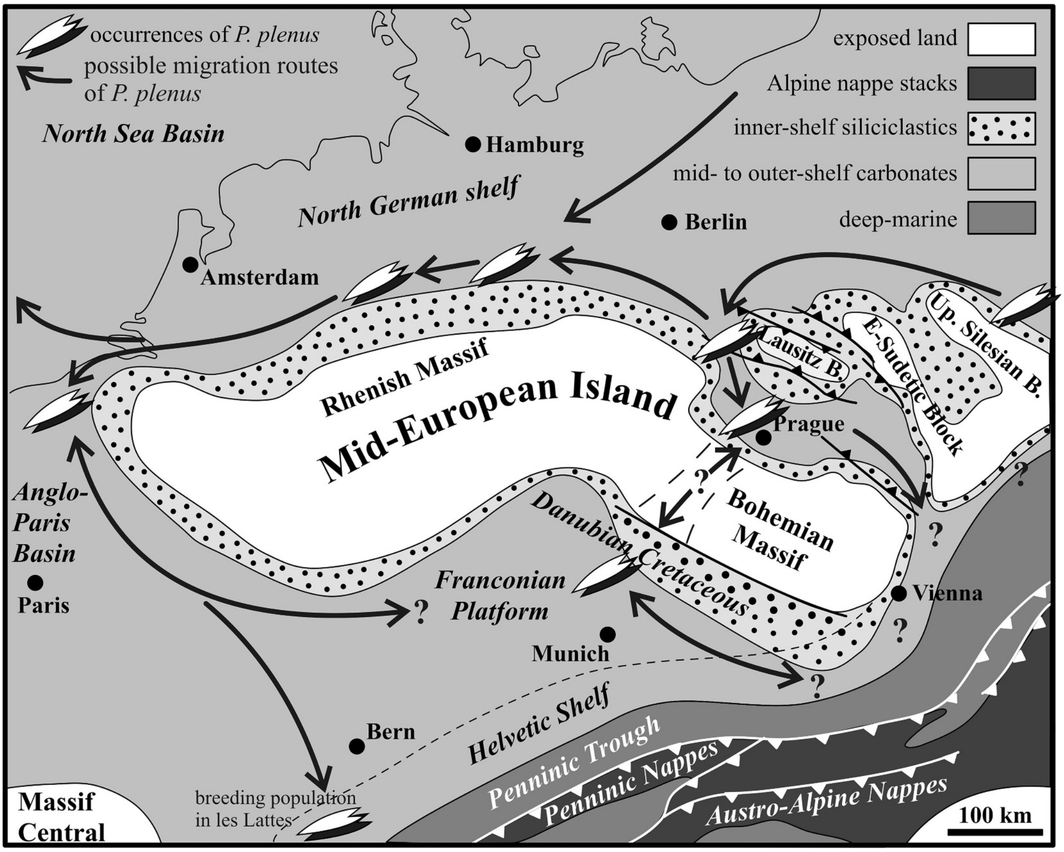
Belemnites are generally rare in the Danubian Cretaceous Group and restricted to the Regensburg and Eibrunn formations. However, the event-like occurrences of belemnites in the Cenomanian of central and NW Europe result in a considerable stratigraphic and palaeoecologic significance of the finds (cf. Ernst *et al.* 1983; Mitchell 2005).

Neohibolites ultimus occurs in the Lower and basal Middle Cenomanian (*Mantelliceras mantelli* to lower *Acanthoceras rhotomagense* zones) of the Tethyan Realm as well as in contemporaneous rocks of the Russian Platform and the southern part of the Central European Subprovince (Christensen 1976, 1990a; Combémorel *et al.* 1981; Wilmsen 1999; Mitchell 2005). *N. ultimus* is particularly common in the lower Lower Cenomanian [e.g., *N. ultimus* is represented by fine specimens in the British Geological Survey (BGS) collections from the *N. carcitanense* Subzone Rye Hill Sands of the Wessex Basin, southern England; it also occurs in the *Inoceramus crippsi* Event in eastern England; pers. comment C.J. Wood] and is one of the last representatives of the genus *Neohibolites* Stolley, which became extinct in the upper part of the *A. rhotomagense* Zone (Combémorel *et al.* 1981). Dacqué's (1939) specimens from the "Cenomaner Grünsandstein, Brandlerberg bei Kelheim" (Text-fig. 3A) can be stratigraphically allocated to the Saal Member of the lower Regensburg Formation. However, an *in-situ* record of an alveolar fragment of *Neohibolites* sp. (Text-fig. 3B) from the middle part of the Saal Member at the type section (Saal an der Donau) from beds with abundant *Inoceramus virgatus virgatus* Schlüter can be unequivocally assigned to the upper Lower Cenomanian *Mantelliceras dixoni* Zone. This fits the stratigraphic position of the single specimen of *N. ultimus* from the Saxonian Cretaceous Basin which was recorded from contemporaneous nearshore sediments of the Meissen Formation by Spaeth and Köhler (1997) and Köhler and Spaeth (1998). Also Ernst and Rehfeld (1997) and Mitchell (2005, *N. ultimus* biohorizon III) recorded belemnite horizons with *N. ultimus* from the *M. dixoni* Zone of the Lower Saxony and Anglo-Paris basins. However, the complete stratigraphic range of *N. ultimus* is more extended, comprising the Early and early Middle Cenomanian (Combémorel *et al.* 1981).

Praeactinocamax plenus is known from the Late Cenomanian *Metoicoceras geslinianum* Zone of the Russian Platform and adjoining areas (e.g., Christensen 1997a; Košťák 2004; Košťák *et al.* 2004; Wiese *et al.* 2009). In Central and northwest Europe, its temporal distribution is even more limited, being stratigraphically restricted to a short interval within the middle part of the *Metoicoceras geslinianum* Zone. This interval defines a stratigraphic event in Europe named the *plenus* Event (Ernst *et al.* 1983; Mitchell 2005). The specimens from the Regensburg area all come from a thin, nodular calcareous bed in the lower part of the Eibrunn Formation ("Kalkmergelbank" of Förster *et al.* 1983); three specimens were recorded from Benberg (north of Regensburg) and nine specimens from Bad Abbach (south of Regensburg; Förster *et al.* 1983; Röper and Rothgaenger 1995). An interval with intensive *Chondrites*, below the *plenus* bed, is interpreted as an equivalent of the *Chondrites* Event of northern Germany (see Ernst *et al.* 1983). The stratigraphic position of the "Kalkmergelbank" within the *M. geslinianum* Zone and, thus, the isochrony of the *plenus* Event, is supported by a rich *M. geslinianum* zonal ammonoid assemblage directly below the "Kalkmergelbank" (Förster *et al.* 1983; Röper and Rothgaenger 1995), the co-occurrence with the inoceramid bivalve *Inoceramus pictus bohemicus* Leonhardt (Tröger *et al.* 2009), and carbon stable isotope stratigraphy (Hilbrecht and Hoefs 1986).

In the Bodenwöhrer Senke (Grub section), the *plenus* Event occurs in the lower Regensburg Formation, i.e. in the upper part of a black marine clay which rests transgressively on top of a Variscan granite and at the base of the overlying glauconitic sandstone (Lower Greensand Bed; Chellouche 2008; Niebuhr *et al.* 2009; see Text-fig. 2). Interestingly, the two levels with *P. plenus* in Grub are separated by an erosion surface at the base of the Lower Greensand Bed which yields mainly fragmented guards of *P. plenus*. The stratigraphic observations from the Grub section correlate very well with the situation in the Plenus Marls Member in southern England, where *P. plenus* likewise occurs in two beds [Jefferies' (1963) beds 3 and 4] separated by an erosion surface representing a parasequence boundary (see Wiese *et al.* 2009 for details). Carbon stable isotope stratigraphy (Chellouche 2008; Wilmsen *et al.* subm.) again supports a strictly isochronous nature of the *plenus* Event within the *M. geslinianum* Zone and highlights the chronostratigraphical significance of (bio-)event stratigraphy (e.g., Wiese *et al.* 2004). On the other hand, it reveals the highly diachronous nature of the lithostratigraphic units of the lower Danubian Cretaceous Group (Text-fig. 2).

Praeactinocamax plenus is widely distributed along the shelves of the northern Tethyan margin, from Turkistan-Tadzhikistan in the east to the Anglo-Paris Basin in the west (e.g., Christensen 1997b; Košťák 2004; Košťák *et al.* 2004). The species (reported as *P.* aff. *plenus*) probably persisted into the early Turonian in NW Siberia (Košťák and Wiese 2008). The species generally occurs north of the palaeobiogeographic boundary of the Tethyan Realm albeit the record from les Lattes (southeastern France) can be regarded as northern Tethyan (Gale and Christensen 1996; Text-fig. 4). Like many other Cretaceous belemnites, *P. plenus* probably had a nektobenthic mode of life and avoided deeper marine environments, being particularly common in inner to mid-shelf settings (e.g., Christensen 1976; Košťák *et al.* 2004; Mitchell 2005; Wilmsen *et al.* 2007; Wiese *et al.* 2009). It is thus also very common around the Mid-European Island (MEI) which provided extensive shallow-marine environments in its periphery (Text-fig. 4). Records of *P. plenus* come from the Bohemian Cretaceous Basin (*e.g.*, Košťák and Pavliš 1997), the Saxonian Cretaceous (*e.g.*, Häntzschel 1933), the Polish Jura Chain (Marcinowski 1972), Lower Saxony (e.g., Wiese *et al.* 2009), the Münsterland Cretaceous Basin (e.g., Christensen *et al.* 1992), southern England (e.g., Jefferies 1962, 1963; Christensen 1974; Mitchell 2005), eastern (Cleveland Basin) and western England (Wessex Basin; see Mortomore *et al*. 2001 and Wiese *et al.* 2009), southeastern France (e.g., Gale and Christensen 1996) and northeastern Bavaria (this study and references above). Faunal similarities, especially the occurrence of *P. plenus* on both sides of the Bohemian Massif (forming the eastern part of the MEI) led Dorn (1958) and Svoboda (1985, 2006) to the inference of a direct marine connection of the Bohemian and the Danubian Cretaceous basins across the Bohemian Massif (Text-fig. 4). However, in the absence of clear geological evidence [i.e., marine Upper Cenomanian sediments from the course of the inferred strait across the Bohemian Massif], a simple migration of *P. plenus* in shallow-marine environments around the MEI would be a much more straightforward explanation for the occurrence of the species in the Danubian Cretaceous (Text-fig. 4). Based on its much more extended stratigraphic range on the Russian Platform (where *P. plenus* appears earlier and disappears later; e.g., Christensen 1997a), the species must have invaded Central Europe as a pulse fauna from the (north-)east. Commonly, this is explained by a short-term cooling ("*plenus* Cold Event" of Gale and Christensen 1996). However, the find of a breeding population as far south as southeastern France (i.e., in a north Tethyan setting; Gale and Christensen 1996) suggest that, during the incursion of the species into Central and NW Europe, water temperature was not an ecological barrier during its migration around the MEI on both its northern and southern margins (it may have even passed the Upper Silesian/East-Sudetic blocks on their southern flanks;



Text-fig. 4. Palaeogeography of central Europe during the Cenomanian–Turonian (modified after Ziegler 1990). Occurrences and possible migration routes of *Praeactinocamax plenus* around the Mid-European Island (MEI) are indicated. A marine strait across the Bohemian Massif is not necessary to explain the occurrence of *P. plenus* in the Danubian Cretaceous Basin (see text for further discussion)

Text-fig. 4). After entering the Saxonian and Bohemian Cretaceous basins, migration of *P. plenus* into the Danubian Cretaceous Basin may have continued around the southern margin of the Bohemian Massif, or counterclockwise along the northern margin of the MEI and via the Anglo-Paris Basin (the latter scenario was also favoured by Košťák *et al*. 2004, p. 517). From studies of the rapid dispersal of Recent marine benthic molluscs along coasts and even across oceans (see e.g. Scheltema 1977) it is apparent that the duration of migration of nektic *P. plenus* across central Europe would be far beyond the resolution of integrated stratigraphy and, thus, must appear as an isochronous event in the stratigraphic record.

CONCLUSIONS

The belemnite records of the lower Danubian Cretaceous Group (DCG, northeastern Bavaria, southern Germany) are compiled (including collection material of the Bayerische Staatssammlung für Paläontologie in Munich and new finds) and placed within the new integrated stratigraphic framework of the group (Niebuhr *et al.* 2009). Three specimens from the lower Regensburg Formation (Saal Member) south of Regensburg can be assigned to *Neohibolites* cf. *ultimus* (d'Orbigny) and are dated as late Early Cenomanian (*Mantelliceras dixoni* Zone). Eight specimens represent *Praeactinocamax plenus* (Blainville) and occur in an event (*plenus* Event) in the lower Eibrunn Formation (Regensburg area) or basal Regensburg Formation (Bodenwöhrer Senke). Independent stratigraphic data (ammonoids, inoceramid bivalves, carbon stable isotopes) suggest that the *P. plenus* belemnite bioevent in the DCG has exactly the same chronostratigraphic position (mid-Late Cenomanian, middle *Metoicoceras geslinianum* Zone) as elsewhere in central and NW Europe. The lithostratigraphic units of the lower Danubian Cretaceous Group (i.e., the Regensburg and Eibrunn formations), however, are characterized by a pronounced diachronism based on their time-transgressive (onlapping) deposition during the Cenomanian–Early Turonian transgression. The distribution of *P. plenus* around the Mid-European Island can be easily explained by migration around the positive area without the necessity of a marine strait across the Bohemian Massif.

Acknowledgements

We thank A. Nützel, S. Schneider und W. Werner (Bayerische Staatssammlung für Paläontologie, München) for the possibility of working on the Dacqué collection. Reviews by M. Košťák (Prague) and F. Wiese (Berlin) are gratefully acknowledged as are numerous helpful comments by C.J. Wood (Minehead) and I. Walaszczyk (Warszawa). Furthermore, we express thanks to Q. Oellinger (Fels-Werke AG, Saal an der Donau) and the Haimerl quarry gravel works (Grub near Roding) for giving access to the Saal and Grub quarries, respectively. T. Pürner (Bayerisches Landesamt für Umwelt, Marktredwitz) und M. Kling (Augsburg) is thanked for the introduction to the sections in the Bodenwöhrer Senke.

REFERENCES

Blainville, H.M.D. de 1825-1827. Manuel de malacologie et de conchyliologie. 664 pp. (1825), 87 pls. (1827). Levrault; Paris and Strasbourg.

Chellouche, P. 2008. Land–Küste–Meer: Stratigraphie, Paläontologie und Sedimentologie der Danubischen Kreide-Gruppe in der östlichen Bodenwöhrer Senke (Oberpfalz, Bayern). Unpubl. Diploma thesis, Würzburg University, 104 pp.

Christensen, W.K. 1974. Morphometric analysis of *Actinocamax plenus* from England. *Bulletin of the Geological Society of Denmark,* **23**, 1–26.

Christensen, W.K. 1976. Palaeobiogeography of Late Cretaceous belemnites of Europe. *Paläontologische Zeitschrift,* **50**, 113–129.

Christensen, W.K. 1990a. Upper Cretaceous belemnite stratigraphy of Europe. *Cretaceous Research,* **11**, 371–386.

Christensen, W.K. 1990b. *Actinocamax primus* Arkhangelsky (Belemnitellidae, Upper Cretaceous): Biometry, comparision and biostratigraphy. *Paläontologische Zeitschrift,* **64**, 75–90.

Christensen, W.K. 1993. *Belemnocamax boweri* Crick, an unusual belemnite from the Cenomanian of northwest Germany and eastern England. *Bulletin of the Geological Society of Denmark,* **40**, 157–166.

Christensen, W.K. 1997a. The Late Cretaceous belemnite family Belemnitellidae: Taxonomy and evolutionary history. *Bulletin of the Geological Society of Denmark,* **44**, 59–88.

Christensen, W.K. 1997b. Palaeobiogeography and migration in the Late Cretaceous belemnite family Belemnitellidae. *Acta Palaeontologica Polonica,* **42**, 457–495.

Christensen, W.K., Diedrich, C. and Kaplan, U. 1992. Cenomanian belemnites from the Teutoburger Wald, NW Germany. *Paläontologische Zeitschrift*, **66**, 265–275.

Combémorel, R., Christensen, W.K., Naidin, D.P. and Spaeth, C. 1981. Les Bélemnites. *Cretaceous Research,* **2**, 283–286.

Dacqué, E. 1939. Die Fauna der Regensburg–Kelheimer Oberkreide. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Neue Folge,* **45**, 218 pp. C.H. Beck; München.

Dorn, P. 1958. Problematik des Vindelizischen Landes. *Geologie*, **7**, 319–341.

Ernst, G. and Rehfeld, U. 1997. Transgressive development in the Early Cenomanian of the Salzgitter area (northern Germany) recorded by sea level controlled eco- and lithoevents. *Freiberger Forschungshefte*, **C 468**, 79–107.

Ernst, G., Schmid, F. and Seibertz, E. 1983. Event-Stratigraphie im Cenoman und Turon von NW-Deutschland. *Zitteliana,* **10**, 531–554.

Förster, R., Meyer, R. and Risch, H. 1983. Ammoniten und planktonische Foraminiferen aus den Eibrunner Mergeln (Regensburger Kreide, Nordostbayern). *Zitteliana,* **10**, 123–141.

Gale, A.S. and Christensen, W.K. 1996. Occurrence of the belemnite *Actinocamax plenus* in the Cenomanian of SE France and its significance. *Bulletin of the Geological Society of Denmark,* **43**, 68–77.

Gümbel, C.W. von 1854. Übersicht über die geognostischen Verhältnisse der Oberpfalz. *Korrespondenz-Blatt des zoologisch-mineralogischen Vereines in Regensburg,* **8**, p. 32, 37–43.

Gümbel, C.W. von 1868a. Verzeichnis der in der Sammlung des zool.-mineral. Vereines in Regensburg vorfindlichen Versteinerungen aus den Schichten der Procän- oder Kreideformation aus der Umgegend von Regensburg. *Korrespondenz-Blatt des zoologisch-mineralogischen Vereines in Regensburg,* **22**, 51–80.

Gümbel, C.W. von 1868b. Geognostische Beschreibung des Koenigreichs Bayern. 2. Abtheilung, Geognostische Beschreibung des Ostbayerischen Grenzgebirges oder des Bayerischen und Oberpfälzer Waldgebirges. 968 pp. Justus Perthes; Gotha.

Gümbel, C.W. von 1891. Geognostische Beschreibung des Koenigreichs Bayern. 4. Abtheilung, Geognostische Beschreibung der Fränkischen Alb (Frankenalb) mit dem anstossenden Fränkischen Keupergebiete. 763 pp. Theodor Fischer; Kassel.

Häntzschel, W. 1933. Das Cenoman und die Plenus-Zone der sudetischen Kreide. *Abhandlungen der Preußischen Geologischen Landesanstalt, Neue Folge,* **150**, 161 pp.

Hilbrecht, H. 1986. Die Turon-Basis im Regensburger Raum: Inoceramen, Foraminiferen und "events" der Eibrunner Mergel bei Bad Abbach. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen,* **172**, 71–82.

Hilbrecht, H. and Hoefs, J. 1986. Geochemical and palaeontological studies of the $\delta^{13}C$ anomaly in the boreal and north Tethyan Cenomanian–Turonian sediments in Germany and adjacent areas. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **53**, 169–189.

Hilbrecht, H., Frieg, C., Tröger, K.-A., Voigt, S. and Voigt, T. 1996. Shallow water facies during the Cenomanian–Turonian anoxic event: bio-events, isotopes, and sea level in southern Germany. *Cretaceous Research,* **17**, 229–253.

Jeffries, R.P.S. 1962. The paleoecology of the *Actinocamax plenus* subzone (lowest Turonian) in the Anglo-Paris Basin. *Palaeontology,* **4**, 609–647.

Jeffries, R.P.S. 1963. The stratigraphy of the *Actinocamax plenus* subzone (Turonian) in the Anglo-Paris Basin. *Proceedings of the Geologists' Association*, **74**, 1–33.

Kauffman, E.G., Herm, D., Johnson, C.C., Harries, P. and Höfling, R. 2000. The ecology of the Cenomanian lithistid sponge frameworks, Regensburg area, Germany. *Lethaia,* **33**, 214–235.

Köhler, S. and Spaeth, C. 1998. The first belemnite record from Early Cenomanian conglomerate of Meissen (Saxony). *Zentralblatt für Geologie und Paläontologie,* **1996**, 1487–1488.

Košťák, M. 2004. Cenomanian through the lowermost Coniacian Belemnitellidae Pavlow (Belemnitida, Coleoidea) of the East European Province. *Geolines,* **18**, 59–109.

Košťák, M. and Pavliš, W. 1997. Biometric analysis of *Praeactinocamax plenus* (Blainv.) from the Bohemian Cretaceous Basin. *Acta Universitatis Carolona - Geologica,* **41**, 1–13.

Košťák, M and Wiese, F. 2008. Lower Turonian record of belemnite *Praeactinocamax* from NW Siberia and its palaeogeographic significance. *Acta Palaeontologica Polonica*, **53**, 669–677.

Košťák, M., Čech, S., Ekrt, B., Mazuch, M., Wiese, F., Voigt, S. and Wood, C.J. 2004. Belemnites of the Bohemian Cretaceous Basin in a global context. *Acta Geologica Polonica,* **54**, 511–533.

Lehner, L. 1937a. Fauna und Flora der fränkischen albüberdeckenden Kreide. I. Die Lamellibranchiaten (ohne Inoceramen), herausgegeben von R. Dehm. *Palaeontographica,* **A 85**, 115–228.

Lehner, L. 1937b. Fauna und Flora der fränkischen albüberdeckenden Kreide. II. Fauna 2. Teil und Flora, herausgegeben von R. Dehm. *Palaeontographica,* **A 87**, 158–230.

Marcinowski, R. 1972. Belemnites of the genus *Actinocamax* Miller, 1823, from the Cenomanian of Poland. *Acta Geologica Polonica,* **22**, 247–256.

Mitchell, S.F. 2005. Eight belemnite biohorizons in the Cenomanian of northwest Europe and their importance. *Geological Journal,* **40**, 363–382.

Naef, A. 1922. Die fossilen Tintenfische. 322 pp. Fischer; Jena.

Naidin, D.P. 1964. Upper Cretaceous belemnites of the Russian Platform and contiguous regions. *Actinocamax, Gonioteuthis, Belemnocamax*, 190 pp. Moscow University Press; Moscow. [In Russian]

Niebuhr, B., Pürner, T. and Wilmsen, M. 2009. Lithostratigraphie der außeralpinen Kreide Bayerns. In: Niebuhr, B. (Ed.), Litho- und Biostratigraphie der außeralpinen Kreide von Bayern. *Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften,* **65**, 7–58.

Orbigny, A. d' 1845. Paléontologie universelle des coquilles et de mollusques. 105 pl., Paris (d'Orbigny).

Pavlow, A.P. 1914. Jurassic and lower Cretaceous Cephalopoda of North Siberia. *Zapiski Imperatorskoj Akademii Nauk, Seriâ 8, Po Fiziko-Matematičeskomu Otdeleniû,* **21**, 1–68. [In Russian]

Röper, M. and Rothgaenger, M. 1995. Neue Fossilfunde aus der Regensburger Oberkreide. Teil 1: Eibrunner Mergel. *Fossilien,* **3/1995**, 180–184.

Scheltema, R. S. 1977. Dispersal of marine invertebrate organisms: Paleobiogeographic and biostratigraphic implications. In: Kauffman, E.G. and Hazel, J.E. (Eds), Concepts and methods of biostratigraphy, pp. 73–108. Dowden, Hutchinson & Ross; Stroudsburg.

Spaeth, C. and Köhler, S. 1997. Erstnachweis eines Belemniten aus dem Untercenoman von Meißen, Sachsen. *Fossilien,* **4/97**, 225–226.

Spaeth, C. 1971. Untersuchungen an Belemniten des Formenkreises um *Neohibolites minimus* (Miller, 1826) aus dem Mittel- und Ober-Alb Nordwestdeutschlands. *Geologisches Jahrbuch, Beihefte,* **100**, 1–127.

Spaeth, C. 1991. Neohiboliten-Leitarten der mittleren Kreide von Helgoland. *Geologisches Jahrbuch,* **A 120**, 281–287.

Stolley, E. 1911. Beiträge zur Kenntnis der Cephalopoden der norddeutschen Unteren Kreide. I. Die Belemniten der norddeutschen Unteren Kreide. 1. Die Belemniten des norddeutschen Gaults (Aptiens und Albiens). *Geologische und Paläontologische Abhandlungen, Neue Folge,* **10**, 201–272.

Svoboda, P. 1985. Spojeni českého křidového moře s bavorským během cenomanu a turonu (The connection of the Bohemian Cretaceous sea with Bavaria during the Cenomanian and the Turonian). *Bohemia Centralis,* **14**, 7–23.

Svoboda, P. 2006. Hercynian Cretaceous and „Plenus Event". *Acta Universitatis Carolinae, Geologica,* **49**, 169–180.

Tröger, K.-A., Niebuhr, B. and Wilmsen, M. 2009. Inoceramen aus dem Cenomanium bis Coniacium der Danubischen Kreide-Gruppe (Bayern, Süd-Deutschland). In: Niebuhr, B. (Ed.), Litho- und Biostratigraphie der außeralpinen Kreide von Bayern. *Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften,* **65**, 59–110.

Trusheim, F. 1935. Die geologische Geschichte Südostdeutschlands während der Unterkreide und des Cenomans. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilagen,* **75**, 1–109.

Wiese, F., Wood, C.J. and Kaplan, U. 2004. 20 years of event stratigraphy in NW Germany; advances and open questions. *Acta Geologica Polonica,* **54**, 639–656.

Wiese, F., Košták, M. and Wood, C.J. 2009. The Upper Cretaceous belemnite *Preaactinocamax plenus* (Blainville, 1827) from Lower Saxony (Upper Cenomanian, northwest Germany) and its distribution pattern in Europe. *Paläontologische Zeitschrift,* **83**, 309–321.

Wilmsen, M. 1999. The Cretaceous belemnite *Neohibolites ultimus* (d'Orbigny, 1845): Its occurrence and significance in the Cenomanian of the North Cantabrian Basin. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte,* **1999**, 295–311.

Wilmsen, M. and Niebuhr, B. 2010. On the age of the Upper Cretaceous transgression between Regensburg and Neuburg an der Donau (Bavaria, southern Germany). *Neues Jahrbuch für Geologie und Paläontologie*, **256**, 267–278.

Wilmsen, M. and Rabe, M. 2008. Belemnites from the lower Middle Cenomanian of Hoppenstedt, northern Germany: significance and integrated correlation. *Cretaceous Research,* **29**, 936–942.

Wilmsen, M., Niebuhr, B., Wood, C.J. and Zawischa, D. 2007. Fauna and palaeoecology of the Middle Cenomanian *Praeactinocamax primus* Event at the type locality, Wunstorf quarry, northern Germany. *Cretaceous Research,* **28**, 428–460.

Wilmsen, M., Wood, C.J., Niebuhr, B. and Kaplan, U. 2009. Cenomanian–Coniacian ammonoids of the Danubian Cretaceous Group (Bavaria, southern Germany). In: Niebuhr, B. (Ed.), Litho- und Biostratigraphie der außer alpinen Kreide von Bayern. *Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften,* **65**, 111–124.

Wilmsen, M., Niebuhr, B., Chellouche, P., Pürner, T. and Kling, M. Facies pattern and sea-level dynamics of the early Late Cretaceous transgression: a case study from the Danubian Cretaceous Group (Bavaria, southern Germany). *Facies* [submitted].

Ziegler, P.A. 1990. Geological atlas of Western and Central Europe. 239 pp., 2nd ed.; Maatschappij B.V.; Shell International Petroleum.

Manuscript submitted: 6th November 2009
Revised version accepted:10th May 2010