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RESEARCH PAPER

The Upper Cretaceous belemnite *Praeactinocamax plenus* (Blainville, 1827) from Lower Saxony (Upper Cenomanian, northwest Germany) and its distribution pattern in Europe

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Abstract Occurrences of the Upper Cenomanian (Upper Cretaceous) belemnite *Praeactinocamax plenus* from the *plenus* Bed of northwest Germany (Söhlde-Loges working quarry near Salzgitter, Lower Saxony) are documented and described for the first time on the basis of two in situ finds. The find horizon and its surrounding beds are re-evaluated in a sequence stratigraphical context. In contrast to the interpretations of other authors, the *plenus* Bed is seen as a pelagization event in a parasequence of transgressively stacked beds, delimited by two significant erosion surfaces below and above. The exclusive occurrence of *P. plenus* in the top part of the *plenus* Bed and its absence from the post-*plenus* Bed succession, in the equivalent of which (higher part of the Plenus Marls Member) it is very common in southern England (Anglo-Paris Basin), is explained by ecological factors in stratigraphically complete sections (intra-shelf depressions) and by gaps in the stratigraphic records in swell settings. The distribution pattern of *P. plenus* suggests a preference for nearshore settings and a demersal mode of life.

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Keywords Upper Cretaceous · Cenomanian · Belemnitellidae · Sequence stratigraphy · Palaeoecology

Zusammenfassung Erstmals werden genau horizontierte Funde des Ober-Cenoman-Belemniten *Praeactinocamax plenus* aus NW Deutschland (Söhlde bei Salzgitter) abgebildet und beschrieben. Das Fundintervall wird sequenzstratigraphisch als Teil einer transgressiven Parasequenz interpretiert. Das ausschließliche Auftreten vom *P. plenus* im oberen Teil der *plenus* Bank NW-Deutschlands und das Fehlen in post-*plenus* Abfolgen (in denen die Art in England häufig ist) kann ökologisch (Nährstoffangebot, demersale Lebensweise) sowie mit lückenhafter Überlieferung erklärt werden.

Schlüsselworter Kreide · Cenoman · Belemnitellidae · Sequenzstratigraphie · Paläoökologie

Introduction

The belemnite *Praeactinocamax plenus* (Blainville, 1827) is an upper Cenomanian representative of the belemnite family Belemnitellidae that is well documented and discussed in the literature. It seems to be common to abundant on the Russian Platform (Naidin 1964). Its occurrence in Europe shows, however, some regional and stratigraphical patchiness, and it is mainly restricted to a short-term incursion epibole within the upper Cenomanian *Metoicoceras geslinianum* ammonite Zone (*plenus* Event, Ernst et al. 1983). Whilst the species is not uncommon in, and gives its name to, the Plenus Marls member of the Chalk Group in southern England (Jefferies 1961; Christensen 1974; Mortimore et al. 2001), as well as in the glauconitic near-shore facies near the Rhenish Massif of Germany (Frieg et al. 1990), it is extremely rare in more distal settings in northwest Germany, which are characterized by limestones, marl/limestone alternations or by the black shales of the oceanic anoxic event OAE II (see Fig. 1 for palaeogeographic overview). From the so-called *plenus* Bed in northwest Germany (Ernst et al. 1983), a hard and splintery white to grey limestone only some few decimetres in thickness, *P. plenus* is frequently mentioned in the literature. From Westphalia, two specimens are recorded (Christensen et al. 1992; Diedrich 2001); occurrences from the top of the *plenus* Bed in Lower Saxony and Sachsen-Anhalt are mentioned (Hilbrecht and Dahmer 1994), but have never been properly documented. There is only one figured specimen from Lower Saxony (Schmid 1965), unfortunately collected loose. In this paper, we figure and describe two specimens of *P. plenus* collected in situ from the top of the *plenus* Bed in Lower Saxony and discuss these occurrences in their lithostratigraphic and biostratigraphic context. Additionally, we will comment on the biogeographical and palaeoecological significance of the finds in the context of records from the *plenus* Bed of Westphalia and the overall distribution of the species in parts of Europe. Essential for the discussion is a critical re-evaluation of the sea-level history of the bed(s) in which it occurs in northwest Germany and England (Anglo Paris Basin, APB; *pars*).

Geological framework

Within the Pläner Limestone Group of northwest Germany (Lower Cenomanian to Lower Coniacian of the Lower Saxony, Subhercynian and Münsterland Cretaceous basins; see Hiss and Schönfeld 2000 and Niebuhr et al. 2000 for geographical details), the so-called Facies Change [boundary between the *Calycoceras* (*Proeucalycoceras*) *guerangeri* and *M. geslinianum* ammonite zones; Fig. 2] marks a significant, locally unconformable lithostratigraphic turnover from white massive nannofossil limestones of the Brochterbeck Formation (Hiss et al. 2007a; see Wilmsen 2003 for details) either towards black shale successions of the OAE II deposited in intra-shelf depressions (Hesseltal Formation: Hiss et al. 2007b) or to red shell-detrital limestones with intercalated marls (Rotpläner), deposited on less subsident intrashelf areas/intra-shelf swells (Söhlde Formation: Hilbrecht and Dahmer 1994; Wiese et al. 2007). In both the Rotpläner and black shale facies, a distinctive white nannofossil limestone bed, only a few dm thick, forms a geographically widespread facies-breaking marker bed, which is referred to as the *plenus* Bed or *plenus* Event in the literature (e.g., Ernst and Wood 1995; Figs. 2, 3). It represents a short-term recurrence of a Brochterbeck Formation-like facies and is readily recognizable at exposure due to its eye-catching pale colour within either black or red strata.

Especially in the broader area around Salzgitter, Vienenburg and Hoppenstedt (Fig. 1), several quarries provide or formerly provided excellent exposures of the Pläner Limestone Formation, and a wealth of publications exist on lithology (Ernst and Wood 1997; Ernst et al. 1998; Hilbrecht and Dahmer 1994; Kott 1985, 1986; Schönfeld et al. 1991; Wilmsen 2003; Wilmsen and Wiese 2004; Wilmsen et al. 2005) and integrated stratigraphy (biostratigraphy, event stratigraphy, tephrostratigraphy, sequence stratigraphy, δ^{13}C curves: Ernst and Wood 1995; Ernst et al. 1983, 1998; Horna and Wiese 1997; Voigt and Hilbrecht 1997; Wiese et al. 2000; Wray 1999; Wray and Wood 2002), to which the reader is referred for further details.

The Söhlde-Loges quarry: lithology, microfacies and depositional setting

The Söhlde-Loges quarry provides an excellent exposure of the Brochterbeck Formation, the Facies Change and the succeeding Söhlde Formation, and has therefore been chosen as the type locality for the latter (Wiese et al. 2007).

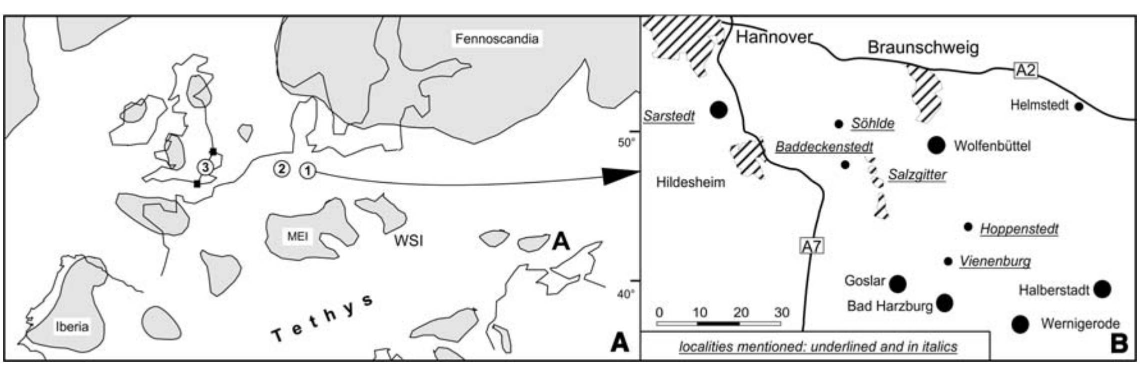

Fig. 1 **a** Simplified palaeogeographic sketch of the Cenomanian/Turonian European shelf sea. *1* Lower Saxony, including the localities Wunstorf and Misburg (see also details in **b**), *2* Westphalia, *3* transect in Fig. 5

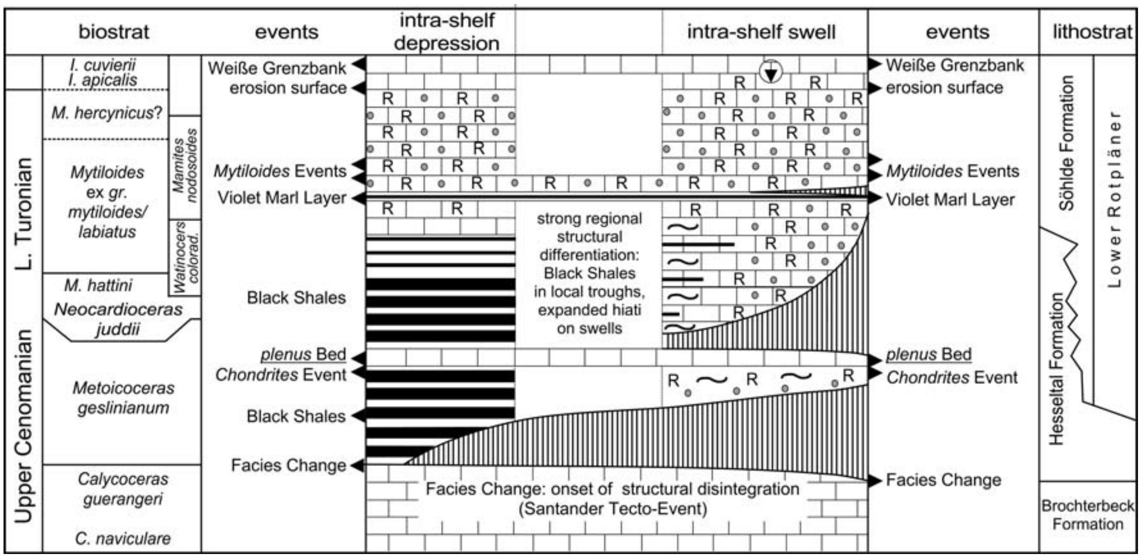

Fig. 2 Lateral lithostratigraphic relationships of the Cenomanian/Turonian boundary interval in northwest Germany with important event beds used for lateral correlation (modified from Wilmsen and Wiese 2004)

The succession has been repeatedly described and is well known in its overall sedimentological, faunal and stratigraphic characteristics (Ernst and Wood 1997; Wiese 2009, with additional references). Here, we will consider in detail a ca. 3 m interval of the exposed section, which spans the Facies Change, the *plenus* Bed and one of the distinctive succeeding lithomarkers, the Violet Marl Layer (Fig. 3a). Thin sections were prepared from the hard limestones for microfacies analysis (Beds 1 and 2 of this interval were too marly for the preparation of thin sections). Microfacies analysis of the interval in question shows comparatively depleted numbers of the main bioclastics that contribute to the compositional variations of the rocks. Apart from the matrix (which can be understood mainly as calcareous nannofossil ooze/debris), calcareous dinoflagellate cysts (c-dinocysts), inoceramid bivalve debris and planktonic foraminifera are the main components. These components have been selected for quantitative analyses and reconstruction of compositional variation with a point-counter ($n = 1{,}000$ counts; Fig. 4).

Lithology and microfacies

The base of the section exposes the Hoppenstedt Member at the top of the Brochterbeck Formation. This member represents a pelagic biosedimentary system deposited with accumulation rates of ca. 20 m/my on a uniform shelf (Wilmsen 2003). The microfacies consist of c-dinocyst wacke- to mudstones with more than 75% matrix and a bioclastic component comprising small c-dinocysts, rare planktonic foraminifera and less than 3% inoceramid debris (Fig. 4). The Facies Change terminates the Brochterbeck Formation and is developed as a well-marked erosion surface in most Söhlde Formation successions. However, at the Söhlde-Loges quarry, it is developed as a rapid but continuous facies shift with a burrow-mottled omission surface (Fig. 3). The succeeding Söhlde Formation consists of red marls, marly limestones and limestones, traditionally referred to as "Rotpläner" (Figs. 2, 3). Bed 2 (c-dinocyst/inoceramid wacke- to packstone) is characterized by a significant decrease in matrix, an increase in c-dinocysts up to 30% (with larger diameters than in the Brochterbeck Formation) and an increase in inoceramid debris up to 17%. The content of planktonic foraminifera, which is generally low in this interval, decreases further to 2%. The *plenus* Bed (Bed 6) reflects macroscopically a short-term recurrence of a nannofossil biosedimentary system like the Brochterbeck Formation, as indicated by a hard and white limestone with increased $CaCO_3$ content; it shows an internal subdivision (a–d) by blood-red marl seams. In 6a, the matrix increases rapidly from about 30% to ca. 80%, and the planktonic foraminiferal content increases to over 5%, while the c-dinocyst and inoceramid content decreases significantly. In the topmost part of the *plenus* Bed (6d), inoceramid debris becomes more frequent again, while c-dinocysts decrease markedly to only ca. 5%; this decrease possibly generates the small increase in the proportion of matrix. Bed 6d yielded the specimens of *P. plenus* described in this paper.

The top of the *plenus* Bed is developed as a conspicuous irregular erosion surface, with lithoclasts up to 10 cm concentrated as a lag in depressions (Hilbrecht and Dahmer 1994; Ernst et al. 1984). These lithoclasts are white coccolithic limestones with the typical *plenus* Bed

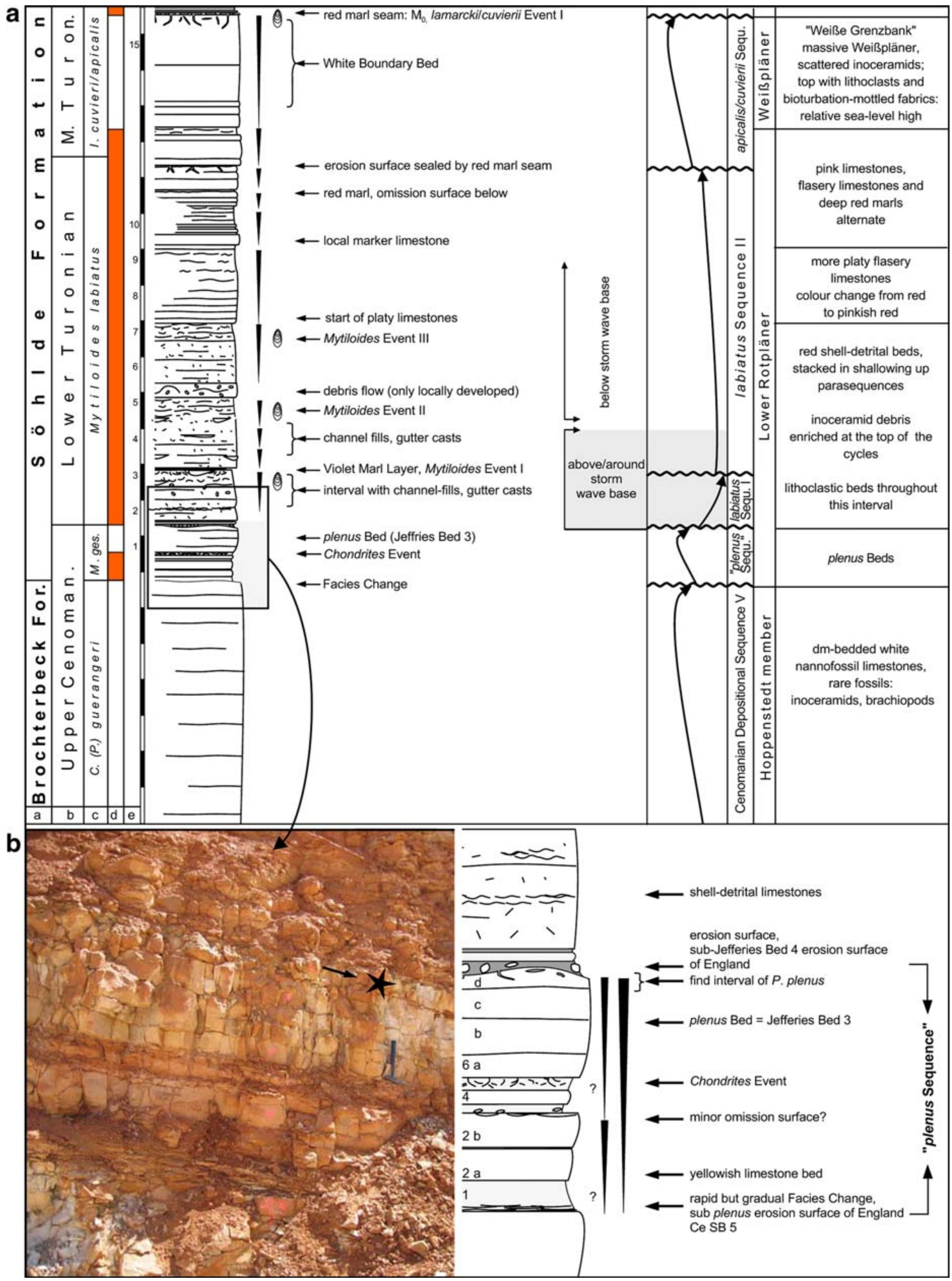

Fig. 3 **a** Lithologic column of the terminal Cenomanian to Lower Turonian of the Söhlde-Loges working quarry with details of biostratigraphy and relative sea-level development of lithological features. *a* Formation, *b* substages, *c* biozone, *d red* intervals are red limestones, *e* thickness in metres. **b** Close-up of the Facies Change and the "*plenus* Sequence" with a detailed profile. *Arrow* and *star* mark the find level of *P. plenus* (*M. ges*: *M. geslinianum*)

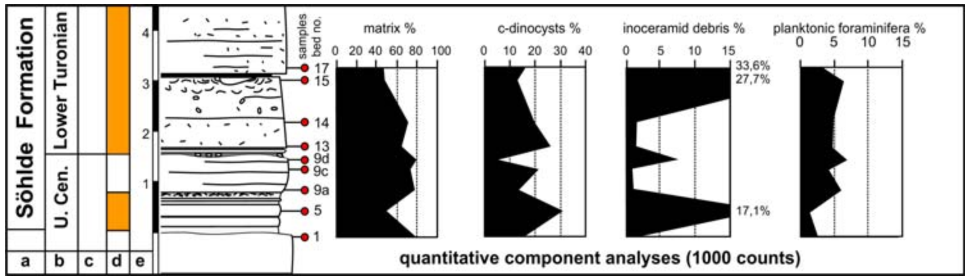

Fig. 4 Quantitative point-counter analyses of selected biogenic components and matrix in the interval between the Facies Change and Violet Marl Layer

microfacies, and there is no doubt that they comprise reworked *plenus* Bed material. The succeeding Rotpläner reflects a progressive establishment of a storm depositional system (Hilbrecht and Dahmer 1994; Wiese 2009), which is associated with a decrease in matrix towards the Violet Marl Layer (sequence boundary) due to winnowing and enrichment in coarse skeletal debris (inoceramid shells: 33%). Microcrinoid debris is not uncommon in this interval. The planktonic foraminifera show no significant trend.

Correlation with the Plenus Marls Member (Holywell Nodular Chalk Formation) of the Anglo-Paris Basin (APB) of southern England and the condensed Hesseltal Formation-type succession in eastern England

In the Chalk Group of the APB, the common occurrence of *P. plenus* is restricted to a single event bed in the Plenus Marls Member at the base of the Holywell Nodular Chalk Formation of the modern lithostratigraphical scheme (see Mortimore et al. 2001 for overview). The Plenus Marls Member comprises an alternation of beds of more argillaceous and less argillaceous chalks, which are traditionally referred to as Jefferies beds 1–8, based on work by Jefferies (1963) in the former Merstham standard section (see also Fig. 5). Recent studies of the member have been based on the greatly expanded section near Eastbourne (Gale et al. 2005) and on a condensed section near Dover (Jeans et al. 1991). (In order to avoid confusion with the numbered beds at Söhlde-Loges quarry, the Jefferies beds will subsequently be referred to in this paper by the abbreviation J followed by the appropriate numbers.) Bed J3 is relatively calcareous, locally indurated and terminates in an erosion surface; the overlying Bed J4 is generally markedly silty. Beds J5, J6 and J8 comprise two calcareous beds separated by a dark coloured argillaceous bed. The main occurrence of *P. plenus* is in beds J3–J5 with an abundance peak in J4. It is rare in bed J3, common in bed J4, and occurs regularly in bed J5. There are also sparse records from bed J6. Jefferies (1963) mentioned a single record of a juvenile from the base of bed J7 and a possible record from bed J8 (Jefferies 1961, 1963; Mitchell 2005).

In eastern England (Lincolnshire and Yorkshire) the post-Facies Change succession is extremely condensed and, in contrast to the Plenus Marls of the APB, includes one or more back shales, of which the most conspicuous is known as the Black Band. At Melton Ross Quarry, Lincolnshire, a relatively uncondensed Hesseltal Formation-type black shale succession has been fortuitously preserved from erosion in a downfaulted block. Here, the *plenus* Bed of northwest German successions is readily recognizable as a massive indurated white limestone bed with large ammonites. It is underlain by several black shales and grades up, without a terminal erosion surface, into a thin silty bed with sparse *P. plenus*. The limestone and the overlying silty bed are considered to equate with beds J3 and J4 of the APB, respectively, and are in turn overlain by the succession of marls that includes the Black Band (Wood and Mortimore 1995; Wood et al. 1997). In the more typical (i.e., condensed) eastern England successions, the limestone equivalent of the *plenus* Bed is very thin and is almost in contact with the Facies change/sub-*plenus* erosion surface, being separated from it by only a few centimetres of green marl with limestone pebbles. The limestone is overlain by a thin silty bed that locally has yielded rare *P. plenus*, but unlike at Melton Ross, the contact between the two beds is sharp, and the top of the limestone is stained black with manganese dioxide.

There is general consensus that the Facies Change correlates with the sub-*plenus* erosion surface of the APB, a widely recognized quasi-global sequence boundary, possibly caused by a glacio-eustatic sea-level fall (Ernst et al. 1983; Gale et al. 1999, 2002; Owen 1996; Wilmsen 2003). In Normandy, France, it equates with the Antifer Hardground 1 (Robaszynski et al. 1998). Given the position of the two beds on the δ^{13}C curve (Gale et al. 2005; Lehmann 1999) and cyclostratigraphic assumptions (Voigt et al. 2008), both Bed J3 and the *plenus* Bed can be understood to be time equivalents (Voigt et al. 2006). The correlation of the upper part of the *plenus* Bed with beds J4 and J5 for cyclostratigraphic (Gale 1995) or with bed J4 for biostratigraphic reasons—the correlation of the *P. plenus* peak occurrences in the two areas—by Wood and Mortimore (1995) appears thus

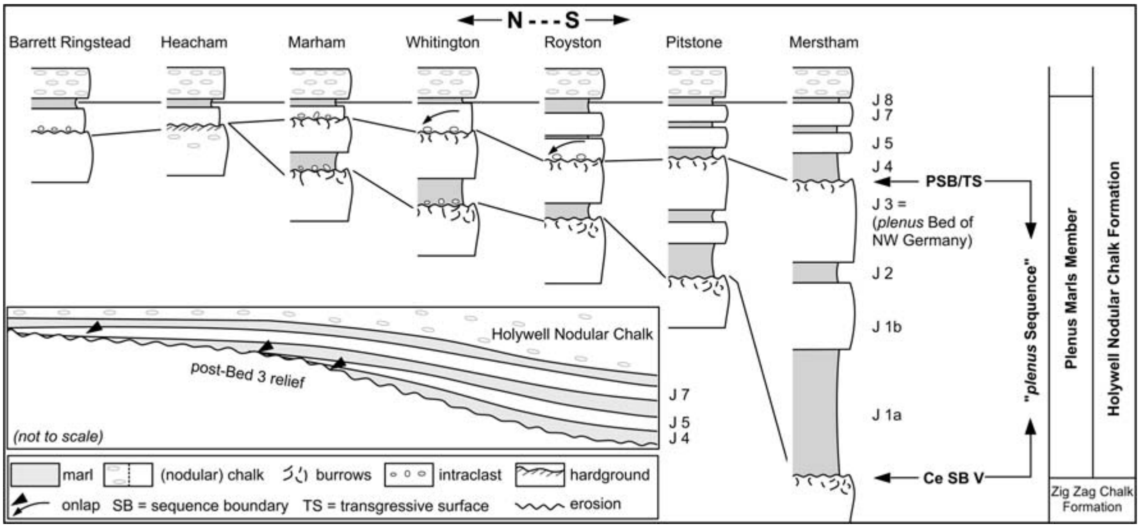

Fig. 5 Reproduction of a N–S-correlation of the *plenus* Marls in England between Barrett Ringstead in the north and Merstham in the south (see also Fig. 1a), based on Jefferies (1963) and Voigt et al. (2006) (with further locality details therein). Note the onlap of J1–J3 and J4–J7, separated by the sub-Jefferies Bed 4 erosion surface. Ce SB 5: Cenomanian Sequence Boundary 5 (see Owen 1996; Wilmsen 2003)

unlikely (Lehmann 1999). Given the correlation of Bed J3 with the *plenus* Bed, the well-developed erosion surface at the top of the *plenus* Bed in Rotpläner successions of northwest Germany is equivalent to the sub-Bed J4 erosion surface of the Plenus Marls Member (Jefferies 1961, 1963) of basinal sections (e.g., Merstham, Fig. 5) and to the Antifer Hardground 2 in Normandy. In conclusion, beds J1–J3 equate stratigraphically with beds 1–6 at Söhlde-Loges.

Palaeontological account

Family Belemnitellidae Pavlow, 1914

Genus *Praeactinocamax* Naidin, 1964

Type species: *Belemnites plenus* Blainville, 1825–1827, p. 376, pl. 11: fig. 3

P. plenus (Blainville, 1825–1827)

Fig. 6a–c

*1825 *B. plenus* DE BLAINVILLE: 376.

1827 *B. plenus* DE BLAINVILLE: pl. 11 bis, fig. 3

1974 *Actinocamax plenus* (Blainville). Christensen: 4–11, 12, pl. 1 figs. 1–3, pl. 2 figs. 1–5, pl. 3 figs. 1–6, pl. 4 figs. 1–5 (with comprehensive synonymy)

1997 *P. plenus* (Blainville). Košták and Pavliš: 2–10, text-fig. 3, 4, pl. 1 figs. 1–4, pl. 2 figs. 1–6.

2004 *P. plenus* (Blainville). Košták: 67–69, pl. 1 figs. 12–15, pl. 2 figs. 1–6, pl. 3 fig. 2, tab. 3

2004 *P. plenus* (Blainville). Košták et al. : 513–517, pl. 1 fig. B–E

2005 *P. plenus* (Blainville). Mitchell: 365, fig. 1, 14, 15

Type: The holotype is the original of *B. plenus* Blainville, 1825, p. 376, later figured by Blainville (1827, pl. 11 bis, fig. 3).

Material: One complete specimen (MB.C.12847) from the top of the *plenus* Bed, marl seam between beds 6c and 6d and one fragment (MB.C.12848) from Bed 6d, 5 cm below top (both Loges working quarry at Söhlde, Lower Saxony). The material is stored at the Naturkundemuseum Berlin.

Description: MB.C.12847 is a medium-sized guard ($L = 77.5$ without mucro, 80 mm estimated with supposed mucro; for abbreviations see Table 1), lanceolate in dorsoventral view and subcylindrical in lateral view. The maximum lateral diameter ($MLD = 11.7$ mm) is situated 30.1 mm (32.6*) from the apex (DAMLD). The ventral side is markedly flattened ($MDVD = 10.5$ mm); the dorsal side is more concave. The dorsolateral compressions

Table 1 Abbreviations and measurements MB.C.12847

L (length): 77.5 mm without mucro preserved, 80* estimated
MLD (maximum lateral diameter): 11.7 mm
MDVD (maximum dorsoventral diameter): 10.5 mm
DAMLD (distance from apex to maximum lateral diameter): 30.1, *32.6
LDAE (lateral diameter at alveolar end): 8.3 mm
DVDAE (dorsoventral diameter at alveolar end): 8.9 mm
CPD (central pit diameter): 1.1 mm
LDLC (length of dorsolateral compression): 36.1 mm
LDLF (length of dorsolateral furrows): 28.8 mm
LVN (length of ventral notch): 1.6 mm

Fig. 6 *Praeactinocamax plenus* (Blainville, 1827) from the top of the *plenus* Bed (Bed 6d) of the Söhlde-Loges working quarry. **a** Dorsal view; **b** lateral view; **c** alveolar fracture. Magnifications: ×1

(DLDL = 36.1 mm) and double furrows (LDLF = 28.8 mm) are fully developed. The alveolar fracture is low cone-shaped and oval-triangular in cross-section (LDAE = 8.3 mm, DVDAE = 8.9 mm) with apparent radial structures forming coarse ribs. The shallow pseudoalveolus is missing; however, the central pit is developed (DCP = 1.1 mm). The remnant of the ventral notch (LVN = 1.6 mm) is well developed (Fig. 6). The guard is smooth; no vascular imprints, striation or granulation are present. The apex is situated centrally, and it is broken at the place of the expected mucro (ca 2.5 mm are missing).

MB.C.12848 is a fragment of a posterior part of a guard; the alveolar end is not preserved, but the guard shows the typical ventral flattening. Traces of predation (shark?) occur, and post-mortem borings by acrothoracic cirripedes are expressed by the ichnogenus *Rogerella*. Although the fragmentary preservation does not permit specific determination, the ventral flattening and the exclusive occurrence of *P. plenus* in this interval in Europe makes the identification as *P. plenus* most likely.

Discussion: The specimen MB.C.12847 represents the typical morphotype of *P. plenus* known from Central Asia in the east to England in the west and to southeast France in the south (Gale and Christensen 1996). It is almost identical with the holotype figured by Blainville (1827). The large northwestern and Central European *P. plenus* populations were analysed statistically by Christensen (1974) and Košťák and Pavliš (1997), who showed the morphological stability of this species, albeit with the possibility of sexual dimorphism (Košťák 2004; Košťák et al. 2004). As *P. plenus* is an extremely well-documented taxon and our specimen can be assigned unequivocally to this species, no more taxonomic comments are required here.

Occurrence: P. plenus occurs throughout the *Metoicoceras geslinianum* Zone on the Russian platform and adjacent areas, i.e., Mangyshlak Peninsula, Kazakhstan (Marcinowski et al. 1996). It has approximately the same stratigraphic range as the index ammonite. In Central and Western Europe, *P. plenus* occurs in only a short interval in the upper part of the *geslinianum* Zone (Jefferies 1961; Mitchell 2005). In northwest Germany, it is restricted to the top of the *plenus* Bed. In the Plenus Marls Member in the Anglo-Paris Basin, its main occurrence is in beds J3–J5, with an abundance peak in J4. It is rare in bed J3, common in bed J4 and occurs regularly in bed J5. There are also sparse records from bed J6. Jefferies (1963) mentioned a single record of a juvenile from the base of bed J7 and a possible record from bed J8. In the condensed Hesseltal Formation type successions in eastern England, its occurrence is restricted to a silty bed overlying the equivalent of the plenus Bed of northwest Germany.

Sea-level development

Several studies provide keys for the recognition of sea-level development/sequence stratigraphic interpretation of chalk sediments and related offshore deposits sediments like the Brochterbeck and Söhlde formations of northwest Germany (Jarvis et al. 2001; Jeans et al. 1991; Robaszynski et al. 1998; Voigt et al. 2006; Wilmsen 2003). The Facies Change, terminating the Brochterbeck Formation, represents a well-developed sequence boundary throughout northwest Germany (Wilmsen 2003). It likewise marks the onset of basin floor movements (Santander tectoevent of Wiese and Wilmsen 1999), resulting in the differentiation into intra-shelf depressions (Hesseltal Formation) and intra-shelf swells (Söhlde Formation). Apart from erosional features, the lowering of sea-level is indicated by an abrupt decrease in $CaCO_3$ values (Schönfeld et al. 1991; Wilmsen et al. 2005) and an increase in coarse bioclastics, here almost exclusively inoceramid debris. Carbonate content and microfacies show that beds 1–5 at Söhlde-Loges quarry reflect a lowered sea-level, while the *plenus* Bed (Bed 6) reflects a short-term period of remarkably uniform sedimentation, facies cross-cutting through the Söhlde and Hesseltal formations. It also onlaps widely onto the Rhenish Massif at the southern margin of the Münsterland Cretaceous Basin, Westphalia (Kalkknollenlage of Hiss 1982; Wilmsen et al. 2005). This wide onlap, a renewed $CaCO_3$ peak and the associated microfacies, specifically the increase in matrix, suggest that the bed represents a short-term, albeit strong, pelagization event and a recurrence of a Brochterbeck Formation-type facies as a result of a high sea-level. This is in accordance with Prauss (2006), who interpreted the base of the *plenus* Bed of Wunstorf, west of Hanover (Lower Saxony), as a maximum flooding interval. We do not follow Wilmsen (2003), who took it as a transgressive surface, as no distinct surface is developed at the base of the *plenus* Bed. Instead, the development from the underlying beds into the *plenus* Bed, although rapid, is always gradual, albeit diagenetically accentuated. A hiatus at the base of the *plenus* Bed (Hilbrecht 1986; Hilbrecht and Dahmer 1994) cannot be observed. At Söhlde-Loges quarry, the succession from Bed 1 to the top of the *plenus* Bed is seen—after the Facies Change sea-level fall—as a transgressively developed set of beds. However, microfacies changes at the top of the *plenus* Bed (6d), specifically the increase in inoceramid debris, may be interpreted to foreshadow the succeeding sea-level fall and changes in the biosedimentary dynamics. The undulating erosion surface on top of the *plenus* Bed marks a renewed lowering of the erosion base level because of a relative sea-level fall, and both stable isotope and biostratigraphic data indicate that there is a considerable hiatus at Söhlde-Loges compared to sections developed in the black shales of the Hesseltal Formation (Voigt and Hilbrecht 1997; Voigt et al. 2008). In accordance with this interpretation are the large (up to 10 cm), partly phosphatized lithoclasts that accumulated as a lag deposit on the erosion surface during transgressive reworking. Above the *plenus* Bed, shell-detrital limestones, the occurrence of gutter casts and small channels show the establishment of a storm depositional system and significant shallowing (Hilbrecht and Dahmer 1994; Wiese 2009).

The same trend can be observed in the Anglo-Paris Basin. To judge from the lateral correlation diagrams given by Jefferies (1963, figs. 7, 10), beds J1 to J3 show stepwise onlap, with Bed J3 representing a first maximum onlap. Basinwards, Bed J3 shows a progressive increase in thickness. No downlap can be observed. As with the *plenus* Bed in northwest Germany, Bed J3 likewise represents a $CaCO_3$ peak and a decrease in sand-sized components and acid insoluble residues (Jarvis et al. 2001; Jeans et al. 1991) and, thus, a short-term pelagization phase. The sub-Bed J4 erosion surface reflects an abrupt lowering of the erosion level, and Bed J4—characterized by coarser clastics, glauconite and significantly lower $CaCO_3$ values—transgressively onlaps only in basinal settings onto Bed J3, while beds J5–J7 onlap onto progressively older strata towards uplifted marginal basin areas (Jefferies 1963; Fig. 5). There, Bed J7 starts to rest directly on the Facies Change in most proximal settings (see also Voigt et al. 2006 for discussion). Lithology and bed geometries, therefore, indicate that bed bundles J1–J3 and J4–J7 reflect individual short-term relative sea-level rises, separated by a period of omission and/or erosion. Thus, Bed J3/*plenus* Bed can be seen as an interbasinal traceable onlapping unit as a result of a high sea-level. An increase of bioclastics foreshadows a sea-level fall in the topmost part of these beds. Apart from England and northwest Germany, the magnitude of the Bed J3/*plenus* Bed sea-level high is also very well documented in Saxony (marginal facies of the Mid-European Island), where *P. plenus*-bearing beds form the first, thin, sealing sheet, which entirely covers the monzonite cliffs ("Klippen Fazies") near Dresden (Voigt et al. 2006, p. 843, fig. 4). As a consequence, the last occurrence of the planktonic foraminifer *Rotalipora cushmanni* in the *plenus* Bed of northwest Germany (Hilbrecht and Dahmer 1994) and in Bed J4 of the Plenus Marls Member in England (Jarvis et al. 1988) may potentially be slightly diachronous.

Given the overall transgressive trend above the Facies Change, we interpret the Facies Change to reflect both a sequence boundary and a transgressive surface. In contrast to the interpretations of other authors (e.g., Owen 1996, Robaszynski et al. 1998), we interpret beds J1–J3 of the APB to represent a sedimentary cycle with transgressively stacked beds that is equivalent to beds 1–6 of the Söhlde-Loges section. Delimited below by a rapid facies change, and above by a well-developed erosional unconformity, this group of beds was previously regarded as a high-frequency third order sequence, the *plenus* Sequence (Wilmsen and Wiese 2004). However, the orbital time scale of Voigt et al. (2007, 2008) shows that the duration of this "sequence" was only ca. 150 ky. Thus, it may be understood rather as a parasequence (4th order cycle) of the DS Ce VI of Wilmsen (2003). In contrast to Voigt et al. (2006), it is interpreted here to be part of a transgressive systems tract, not a lowstand systems tract. A shelf margin wedge, as suggested, e.g., by Robaszynski et al. (1998), is not developed, this being shown by the onlapping sets of beds and the entire lack of downlap geometries. The application of the term shelf margin wedge in this context is misleading in any case. In a purely sequence stratigraphic sense, such a sediment body is expected to occur attached to the shelf margin during sea-level lowstand. However, the APB was an intra-shelf basin positioned well on the European Cretaceous shelf (Ziegler 1988). The wedge-shaped geometry of the sediments observed may thus be better explained by the interplay of uplift and sea-level fall, resulting in erosional loss of previously deposited strata in uplifted areas. As graphically presented by Jefferies (1961) and discussed by Jeans et al. (1991), the depositional history of the Plenus Marls Member is associated with tectonic movements that are the expression in the APB of the subsequently recognized Santander Tectoevent of Wiese and

Wilmsen (1999). The onset of slow uplift near basinal margins/tectonic structures in the uppermost *guerangeri* Zone resulted in stronger erosion during the sea-level falls creating the Facies Change, with a low-angle erosional unconformity in these areas. The transgressive onlap of beds J1–J3 levelled the weak relief. Repeated relative sea-level fall during the deposition of the top of Bed J3 again resulted in the development of an erosion surface mainly in the marginal areas, where uplift still continued. Beds J4–J7 progressively sealed the relief during the succeeding transgression.

Migration pattern and palaeoecology of *P. plenus*

Several belemnite incursion events are recognized in the Cenomanian of Europe. In the Lower to lower Middle Cenomanian, isolated occurrences of representatives of *Neohibolites* reflect the stepwise extinction of the genus in Europe (Christensen 1997b; Mitchell 2005). The event-like incursion of *Praeactinocamx primus* (early *rhotomagense* Zone, Middle Cenomanian) and *P. plenus* (*geslinianum* Zone, Upper Cenomanian) represents a westward immigration of newly evolved Belemnitellidae from the Russian Platform into Europe (e.g., Ernst et al. 1983; Jefferies 1961; Košták et al. 2004; Mitchell 2005; Wilmsen et al. 2007). These short-term immigration events are recorded in transgressive sediments, which, however, represent an even lower sea-level than the terminal sediments of the previous sequence. Thus, migration must have happened during low or lowered sea-level, which is in accordance with Mitchell (2005). Immigration is—in contrast to Mitchell (2005)—associated with seawater cooling, as indicated by the associated fauna (Gale and Christensen 1996; Jefferies 1961; Wilmsen et al. 2007) and δ^{18}O data (Voigt et al. 2004). However, the geographically patchy occurrence of *P. plenus* and its disparate occurrence in the top of Bed J3/the *plenus* Bed and Bed J4 in the APB, as well as its absence in post-*plenus* successions in northwest Germany, require discussion.

In the area of its inferred regional provenance (Russian Platform), mass or abundant occurrences, respectively, of *P. plenus* are recorded mainly from proximal settings, e.g., from the Mangyshlak peninsula, Kazakhstan (Marcinowski et al. 1996; Naidin 1964) and southern Russia (Naidin 1964). All these records include adults and juveniles, thus most probably representing breeding populations. Occurrences in shallow marine settings are recorded from the APB (*P. plenus* in Bed J4: the main *P. plenus* occurrence; Jefferies 1963), Les Lattes, southeast France (Gale and Christensen 1996), Poland (Marcinowski 1972) and from marginal settings close to the Bohemian Massif or the Mid-European Island (Bohemian Cretaceous Basin: Häntzschel 1933; Košták and Pavliš 1997; Seifert 1955; Bavaria: Dacqué 1939). *P. plenus* also occurs in numbers in nearshore/proximal settings near the Rhenish Massif, Westphalia (Frieg et al. 1990), but, with increasing distance from these settings, its abundance decreases dramatically within only a few kilometres, and it becomes restricted to an event-like occurrence, the *plenus* Bed, in the offshore parts of the north-west German Cretaceous basins (Münsterland, Lower Saxony, Subhercynian Cretaceous basins). Most records of *P. plenus* are from the interval around the Facies Change (e.g., Stille 1905) or from the *plenus* Bed without precise localization within the bed (Christensen et al. 1992; Heinz 1928). From Baddeckenstedt, only ca. 8 km S of Söhlde-Loges, Schönfeld et al. (1991) reported three specimens from the top of the *plenus* Bed, referring to an oral communication by H. Hilbrecht, and Hilbrecht and Dahmer (1994) mentioned that *P. plenus* came from the uppermost part of the *plenus* Bed at Söhlde Loges; however, none of these finds has ever been properly and photographically documented. So far, only a single specimen with red limestones attached to it, collected loose from the Cenomanian/Turonian boundary interval, was figured from the Sack Syncline, Lower Saxony (Schmid 1965). A further record is in Schlüter (1876), who recorded a single find from Rotpläner facies without any details of the find locality and level. Thus, where the find levels are given, all records relate to the uppermost part of the *plenus* Bed. The same level is also indicated by Diedrich (2001) from Westphalia. There are no known records anywhere in Germany from below or above the equivalent of Bed 6d at Söhlde-Loges.

The known preference of *P. plenus* and other belemnitellids for shallower settings is well known (see above; Naidin 1964, 1969; Christensen 1990, 1997a, b; Gale and Christensen 1996; Košták et al. 2004). Thus, a sea-level fall and resulting large interconnected shelf areas favoured westward belemnite migration out of the EEP into the western European shelf seas. Mitchell (2005) and Wilmsen et al. (2007) suggested a transgressive setting for the development of the two *Praeactinocamax* incursion events into Western and Central Europe, as they occur in the beds overlying a parasequence boundary (Wilmsen 2007). However, in the case of the *plenus* Event, the occurrence of *P. plenus* already in the upper part of Bed J3 in the APB demands a slightly modified view, because this is below the inferred parasequence boundary and the succeeding transgressive horizons. The following model may explain the observed distribution pattern as an interaction among falling sea-level, immigration and the taphonomy/sedimentary record (see Fig. 7).

(1) Falling sea-level progressively created conditions for migration by the expansion of shelf settings with

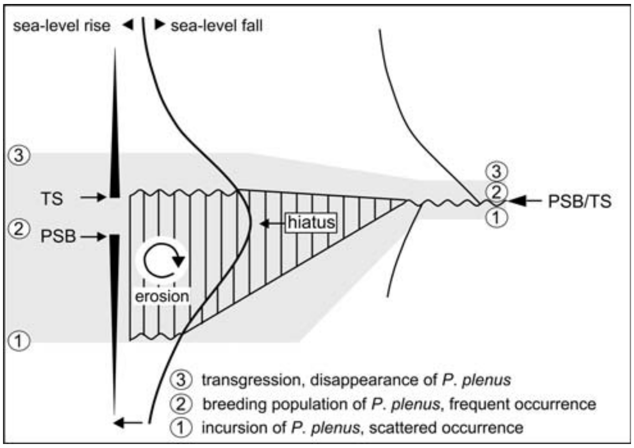

Fig. 7 Possible relationship between sea-level development, belemnite immigration and its geological expression (see explanation in the text)

favourable depths for migration. As the *plenus* Bed/Bed J3 shows a remarkable development with comparable lithology and only limited thickness variations throughout Europe, it represents a period devoid of noteworthy relief and even minor sea-level fluctuations.

(2) With continuous sea-level fall, *P. plenus* became widespread in appropriate settings, with first occurrences during parasequence highstand and maximum occurrence during early transgressive settings. Statistical analyses of *P. plenus* from Bed J4 in southern England revealed the presence of both juveniles and adults, indicating the existence of a breeding population (Christensen 1974). It would be interesting to re-investigate the rare *P. plenus* records from the top of Bed J3 to see whether or not these first migrants comprised adult individuals only.

(3) Shallowing progressively generated settings favourable for the migration initially of scattered immigrants (beginning of grey shaded interval in Fig. 7a: temporal development), following which a large population became established. Vice versa, increasing water depths caused a loss of favourable habitats and the progressive disappearance of *Praeactinocamax*. Lithologically, however, due to erosion in connection with the parasequence boundary (Fig. 7b: sedimentological expression), large amounts of information are not preserved because of the lowered erosion base level during sea-level fall. In addition, information may be artificially accentuated in the transgressive beds due to low accumulation rates and/or slight condensation resulting from winnowing of the fine-grained components during initial transgression. Thus, only the first immigrants are recorded (top Bed J3/*plenus* Bed). The period of progressive establishment of a population is sedimentologically not recorded due to a hiatus. With renewed sedimentation, the flood occurrence of *P. plenus* occurs “abruptly” in Bed J4. With further transgression, the species becomes rare again.

The above model can explain the occurrences of *P. plenus* already in Bed J3/top *plenus* Bed, but it fails to explain the disparate distribution compared to that in Bed J4 in the APB. It likewise fails to explain the absence of *P. plenus* above the *plenus* Bed in northwest Germany. We discuss several possible reasons:

– As already discussed, *P. plenus* favoured proximal parts of the depositional area, which may be an expression of either a food-related fixation (Mitchell 2005) or the presence of food in general. Lithologically similar to Bed J4 of the APB, the Middle Cenomanian *primus* Event of northwest Germany shows high faunal abundance and diversity, best explained by the occurrence of a sufficient food supply in mesotrophic waters (Wilmsen et al. 2007). The occurrence of *P. plenus* in the upper part of Bed J3 (Mitchell 2005) is associated with a Brochterbeck Formation-type facies comparable to that of the *plenus* Bed of northwest Germany, which represents a nutrient-depleted biosedimentary system with the low abundance-low diversity faunas of an open oceanic system (Gale et al. 2000; Wilmsen 2003). Thus, even though a minor sea-level fall can be detected in the upper part of Bed J3/*plenus* Bed, depletion of nutrients may have hindered migration of large populations into offshore settings.
– The absence of *P. plenus* in stratigraphically more or less complete but distal/basinal sections may be an expression of food deficiency in these areas (see above). However, these sections, spanning the Cenomanian/Turonian boundary interval without any significant hiatuses, are mainly characterized by black shales of the OAE II, e.g., Lengerich and Halle, Westphalia (Lehmann 1999; Voigt and Hilbrecht 1997) or Misburg and Wunstorf, Lower Saxony (Hilbrecht and Dahmer 1994; Wood and Ernst 1998). Although nektonic organisms like ammonites and fish are well documented from the black shales (Breitkreutz et al. 1991; Diedrich 2001)—indicating an oxygenated water column—belemnites are absent. A similar mode of occurrence is observed in the Bohemian Cretaceous Basin, where *P. plenus* is absent from the black sediments of the OAE II of the Pecínov Member (distal offshore; Košťák et al. 2004; Svoboda 2006). This suggests that *P. plenus* avoided the open water column and was most likely a demersal feeder in shallower/more proximal settings with higher nutrient flux (Mitchell 2005).

– The Rotpläner facies represents distal albeit shallow water shelf settings (Hilbrecht and Dahmer 1994; Kott 1985) and, thus, a potentially favourable habitat for belemnitellids. However, as can be seen from the δ^{13}C curves for the Söhlde-Loges section (Voigt and Hilbrecht 1997), there is a considerable hiatus in this section, and the stratigraphic equivalent of bed J4 is not preserved. Thus, belemnite finds cannot be expected there as these beds fall stratigraphically outside the stratigraphic range of the *P. plenus* epibole.

Summary of main conclusions

(1) Beds 1–6 of Söhlde-Loges (Lower Saxony, NW Germany) and beds J1–J3 of the Plenus Marls Member (Anglo Paris Basin) are a correlative set of strata, which represents a fourth order cycle.

(2) After the "Facies Change" glacio-eustatic sea-level fall, this cycle reflects renewed transgression, with Bed J3/*plenus* Bed as a short-term and widespread pelagization event within Europe.

(3) After the "Facies Change" glacio-eustatic sea-level fall, it is not the transgressive beds J1/J2 of the APB and their equivalents in the northwest German succession that are associated with a belemnite incursion, albeit shallowing may have triggered migration. Instead, a short-term westward immigration event of belemnitellids from the Russian Platform into Europe, associated with an incursion of cool water masses, took place later, during the deposition of beds J3/J4, in the course of a fourth order transgressive (beds J1–J3)/regressive (bed J4) cycle (initial transgression of the Cenomanian depositional sequence 6). This immigration pattern mirrors that of the earlier *primus* Event, where the incursion of the belemnite *Praeactinocamax primus* happened after the first transgressive parasequence of the transgressive systems tract.

(4) The first scattered and rare *P. plenus* immigrants appeared during the initial sea-level fall and are preserved in the top of Bed J3/*plenus* Bed. A uniform depositional area enabled the isochronous and widespread distribution of these first pioneers. A larger (breeding?) population became briefly established during the following sea-level low and is preserved in bed J4. With the succeeding transgression and the flooding of favourable habitats, *P. plenus* disappeared again.

(5) The geographical distribution pattern of *P. plenus* and migration during falling sea-level supports the idea of a demersal mode of life in more near-shore or shallower habitats and an avoidance of too distal settings. This also explains its absence in black shales.

(6) The absence of *P. plenus* in Rotpläner Facies (other than in the top of the *plenus* Bed) is caused by depositional gaps in these settings.

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