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Eight belemnite biohorizons in the Cenomanian of northwest Europe and their importance

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Eight belemnite biohorizons (BB) are recognized in the Cenomanian of northwest Europe, and can be related to both the ammonite zonal/subzonal and Cenomanian cyclostratigraphic schemes. These biohorizons are: BB1 (*Neohibolites praeultimus*) in the basal *Neostlingoceras carcitanense* Subzone (*Mantelliceras mantelli* Zone); BB2 (*Neohibolites ultimus*) in the upper *N. carcitanense* Subzone (*M. mantelli* Zone); BB3 (*N. ultimus*) in the *Sharpeiceras schluteri* Subzone (*M. mantelli* Zone); BB4 (*N. ultimus*) at the base of the *Mantelliceras dixoni* Zone; BB5 (*N. ultimus*) in the *Cunningtoniceras inerme* Zone; BB6 (*Praeactinocamax primus* and *Belemnocamax boweri*) in the lower *Acanthoceras rhotomagense* Zone; BB7 (*B. boweri*) in the middle *A. jukesbrownei* Zone; and BB8 (*P. plenus*) in the mid *Metoicoceras geslinianum* Zone. Belemnites are associated with deposits overlying the transgressive surfaces in the early transgressive systems tracts (BB2–4, BB6–8) or, rarely, with higher-frequency transgressive surfaces in lowstand deposits (BB5). Early transgressive systems tracts also commonly have small positive δ^{13}C excursions, although there is no one-to-one correspondence between the excursions and the belemnite biohorizons. A review of δ^{18}O curves for the Cenomanian Stage suggests little evidence for a temperature control on the distribution of belemnites.

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1. INTRODUCTION

The Cenomanian represented an important interval of palaeogeographical turn-over for the belemnites. With the progressive demise of the last widespread Tethyan belemnite genus *Neohibolites* in the Late Albian to Early/Middle Cenomanian, a relict, bipolar belemnite distribution appeared with low-diversity belemnitellid assemblages in the Boreal Realm, and low-diversity dimitrobelid assemblages in the Austral Realm (Doyle 1992a). Thus, late Cretaceous belemnite faunas were restricted to relatively high latitudes, with the majority of the Tethyan Realm lacking belemnites. Why belemnites disappeared from the Tethyan Realm remains an enigma. Perhaps the niche formerly occupied by the belemnites was taken over by other organisms (such as *Loligo*-like coleoids) that had fragile horny pens and, consequently, very low fossilization potentials.

The taxonomy of European Cenomanian belemnites is now generally well known (e.g. Spaeth 1971; Christensen 1974, 1976, 1990, 1993, 1997a; Christensen *et al.* 1992, 1993; Gale and Christensen 1996), but their detailed occurrence is less well understood. General summaries of their stratigraphic distribution have been given by Sharpe (1853–1857), Wright and Wright (1951), Swinnerton (1936–1955), Christensen (1974, 1990, 1993, 1997a), Christensen *et al.* (1992, 1993), Combémorel *et al.* (1981) and Doyle (1987). These studies largely related

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the distribution of belemnites to ammonites or, for the older works, ammonite–echinoderm subzones or zones. This has resulted in the suggestion that belemnites had extended ranges in the Cenomanian.

Many Cenomanian successions in northwest Europe are represented by decimetre- to metre-scale rhythmicity (Gale 1990, 1995; Paul *et al.* 1994). Each rhythm is represented by a marl–chalk couplet with bioturbated boundaries (omission surfaces). This rhythmicity is now attributed to climatic forcing driven by the Milankovitch 20 000 year precession cycle (Ditchfield and Marshall 1989; Gale 1990, 1995; Paul *et al*. 1994). By integrating ammonite and inoceramid zonations with short-lived appearances of certain macrofaunal elements (including cephalopods, bivalves, brachiopods and serpulids: Ernst *et al.* 1983; Gale 1989, 1990, 1995; Gale and Friedrich 1989; Mitchell *et al.* 1996), carbon stable isotope excursions (Paul *et al.* 1994; Jenkyns *et al.* 1994; Mitchell *et al.* 1996) and distinctive couplet stacking patterns (Gale 1990, 1995; Mitchell *et al.* 1996), the cyclostratigraphic timescale has been linked between sections in northwest Europe (Gale 1990, 1995; Paul *et al*. 1994). Couplets were numbered in five groups lettered A to E, each group having the following number of couplets: A, 51; B, 49; C, 46; D, 49; and E, 17 (Gale 1995). This cyclostratigraphic scheme can also be related to sequence stratigraphic interpretations of the Cenomanian Stage (Owen 1996; Mitchell *et al*. 1996; Robaszyski *et al*. 1998; Wilmsen 2003) and offers the excellent opportunity to compare the distribution of fossil organisms using an independent stratigraphic timescale.

Recent studies have given much more accurate data on belemnite distributions related to measured sections or Gale's cyclostratigraphic scheme (e.g. Jefferies 1962, 1963; Christensen *et al*. 1992; Paul *et al*. 1994, 1999; Gale and Christensen 1996; Wittler 1996; Mitchell and Carr 1998; Lehmann 1999). This has resulted in a new understanding of belemnite distribution. Rather than extended ranges, many belemnites appear to occur over very brief stratigraphic intervals. Several belemnite 'events' have been recognized (e.g. *Aucellina*/*ultimus* event, *primus* event, *plenus* event) in northwest Europe (Ernst *et al.* 1983).

In this paper, the distribution of accurately located belemnites (collected over a period of more than 15 years) from three measured sections in the Cenomanian of northeast England is presented. These occurrences are compared with belemnite distributions in southern England and northern Germany. The stratigraphic distribution of the belemnites is correlated, as far as possible, with Gale's cyclostratigraphic timescale, allowing a detailed comparison between the different regions.

2. TAXONOMIC STATUS OF THE BELEMNITES

The belemnites from the Cenomanian of northwest Europe are represented by six species, representing four genera and two families. A brief review of the Cenomanian belemnites is provided below. Figure 1 shows representatives of the species present.

Neohibolites and *Parahibolites*, the last representatives of the suborder Pachybelemnopseina (family Mesohibolitidae), occur in the Cenomanian Stage, although only *Neohibolites* has been widely reported from the Cenomanian of northwest Europe (Stolley (1920) reported very rare cf. *Parahibolites tourtiae* (Weigner) from the Münster Basin). At present, two Cenomanian species of *Neohibolites* are recognized: *Neohibolites praeultimus* Spaeth and *N. ultimus* (d'Orbigny). *Neohibolites praeultimus* from the Upper Albian of northwest Germany was fully described by Spaeth (1971). *Neohibolites* has a continuous record through the Aptian and Albian at Speeton, with the last representatives limited to the basal Cenomanian (Mitchell, 1995). Above this level, belemnites occur only in narrow stratigraphic intervals of the Cenomanian of northwest Europe. *Neohibolites ultimus*

Figure 1. Representative belemnites from the Cenomanian of NW Europe. (**1**,**2**) *Neohibolites praeultimus* Spaeth, no. C20585, bed RC1E, lower Lower Cenomanian, Speeton; ventral (1) and right lateral views (2). × 1. (**3**–**11**) *Belemnocamax boweri* Crick, nos. C20562 (3–5), C20015 (6–8), C20016 (9–11), bed SLC11C, Middle Cenomanian, Speeton. (3, 6, 9) Ventral views. (4, 7, 10) Left lateral views. (5, 8, 11) Dorsal views. All × 3. (**12**, **13**) *Praeactinocamax primus* (Arkhangelsky), no. C20582, bed SLC11C, Middle Cenomanian, Speeton; ventral (12) and left lateral views (13). × 2. (**14**, **15**) *Praeactinocamax plenus* (Blainville), no. C18012, Plenus Marls Bed 4, Eastbourne Sussex; ventral (14) and left lateral views (15). × 1. All specimens coated in magnesium oxide. All specimens to be deposited in Department of Palaeontology, Nationaal Natuurhistorisch Museum, Leiden, The Netherlands.


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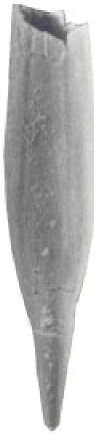
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was described originally from France by d'Orbigny (1847). More recent descriptions have been given by Wright and Wright (1951), Christensen (1990) and Doyle (1987). A local abundance of this species in the early Cenomanian of northwest Germany is known as the *Aucellina*/*ultimus* 'event' (Ernst *et al*. 1983).

The earliest representatives of the boreal Belemnitellidae appeared in the Cenomanian Stage. These include three species: *Praeactinocamax primus* (Arkhangelsky), *P. plenus* (Blainville) and *Belemnocamax boweri* Crick. Taxonomic treatments of these species have been given by Christensen (1974, 1990, 1993), Christensen *et al*. (1992) and Gale and Christensen (1996). Cenomanian *Praeactinocamax* (formerly *Actinocamax*) are widely distributed in Europe and European Russia where they extend from Northern Ireland to the Urals and southern France (Hancock 1961; Christensen 1974, 1976, 1990, 1997a; Christensen *et al*. 1992; Gale and Christensen 1996; Ali-Zade 1972; Naidin 1964). *Belemnocamax* has been recorded only from northeast England and northwest Germany (Crick 1910; Christensen 1990, 1993; Christensen *et al*. 1992; Mitchell *et al*. 1996; Wittler 1996; Lehmann 1999).

3. DISTRIBUTION OF BELEMNITES IN NORTHEAST ENGLAND

In northeast England, belemnites have been collected in detail from three sections: Speeton, South Ferriby and Hunstanton (Figure 2). Speeton is a relatively deep-water site (outer shelf) within the confines of the Cleveland Basin (Mitchell 1995; Mitchell and Langner 1996; Underwood and Mitchell 1999; Figure 2 herein). The stratigraphy of the Cenomanian has been described by several authors (e.g. Jeans 1980; Mitchell 1995, 1996; Mitchell *et al*. 1996; Gale 1995) and was summarized by Mortimore *et al*. (2001). The succession consists of hard chalks and thin marls, and can be correlated against the standard ammonite zonation of northwest Europe by the use of numerous lithological, geochemical (δ^{13}C excursions) and faunal biohorizons (Figure 3). Additionally, the well-developed rhythmicity allows Gale's (1995) cyclostratigraphic scheme for the Cenomanian to be employed (Figure 3).

South Ferriby is situated towards the northern end, and Hunstanton on the southern margin, of the East Midlands Shelf (Figure 2). The successions consist of hard chalks with few marls and the sections are interpreted to have been deposited at shallower water depths (shallow shelf) than the succession at Speeton (Jeans 1980; Mitchell and Langner 1996; Underwood and Mitchell 1999). Similar faunal horizons to those at Speeton enable a correlation with the standard ammonite zonal scheme (Figures 4, 5), although in most cases individual rhythms of Gale's

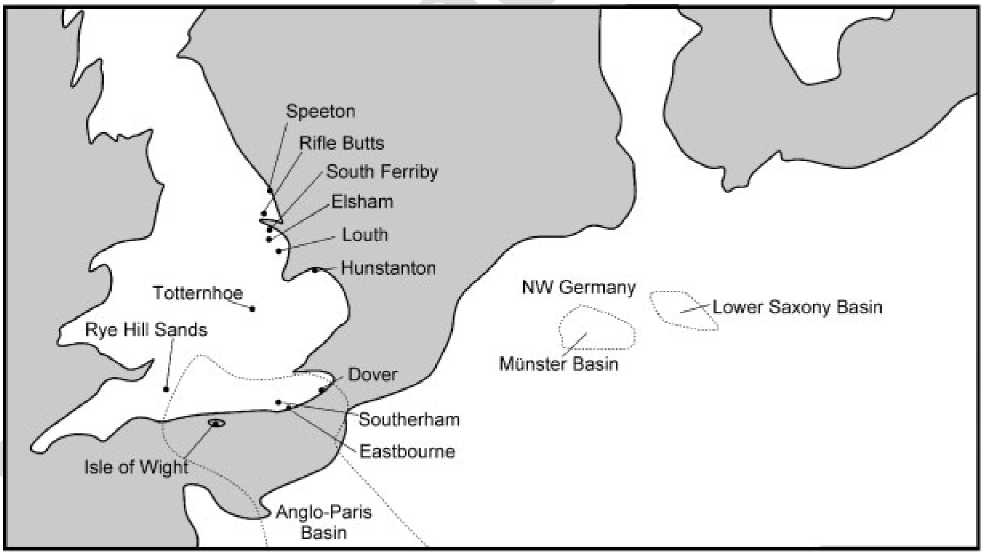

Figure 2. Distribution of sections in northwest Europe mentioned in the text.

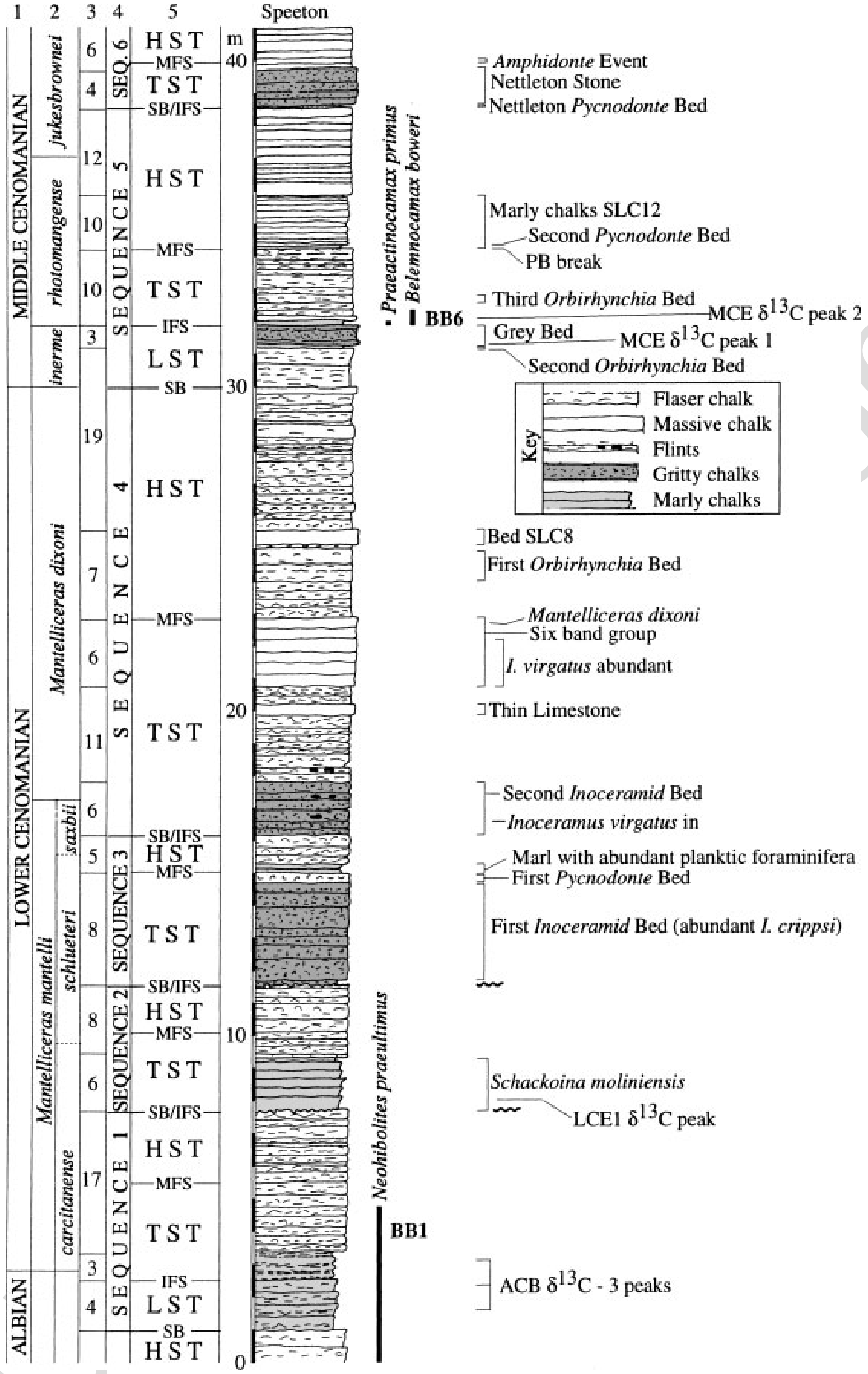

Figure 3. Distribution of belemnites, faunal marker horizons and δ^{13}C excursions in the Cenomanian of Speeton. Key: 1, stages; 2, ammonite zones; 3, number of couplets; 4, sequences; 5, systems tracts. Graphic log shows weathering profile.

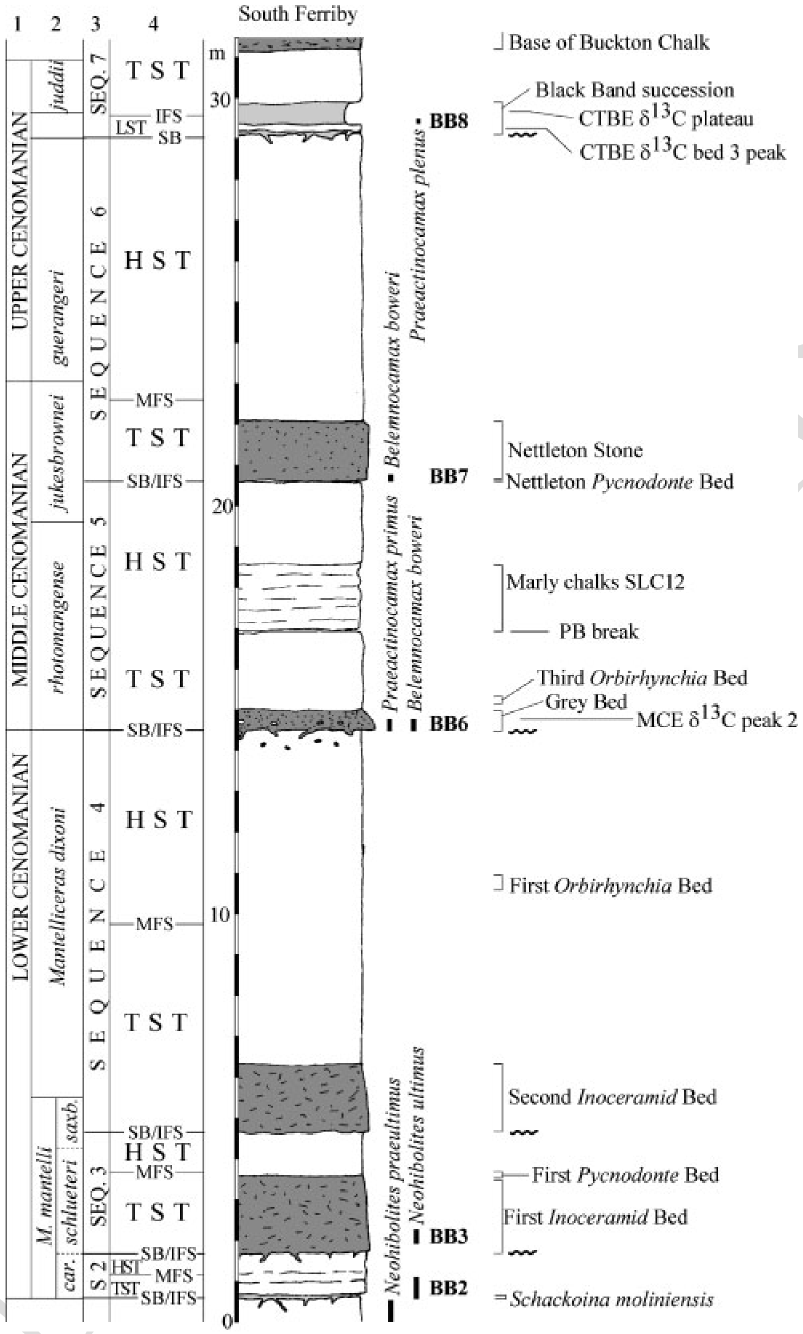

Figure 4. Distribution of belemnites, faunal marker horizons and δ^{13}C excursions in the Cenomanian of South Ferriby. Key: 1, stages; 2, ammonite zones; 3, sequences; 4, systems tracts. Graphic log shows weathering profile. See Figure 3 for key to symbols.

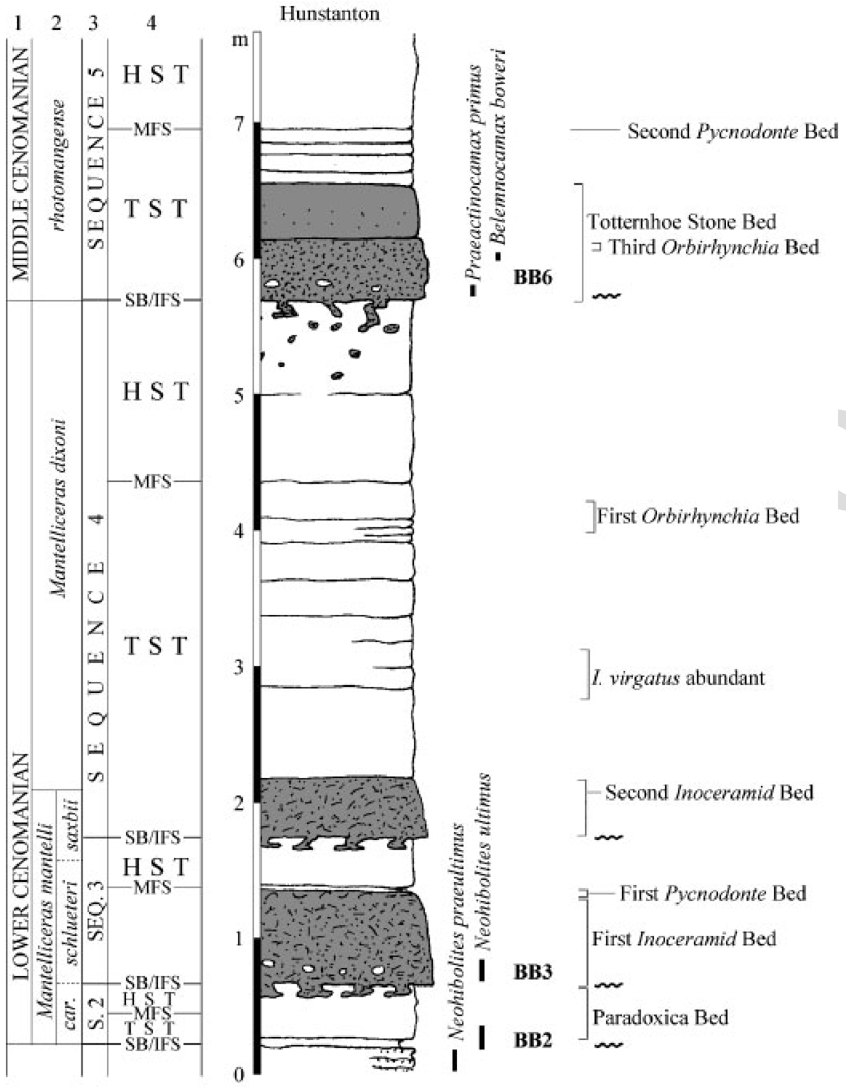

Figure 5. Distribution of belemnites and faunal marker horizons in the Cenomanian of Hunstanton. Key: 1, stages; 2, ammonite zones; 3, sequences; 4, systems tracts. Graphic log shows weathering profile. See Figure 3 for key to symbols.

(1995) cyclostratigraphic scheme cannot be recognized in these shallow water sites. The section at South Ferriby has been described by Jeans (1973) and Paul *et al.* (1994), and the section at Hunstanton by Owen (1995), Jeans (1973, 1980) and Mortimore *et al.* (2001).

Belemnites occur at six levels in the Cenomanian of northeast England (Figures 3–5). These occurrences are described below as belemnite biohorizons. For completeness, the two belemnite biohorizons not represented in northeast England are also described.

3.1. Belemnite Biohorizon 1 (BB1: Neohibolites praeultimus *biohorizon)*

At Speeton, *Neohibolites praeultimus* occurs in abundance in the upper Upper Albian (Dulcey Dock and Weather Castle Members of the Hunstanton Formation) and continues into the lower part of the Red Cliff Hole Member (Hunstanton Formation) (Mitchell 1995). *Neohibolites praeultimus* occurs together with specimens of *Aucellina* showing a striate microsculpture (Mitchell 1995). The Albian–Cenomanian boundary can be accurately placed at Speeton by comparison with detailed stable carbon isotope excursions across the Albian–Cenomanian boundary between Mont Risou in southeast France and Speeton (Mitchell 1995; Gale *et al*. 1996; Mitchell *et al.* 1996). At Speeton, the base of the Cenomanian is placed in the upper part of the Weather Castle Member (Mitchell 1995).

In northeast England, other records of *N. praeultimus*, probably of earliest Cenomanian age, have been given by Morter and Wood (1983). In the basal unit of the Cambridge Greensand in Ely-Ouse Borehole No. 6 (East Anglia), *N. praeultimus* occurs with specimens of *Aucellina* carrying a striate microsculpture (Morter and Wood 1983, p. 519). This unit was tentatively correlated with the base of the Red Cliff Hole Member at Speeton by Mitchell (1995). Morter and Wood (1983, p. 520) also reported *N. praeultimus* from a splintery limestone above bed 19 of the Gault Clay in the BGS borehole at Gayton (East Anglia), which may also be of the same age.

3.2. Belemnite Biohorizon 2 (BB2: Neohibolites ultimus *biohorizon I)*

Moderately common specimens of *N. ultimus* occur in the lower part of the Paradoxica Bed at South Ferriby and Hunstanton (Figures 4, 5). The lower part of the Paradoxica Bed contains *Aucellina* with an elongate–reticulate microsculpture and the brachiopod *Atactosia jeansi* Mitchell (Mitchell 1996; Mitchell and Veltkamp 1997). *Neohibolites ultimus* also occurs in the red clay that underlies the Paradoxica Bed at Hunstanton (Owen 1995). Burrows piped down from this clay at South Ferriby contain the planktic foraminiferan *Schackoina moliniensis* Reichel, that demonstrates a correlation with the upper part of the Red Cliff Hole Member of the Hunstanton Formation at Speeton (Mitchell and Veltkamp 1997). This level is equivalent to the *ultimus–Aucellina* 'event' of the event stratigraphy of Ernst *et al*. (1983) and can be placed in the uppermost *Neostlingoceras carcitanensis* Subzone of the *Mantelliceras mantelli* Zone (Mortimore *et al*. 2001).

3.3. Belemnite Biohorizon 3 (BB3: Neohibolites ultimus *biohorizon II)*

Rare examples of *Neohibolites ultimus* occur in the lower part of the First Inoceramus Bed at South Ferriby (Figure 4; Mitchell 1995; Mitchell and Veltkamp 1997), and in the First Inoceramus Bed at Hunstanton (Figure 5; Gallois 1994; Mortimore *et al*. 2001). The First Inoceramus Bed contains *Inoceramus crippsi crippsi* Mantell in flood abundance and the oyster *Rastellum colubrinum* (Lamarck) indicating the *Sharpeiceras schlueteri* Subzone of the *Mantelliceras mantelli* Zone (Gale and Friedrich 1989; Mortimore *et al*. 2001). This is confirmed by the report of a single *Sharpeiceras schlueteri* from this bed (Mortimore *et al*. 2001).

3.4. Belemnite Biohorizon 4 (BB4: Neohibolites ultimus *biohorizon III)*

In northwest Germany, *Neohibolites ultimus* has been reported from the 'Sponge Bed' by Ernst and Rehfeld (1997). The coarse-grained chalk beds of the 'Sponge Bed' are rich in anastomosing becksiid sponges and inoceramid debris, and occur at the base of the *M. dixoni* Zone (Wilmsen 2003). These beds are equivalent to the Second Inoceramus Bed in northeast England (Mitchell *et al*. 1996; Mortimore *et al*. 2001). This belemnite biohorizon has not been identified in northeast England and is referred to here as BB4 (*Neohibolites ultimus* biohorizon III).

3.5. Belemnite Biohorizon 5 (BB5: Neohibolites ultimus *biohorizon IV)*

Neohibolites ultimus was recorded from couplet B39 at Eastbourne by Mitchell and Carr (1998). A single coleoid arm hook has also been collected from the lower part of couplet B39A at Folkestone (Mitchell and Carr 1998), which is tentatively attributed to *Neohibolites*, as no other coleoids are presently known from this level. A.S. Gale (personal communication 1998) has also collected *Neohibolites* from a similar level in the Southernham Grey Pit in Sussex (Figure 2). Couplet B39 is in the *Cunningtoniceras inerme* Zone of the lower Middle Cenomanian (Gale 1995). This belemnite biohorizon has not been identified in northeast England, possibly because in many sections this interval is not preserved due to erosion before the deposition of the Totternhoe Stone; it is referred to here as BB5 (*Neohibolites ultimus* biohorizon IV).

3.6. Belemnite Biohorizon 6 (BB6: Praeactinocamax primus *and* Belemnocamax boweri *biohorizon)*

At Speeton, *Praeactinocamax primus* is rare (four specimens collected over 15 years) and occurs in bed SLC11C, which is couplet C1 (lower *Turrilites costatus* Subzone, *Acanthoceras rhotomagense* Zone) of Gale's cyclostratigraphic scheme (Paul *et al.* 1994; Gale 1995; Mitchell *et al.* 1996). *Belemnocamax boweri* is considerably more common and is largely restricted to bed SLC11C (63 specimens), but single specimens have also been collected in beds SLC11D and SLC12A (Figure 3). Therefore, *B. boweri* ranges through couplets C1 and C2 at Speeton.

At South Ferriby and Hunstanton, *Praeactinocamax primus* is fairly common near the base of the Totternhoe Stone (Figures 4, 5; Paul *et al*. 1994; Christensen 1990; Mortimore *et al*. 2001). *Belemnocamax boweri* also occurs in the Totternhoe Stone at South Ferriby and Hunstanton (Figures 4, 5), but is rarer than *P. primus* (Whitham 1991; Paul *et al*. 1994; Christensen 1993; Mortimore *et al*. 2001). *Praeactinocamax primus* has also been reported from the Totternhoe Stone of Melton (Whitham 1991) and Totternhoe (Christensen 1990). *Belemnocamax boweri* has been reported from the Totternhoe Stone of Louth (Crick 1910) and Rifle Butts (Wright and Wright 1951).

3.7. Belemnite Biohorizon 7 (BB7: Belemnocamax boweri *biohorizon)*

Whitham (1991) recorded an example of *B. boweri* from a loose block that was derived from the Nettleton *Pycnodonte* Bed at South Ferriby (Figure 4). The Nettleton *Pycnodonte* Bed is within the *Acanthoceras jukesbrownei* Zone (Gaunt *et al.* 1992; Mitchell *et al*. 1996) at the base of the Nettleton Stone (couplet D1 of Gale 1995). Hopefully *in situ* specimens will be collected from this horizon in the future to confirm the record.

3.8. Belemnite Biohorizon 8 (BB8: Praeactinocamax plenus *biohorizon)*

Praeactinocamax plenus is very rare at South Ferriby. Whitham (1991; personal communication 1994) recorded *P. plenus* from the Black Band succession above the basal chalk bed at South Ferriby (Figure 4). This is below the main occurrence of black shale in the upper part of the Black Band. An unpublished δ^{13}C curve demonstrates that this is in the build-up phase of the carbon isotope excursion associated with the Cenomanian–Turonian Boundary Event (CTBE), with peak values occurring in the black shales above the occurrence of the belemnites (Figure 4). *Praeactinocamax plenus* has also been recorded at a similar level in the Black Band succession at Elsham (Mortimore and Pomerol 1991).

4. BELEMNITES IN THE CENOMANIAN OF SOUTHERN ENGLAND

Belemnites have been widely reported from the Cenomanian Stage of southern England (e.g. Sharpe 1853–1857; Wright and Wright 1951; Jefferies 1962, 1963; Paul *et al*. 1994, 1999; Mitchell and Carr 1998; Mortimore *et al*. 2001). These are discussed below.

4.1. Neohibolites ultimus

Neohibolites ultimus is well known from the Rye Hill Sands of Warminster (Swinnerton 1936–1955, p. 78, pl. 18, figures 39–42). These sands also yield *Aucellina* with a striate microsculpture and can be placed in the *Neostlingoceras carcitanensis* Subzone of the *Mantelliceras mantelli* Zone (Mortimore *et al*. 2001, p. 152). This represents Belemnite Biohorizon 2 (*Neohibolites ultimus* horizon I).

Neohibolites ultimus has also been recorded from the Glauconitic Marl of the Isle of Wight (Sharpe 1853–1857; Wright and Wright 1951). Gale *et al*. (1996) noted that the Glauconitic Marl on the Isle of Wight contained a remanié *N. carcitanense* Subzone fauna and an indigenous *S. schlueteri* Subzone fauna. The belemnites could, therefore, belong to either subzone (BB2 or BB3, *Neohibolites ultimus* biohorizon I or II). *Neohibolites ultimus* biohorizon IV (BB4) is recognized at Eastbourne and Southerham (see section 3.5).

4.2. Praeactinocamax primus *biohorizon*

Praeactinocamax primus has been recorded in the lower part of couplet C1 at Folkestone and Southerham (Paul *et al*. 1994). This is near the base of the *T. costatus* Subzone of the *A. rhotomagense* Zone, and can be correlated with the *P. primus* occurrence (belemnite biohorizon 6) in bed SLC11C at Speeton (Paul *et al*. 1994; Gale 1995).

Kennedy (1970) also reported a specimen of *P. primus* from the basement bed of the Cenomanian in Dorset of Middle Cenomanian age. This specimen was discussed by Christensen (1990) and although not typical of examples of *A. primus*, there is no reason to believe that it was derived from any level other than the equivalent of bed C1.

Wright and Wright (1951) recorded *B. boweri* from the Isle of Wight. This specimen was examined by Christensen (1993), who concluded that it was a fragment of a crustacean. Therefore, *B. boweri* is unknown in belemnite biohorizon 6 of southern England.

4.3. Praeactinocamax plenus *biohorizon*

Jefferies (1962, 1963) undertook a detailed study of the Plenus Marls and introduced a bed numbering scheme (beds 1 to 8). He recognized that the belemnite now called *Praeactinocamax plenus*, after which the unit was named, did not occur throughout, and was restricted to the interval from the topmost part of bed 3 to bed 6, but with the main flood abundance in bed 4. Jefferies (1962, 1963) recorded the belemnite from numerous sections throughout southern England and northern France. Recent collections have confirmed this distribution (e.g. Gale and Christensen 1996; Paul *et al*. 1999), although Gale and Christensen (1996) also reported rare occurrences in bed 8. The Plenus Marls are of *Metoicoceras geslinianum* Zone age and the belemnites are confined to the middle of this zone (Gale 1995). This biohorizon can be traced into the Tethyan Realm of southeast France, some 540 km south of its most southern occurrence in the Anglo-Paris Basin (Gale and Christensen 1996).

The stable carbon isotope excursion associated with the Cenomanian–Turonian boundary event the begins in the lower part of the Plenus Marls, reaches a first peak in Plenus Marls bed 3, a second peak in Plenus Marls bed 8 and remains on a plateau for the lower part of the Melbourne Rock Beds, before dropping to a new post-excursion base level (Schlanger *et al*. 1987; Gale *et al.* 1993; Paul and Mitchell 1994; Mitchell *et al*. 1996; Paul *et al*. 1999). The belemnites, therefore, occur in the build-up phase of the excursion before the plateau phase, as in the condensed sections in northeast England.

5. BELEMNITES IN THE CENOMANIAN OF NORTHWEST GERMANY

Belemnites, although well reported, are very rare (Christensen 1997b; W. Riegraf personal communication 2003) in the Cenomanian of northwest Germany (Figure 6). These rare records are discussed below.

5.1. Neohibolites ultimus

The main occurrence of *N. ultimus* is in the *Aucellina*/*ultimus* 'event' (Ernst *et al*. 1983; Lehmann 1999). This is the level from which Spaeth (1971) analysed a large population (63 specimens) of *N. ultimus*. The *Aucellina*/*ultimus* 'event' yields specimens of *Aucellina* with an elongate–reticulate microsculpture (Morter and Wood 1983), and is therefore of *N. carcitanensis* Subzone age, equivalent to the Paradoxica Bed of northeast England and the Glauconitic Marl of southern England. This represents BB2 (*N. ultimus* horizon I).

Christensen *et al.* (1992) recorded an example of *N. ultimus* from Teutoburger Wald in northwest Germany. This horizon is probably in the lower part of the *Mantelliceras mantelli* Zone according to Christensen *et al*. (1992) and might represent BB3. Ernst and Rehfeld's (1997) record of *N. ultimus* from the 'Sponge Bed' at the base of the *M. dixoni* Zone represents BB4 (see section 3.4).

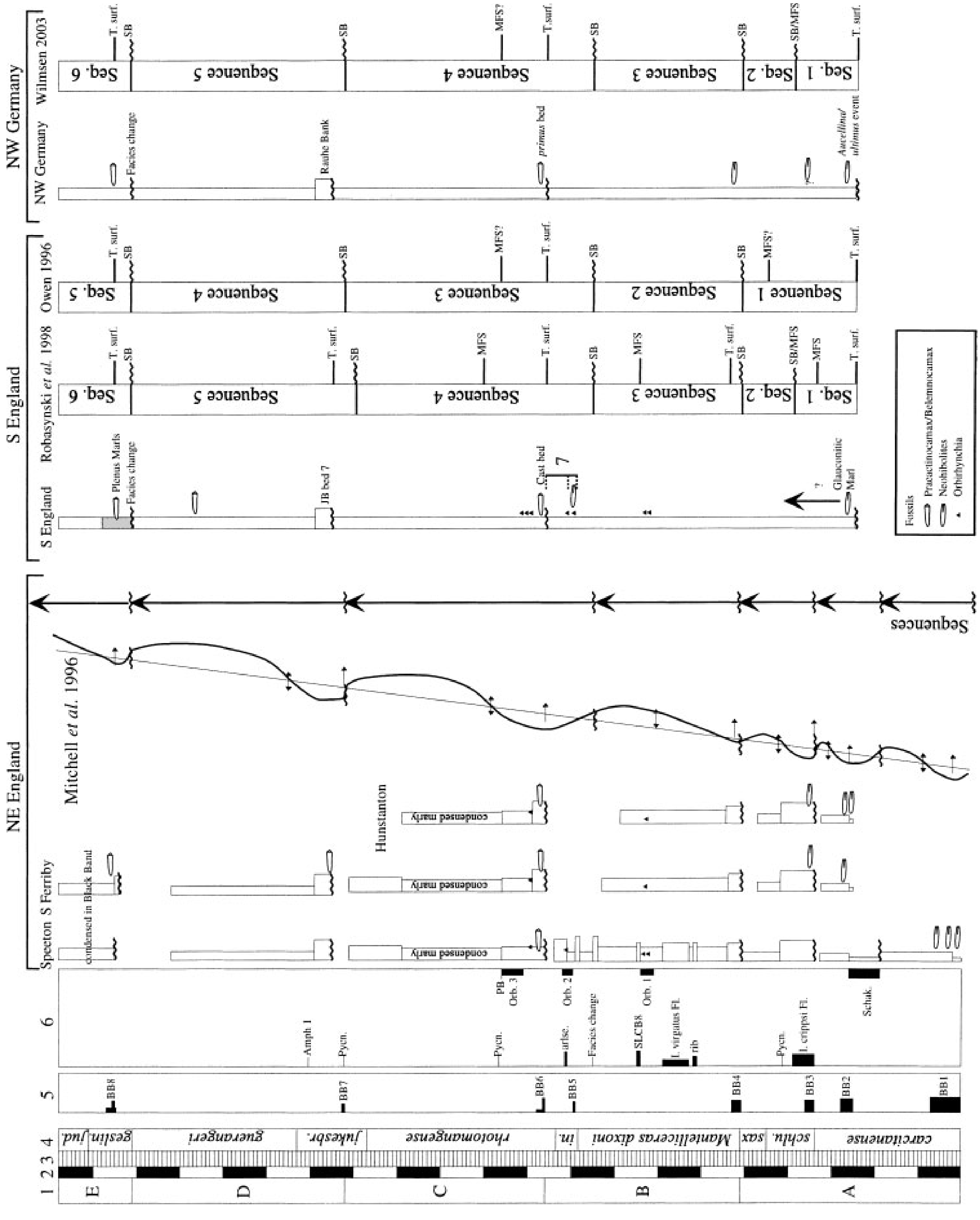

Figure 6. Distribution of belemnites in the Cenomanian of northwest Europe based on a Milankovitch cyclostratigraphy. Key: 1, couplet divisions; 2, groups of ten couplets; 3, individual couplets; 4, ammonite zones; 5, belemnite bioevents; 6, other bioevents; 7, flooding surfaces from Mitchell and Carr (1998); ellipses = belemnite occurrences; triangles = *Orbirhynchia* beds. Belemnite bioevents correlate well with sea-level curve derived from northeast England.

5.2. Praeactinocamax primus *and* Belemnocamax boweri

In northwest Germany a *primus* 'event' was recognized by Ernst *et al.* (1983) and the nominate belemnite recorded widely. However, the *primus* 'event' was not limited to the occurrence of the named belemnite, but extended through up to 8 m of chalks and marls of lower Middle Cenomanian age (e.g. Meyer 1990; Lehmann 1999). *Praeactinocamax primus* is much more restricted in its distribution and occurs in the '*primus* bed' (e.g. Meyer 1990; Christensen 1990; Christensen *et al*. 1992; Gale 1995; Wittler 1996; Lehmann and Wiedmann 1996; Mitchell *et al*. 1996; Lehmann 1999; Wilmsen 2003). *Belemnocamax boweri* is also reported from the '*primus* bed' (Christensen *et al*. 1992; Christensen 1993; Lehmann 1999). The '*primus* bed' was correlated with couplet C1 by Gale (1995), Mitchell *et al*. (1996) and Wilmsen (2003). This represents BB6 (*P. primus* horizon of northeast England).

5.3. Praeactinocamax plenus

Praeactinocamax plenus is very rare throughout much of northwest Germany and only a few detailed occurrences have been documented. Specimens from basin facies (Schmid 1965; Christensen *et al*. 1992) cannot be accurately placed within the stratigraphic succession. A limestone in the shallow water facies has commonly been called the Plenus Bank and a few recent records confirm the occurrence of *P. plenus* in this bed (see Lehmann 1999). The Plenus Bank is in the lower part of the δ^{13}C excursion at the Cenomanian–Turonian boundary (Lehmann 1999, figures 14, 16) and its distribution is therefore similar to that in southern England (i.e. BB8, *P. plenus* horizon of northeast England).

6. SEQUENCE STRATIGRAPHY OF THE CENOMANIAN

Jeans (1968, 1973, 1980) recognized five lithological cycles in the Cenomanian of NE England. These were best developed on the shallow-water East Midlands Shelf, but could also be traced into the adjacent basins. On the shelf, each cycle was represented by a lower unit of sand-grade chalk overlying a single or group of bored or burrowed erosion surfaces. The coarse-grained beds were overlain by micritic chalks. Jeans (1980) attributed the generation of the basal erosion surfaces to the shallowest water phase and the fining-upward cycles were attributed to an upward increase in water depth. These cycles were the basis of the sequence stratigraphic interpretation of Mitchell *et al*. (1996), with the sand-grade chalks on the East Midlands Shelf attributed to all or part of the transgressive systems tracts. At Speeton, an additional cycle is present across the Albian–Cenomanian boundary (Underwood and Mitchell 1999). Mitchell (1996) demonstrated how benthic foraminiferal assemblages could be used to constrain sea-level variations in the lower Middle Cenomanian. A detailed discussion of the sequence stratigraphy of the Cenomanian of northeast England is beyond the scope of this paper.

Sequence stratigraphic schemes have also been developed for the Cenomanian of the Anglo-Paris Basin and the Münster Basin (Owen 1996; Robaszynski *et al*. 1998; Wilmsen 2003; Figure 6 herein). The Cenomanian sequence stratigraphic schemes for the Anglo-Paris Basin of Owen (1996) and Robaszynski *et al*. (1998) are very similar for the interval from the base of the *Mantelliceras dixoni* Zone to the top of the Cenomanian, and agree with the sequences in northeast England (Jeans 1968, 1973, 1980; Mitchell *et al*. 1996). In the *Mantelliceras mantelli* Zone, however, Owen (1996) recognized only a single sequence (sequence boundary in the late Albian), whereas Robaszynski *et al*. (1998) recognized two sequences (sequence boundaries in the latest Albian and at the base of the *Mantelliceras saxbii* Subzone; see Gale (1995) for ammonite subzonal boundaries). In the Münster Basin, Owen (1996) recognized six sequences. His results were similar to those he reported from the Anglo-Paris Basin, except that an extra sequence boundary was placed at the base of the *primus* 'event' (i.e. low in the *A. rhotomagense* Zone). Wilmsen (2003) interpreted this 'extra' sequence boundary as a transgressive surface.

The sequence stratigraphic interpretations of the Cenomanian of northeast England, the Anglo-Paris Basin and the Münster Basin have much in common. The differences are largely restricted to the *M. mantelli* Zone. The *M. mantelli* Zone is developed in condensed facies in many parts of northwest Europe (Gale 1995; Gale *et al*. 1996), and this might explain the different interpretations. Herein, the scheme for northeast England is used, since this is the area where the best belemnite biohorizon record is preserved.

7. PALAEOBIOLOGY OF BELEMNITES

Christensen (1997b) discussed the distribution of *Praeactinocamax* in northwest Europe (his Central European Belemnite Province). He recognized two immigration events, *P. primus* in the earliest Middle Cenomanian and *P. plenus* in the middle late Cenomanian, which were associated with rapid sea-level rises and cool climatic phases (the so-called Primus and Plenus Cold Events). Christensen (1976) noted that adult and juvenile growth stages were preserved in shallow-water chalks (i.e. deeper shelf deposits), suggesting the presence of breeding populations. Yet in deeper-water basinal deposits, only rare adult growth stages were present, suggesting the lack of breeding populations and the death of stray adult animals. He therefore suggested that belemnites were largely restricted to shallow-water environments.

Belemnites are abundant fossils in the Jurassic and Lower Cretaceous of Great Britain, and their distribution is briefly discussed here in connection to the mode of life of belemnites. They are abundant in shelf mudstones (e.g. the Pleinsbachian Belemnite Marls of Dorset; the Toarcian Whitby Mudstone Formation of Yorkshire; the Callovian–Oxfordian Oxford Clay of Dorset, Wiltshire and Cambridgeshire; and the Lower Cretaceous Speeton Clay of Yorkshire) and sandstones (e.g. the Upper Toarcian Bridport Sands of Dorset; the Blea Wyke Sands of Yorkshire; and the Kellaways Sandstone of Wiltshire) (Phillips 1865–1909; Lang 1928; Doyle 1990, 1992b; Page and Doyle 1991; Swinnerton 1936–1955). They also occur commonly in condensed ironstone and carbonate facies (e.g. the Upper Toarcian Cotswold Cephalopod Bed of Gloucestershire; the mid-late Toarcian Raasay Ironstone of Raasay and Skye; and the Aalenian–Bajocian Inferior Oolite of Dorset and Somerset) (Phillips 1865–1909; Doyle 1990; Mitchell, unpublished research), which accumulated on shelves starved of clastic influx. These facies are commonly called cephalopod limestones because of the abundance of belemnites and ammonites.

In contrast, belemnites are rare or absent in organic-rich facies associated with oceanic anoxic events (OAEs). For instance, in the Whitby Mudstone Formation (northeast England), belemnite diversities range from six to 15 specie, yet during the lower Toarcian OAE, diversity fell to two species (Doyle 1990). Similarly, belemnites are rare or absent in shallow-water carbonate sand (skeletal and oolitic) and reef facies (Mitchell, unpublished research). Thus, belemnites are extremely rare in the oolitic and bioclastic carbonates of the Aalenian–Bathonian Inferior oolite of the Cotswolds, and in the oolitic sandstones and coral boundstones of the Oxfordian Corallian deposits of Dorset, Wiltshire and Yorkshire.

Consequently, the normal habitat for belemnites appears to have been the deeper area of the shelf (clays, sands and condensed facies). They were absent from shallow-water carbonate sand and reef facies, anoxic shale deposits associated with OAEs and deep-water basinal deposits. It is likely that the distribution of belemnites was controlled by their food preference or their reproduction strategies. The lack of belemnites in deep-water deposits (Christensen 1976) suggests that they did not feed on surface prey as in many modern pelagic squid. Belemnites possibly had an epi-nektonic lifestyle, catching benthic prey (maybe small crustaceans) in the same way as many cuttlefish do today.

8. CONTROLS ON THE DISTRIBUTION OF BELEMNITES IN THE CENOMANIAN

Belemnites occur at eight levels (belemnite biohorizons) within the Cenomanian of northern Europe. Within the limitations of correlation, it appears that many of these occurrences can be traced from region to region and that these biohorizons were isochronous across northwest Europe (Figure 6). Above the basal Cenomanian, there is no continuous belemnite record in northwest Europe and this indicates that the biohorizons must record short-lived influxes of belemnites from other regions. The belemnite biohorizons are represented by influxes of mesohibolitids in the Lower to lowermost Middle Cenomanian, but by appearances of belemnitellids in the mid-Middle to Upper Cenomanian. The different taxonomic composition of the belemnite biohorizons is particularly significant, since the mesohibolitids were a Tethyan group that had their main centre of evolution in southern Europe (Doyle 1992a; Mutterlose *et al*. 1983), whereas the belemnitellids were a Boreal group and had their centre of evolution within the Russian Platform (*Praeactinocamax*) or North Sea region (*Belemnocamax*) (Naidin 1964; Christensen 1976, 1997a).

The belemnite biohorizons are clearly related to the sequence stratigraphy of the Cenomanian of northwest Europe (Figure 6). Belemnite biohorizons occur within the transgressive systems tract (and locally the lowstand deposits) of the recognized sequences. In the following sections, the distribution of belemnites is considered in relation to the sequence stratigraphy, and the carbon and oxygen stable isotopes.

8.1. Sea-level fluctuations

Christensen (1976) and Gale and Christensen (1996) suggested that belemnitellid belemnites appeared in the Cenomanian at times of lowered sea level. So belemnites might, therefore, be expected to be preserved in the deposits of the lowstand systems tract.

Marginal facies of the Cenomanian are preserved in Devon (Owen 1996; Mortimore *et al*. 2001). Here, belemnites are either absent or occur (as far as it is possible to determine) at the same levels as they occur in the more basinal successions. There is, therefore, no evidence that belemnites simply migrated from the shelves into the basins during lowered sea levels; rather it is likely that belemnites migrated into both basins and shallows at specific levels. In the case of northeast England, belemnite biohorizons are better represented in the shallow-water sections on the East Midlands Shelf (South Ferriby and Hunstanton) than in the deeper-water Cleveland Basin (Speeton) (Figure 6), possibly reflecting the creation of ideal habitats close to these sites at these times. Belemnite occurrences in deeper water could be rare straying adults or dead specimens that floated in, prior to them sinking when their phragmocones became water-logged. Thus, belemnite biohorizons indicate that belemnites migrated only at specific intervals of time into northwest Europe and that they occupied sufficiently shallow-water habitats at these times.

In all cases, other than BB5, the belemnites are associated with the transgressive surfaces overlying the lowstand deposits (or sequence boundary where lowstand deposits are absent). Therefore, belemnites are associated with transgressive intervals, at a time when sea levels were still relatively low. Perhaps low sea levels created suitable migration routes (extensive suitable shelf regimes), while early transgressive intervals promoted current systems, allowing the dispersal of belemnites or their prey.

Belemnite biohorizon 5 occurs in the lowstand deposits of sequence 5. Mitchell and Carr (1998) argued for higher frequency sea-level cycles in the mid-Cenomanian at Folkestone. Their cycle 7 had belemnite biohorizon 5 at the base, cycle 8, the *arlesiensis* fauna (Paul *et al*. 1994; Gale 1995) at the base, and cycle 9, belemnite biohorizon 6 at the base. BB5, the *arlesiensis* bed fauna and BB6 can be attributed to higher frequency sea-level cycles in the Cenomanian (compare with Gale *et al*. 2002; Wilmsen 2003).

8.2. Carbon stable isotopes

Small positive carbon stable isotope excursions are now known to be commonly associated with the transgressive deposits of sequences in the Cenomanian (Paul *et al*. 1994, 1999; Mitchell *et al*. 1996; Jarvis *et al*. 2001; Figure 6 herein). Although both belemnite biohorizons and small $\delta^{13}C$ excursions occur within transgressive systems tracts, there is no one-to-one correspondence in their stratigraphic distribution. Therefore, both appear to be related to sea-level changes, but not necessarily in the same way.

A very large positive carbon stable isotope excursion is associated with the AOE at the Cenomanian–Turonian boundary event (CTBE) (e.g. Schlanger *et al.* 1987; Gale *et al.* 1993; Paul and Mitchell 1994; Mitchell *et al.* 1996; Paul *et al.* 1999). The OAE is recognized by the widespread deposition of laminated, organic-rich mudstones. Such mudstones were deposited in the Münster Basin, the Cleveland Basin and across much of the East Midlands Shelf. The apparent dislike of belemnites for these organic-rich sediments may explain the relative abundance of *P. plenus* in belemnite biohorizon 8 in the Anglo-Paris Basin where organic-rich deposits are lacking, compared to its extreme rarity at the same level in the Münster and Cleveland Basins, as well as on the East Midlands Shelf, where organic-rich sediments were deposited.

8.3. Oxygen stable isotopes and palaeotemperatues

Arkhangelsky (1916) first suggested that the distribution of the belemnite *Praeactinocamax* (then *Actinocamax*) might be temperature related. Jefferies (1963) placed *Praeactinocamax* (then *Actinocamax*), *Lyropecten arlesiensis* (Woods) and *Oxytoma seminudum* (Dames) into his 'cold Boreal fauna', and linked their appearance to a cold water influx in Plenus Marls beds 4 to 6. Gale and Christensen (1996) used the terms Primus and Plenus Cold Events for these intervals, suggesting that belemnites migrated towards the south because of cooling.

Many studies of oxygen isotope compositions of bulk chalks from the Cenomanian of northwest Europe have been published. I consider some of the critical intervals here, and how oxygen isotope palaeothermometry might relate to belemnite biohorizons. Jenkyns *et al.* (1994, figure 4) presented an oxygen stable isotope curve for the Cenomanian of Kent. Warm temperatures (relatively negative δ^{18}O values) occur in the Glauconitic Marl followed by cooler temperatures (less negative δ^{18}O values) in the Chalk Marl. Warmer values occur again throughout the Grey Chalk, followed by the warmest values of all associated with the Plenus Marls and Melbourne Rock. The apparent warming across the Chalk Marl/Grey Chalk boundary broadly corresponds to the PB[Q1] break where abundant planktic foraminifers appear (Carter and Hart 1977; Paul *et al.* 1994). The appearance of abundant planktic foraminifers, including the Tethyan genera *Praeglobotruncana* and *Rotalipora*, at the PB Break in the Anglo-Paris Basin and northeast England is most easily explained by warming. Abreu *et al.* (1998) suggested that this general warming trend represented a major cycle that began in the Aptian and ended with the warmest values around the Cenomanian–Turonian event. Q1

By reference to the Jenkyns *et al.* (1994) curve, the appearance of *Praeactinocamax* in the Plenus Marls would not be consistent with a cool water pulse (as maintained in Košták and Wiese 2002, p. 63), as this interval represents the warmest interval in the Cretaceous. However, the warm pulse in the Glauconitic Marl could be related to the appearance of *Neohibolites* of Tethyan affinity in belemnite biohorizon 2 of northeast England.

Paul *et al.* (1994) undertook a detailed study of the mid-Cenomanian interval in southern England. δ^{18}O curves were presented for Folkestone and Southerham together with the distribution of macrofossils including *Praeactinocamax primus*. Strong oscillations in δ^{18}O values occur between marls and limestones. This was originally interpreted as a palaeoceanographic signal with chalks formed as productivity events during elevated temperatures (Ditchfield and Marshall 1989). However, Mitchell *et al.* (1997) demonstrated that this was a diagenetic signal due to preferential cementation of the chalk beds creating more negative δ^{18}O values, due to precipitation of cements at elevated temperatures and/or with a significant meteoric input. The δ^{18}O values of successive marls show little change up-section. The levels with belemnites in the Middle Cenomanian (i.e. B39, C1) do not have significantly different values to those without. B39 is associated with the influx of a 'warm-water' Tethyan form (*N. ultimus*), whereas C1 is associated with the influx of 'cold-water' Boreal forms (*P. primus* and *B. boweri*). Because of the lack of difference in oxygen stable isotopes at these levels, there appears to be no obvious evidence that temperature variations controlled the distribution of belemnites in the Middle Cenomanian.

Detailed δ^{18}O curves have also been published for the Cenomanian–Turonian Boundary Event in southern England (e.g. Jarvis *et al.* 1988; Lamolda *et al.* 1994; Paul *et al.* 1999); summarized by Keller *et al.* 2001). The strong oscillation in δ^{18}O values between marls (less negative values) and chalks (more negative values) is particularly striking, and almost certainly represents a diagenetic signal (Paul *et al.* 1999). A broad trough towards relatively less negative δ^{18}O values is seen at Eastbourne (Plenus Marls beds 2 to 4) and Dover (Plenus Marls beds 4 to 5) in many curves. These are the thicker marly intervals; they certainly reflect a sampling bias for marls and, by comparison with the Middle Cenomanian results of Mitchell *et al.* (1997), may therefore preserve a less diagenetically modified signal. If just the marls are considered in more detailed curves (e.g. Paul *et al.* 1999, figure 4), no obvious cooling appears to be associated with the supposed 'Plenus Cold Event' (Plenus Marls beds 4 to 8). In view of the clear diagenetic overprinting of the oxygen isotope values of bulk carbonate samples from the chalks of northwest Europe, there is no evidence that the occurrence of *Praeactinocamax* in either BB6 or BB8 was related to a short-lived influx of cold water, particularly as the Plenus Marls represent the warmest interval in the Upper Cretaceous (Jenkyns *et al.* 1994; Abreu *et al.* 1998).

The results presented here, that oxygen stable isotopes do not correlate with the appearance of short pulses of warm or cold water cephalopod faunas, agree with studies on the Jurassic of Poland (Wierzbowski 2002). In Poland, Wierzbowski (2002) found no correlation between oxygen stable isotopes (which remained essentially uniform implying uniform temperatures) of skeletal calcite in belemnite and brachiopod shells, and the short-lived appearance of Tethyan ammonites. Rather than being temperature related, he suggested that the ammonite influxes might occur at times of increased water depth.

9. DISCUSSION

Belemnites clearly appear in the Cenomanian at intervals of changing sea level, specifically transgressive surfaces associated with the lower parts of transgressive systems tracts, and in one case at a transgresive surface within a lowstand systems tract. The appearance of different types of supposedly temperature-restricted belemnites (i.e. mesohibolitids in the Early to earliest Middle Cenomanian and belemnitellids above) at the same point in different depositional sequences requires some discussion. The control of global(?) sea-level fluctuations in the Cretaceous is highly controversial, with some authors in favour of glacial-eustatic control (e.g. Miller *et al.* 1999, 2003; Gale *et al.* 2002) and others against (e.g. Huber *et al.* 1995; Price 1999). Glacial-eustacy has been used to explain sea-level changes in the Cenomanian (e.g. Gale *et al.* 2002) and also to explain the presence of dropstones within the Plenus Marls (e.g. Jeans *et al.* 1991). If glacial-eustatic processes did control sea level in the Cenomanian, then rapid melting of the ice caps could explain cold-water pulses associated with the bases of transgressive systems tracts (e.g. the so-called Primus and Plenus Cold Events). Yet, all other transgressive surfaces at the bases of the transgressive systems tracts in the Lower Cenomanian are associated with the influx of mesohibolitids of southern (warm-water) affinity. Equally, dropstones are not produced solely by melting icebergs; they can form by other means, including release of animal gastroliths and debris dropped from the roots of floating plants (e.g. Bennett *et al.* 1996). Thus, dropstones, unless associated with other evidence of glaciation (such as diamictites), are not specifically indicative of glaciations or, therefore, cold-water fluxes. It is obvious that a detailed study of oxygen stable isotopes in unaltered skeletal calcite (e.g. brachiopods) across several Cenomanian belemnite biohorizons is urgently needed to determine if a palaeotemperature signal is recorded in these intervals.

It is entirely possible that the formation of belemnite biohorizons was controlled by other mechanisms. Belemnites clearly lived in shelf environments, and were largely absent from deep-water basins and shallow-water carbonate (bioclastic and oolitic) sands and reefs. The cosmopolitan distribution of belemnites in the Early Cretaceous was replaced by a bipolar distribution in the Late Cretaceous. This change in distribution pattern occurred during the Cenomanian. This is manifested in northwest Europe by a change from an *in situ* evolution of *Neohibolites* stock from the Aptian to lowermost Cenomanian, to the periodic development of belemnite biohorizons in the rest of the Cenomanian. It is likely that this expulsion of belemnites from the Tethyan Realm during the Cenomanian was caused by the evolution of other organisms, such as other coleoids, that were able to displace the belemnites from their niches. Thus, belemnites were probably forced into more restricted environments where they could out-compete their competitors. Maybe the environments that existed during the early part of the Cenomanian transgressive systems tract (possibly higher nutrient fluxes, e.g. Mitchell *et al.* 1996; Wilmsen 2003) provided the ideal environments for the spread of both Boreal- and Tethyan-derived belemnites.

Much has been suggested for a southward migration of the belemnitellid *Praeactinocamax* at the levels of BB6 and BB8. *Praeactinocamax* has been assumed to have had its evolutionary centre on the Russian Platform (Arkhangelsky 1916; Jefferies 1962, 1963; Christensen 1976, 1997b), and spread southwards to occupy environments in northwest Europe only during BB6 and BB8. The study by Gale *et al*. (1999) on sections at Mangyshlak in western Kazakhstan, indicates that *P. plenus* had a similarly restricted stratigraphic distribution (i.e. BB8) on this part of the Russian Platform as in northwest Europe. Therefore, rather than the Russian Platform being seen as the evolutionary centre for *Praeactinocamax*, it might simply record the same migration events as represented by BB6 and BB8 in northwest Europe. In all likelihood, *Praeactinocamax* evolved in a restricted area, maybe somewhere in the northern part of the North Sea, during the Late Albian/Early Cenomanian interval as a descendent from the *Neohibolites* stock. Subsequently, it was only able to extend its distribution when conditions were optimum; perhaps changing nutrient fluxes during transgressions produced a significant change in the trophic structure and composition of marine communities to allow migration. Initially, facing competition with *Neohibolites*, which was equally only able to migrate into northwest Europe from southern Europe at these times, it was unable to penetrate into the Central European Belemnite Province. Following the extinction (or southern restriction?) of *Neohibolites* in the early Middle Cenomanian, *Praeactinocamax* then occupied this niche during BB6 and BB8.

Belemnocamax has an even more restricted geographic range than *Praeactinocamax*, being restricted to northern Germany and northeast England. Its ancestor is unknown (Christensen 1997a, b), but it presumably also evolved in a restricted area of the North Sea, and spread into northeast England during BB6 and BB7, and into northern Germany during BB6.

10. CONCLUSIONS

Belemnites occur within eight narrow intervals in the Cenomanian of northwest Europe. Their distribution is consistent within the limits of cyclostratigraphic correlation. Belemnites do not have extended ranges as suggested by plotting occurrence against ammonite zonal schemes. Belemnites are associated with transgressive surfaces at the base or in the lower part of transgressive systems tracts, or, rarely, at transgressive surfaces in lowstand systems tracts.

There is no evidence that the distribution of belemnites in the Cenomanian correlates directly with either the δ^{13}C or δ^{18}O records. Although both belemnites and δ^{13}C excursions are associated with transgressive surfaces, there is no one-to-one correlation between these. Comparisons of the distribution of belemnites with various published δ^{18}O curves indicates no evidence that Boreal belemnites appeared during ‘cold intervals’, or that Tethyan belemnites appeared during ‘warm intervals’. Consequently, there is little evidence that temperature controlled the distribution of belemnites in the Cenomanian.

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