

Palaeobiogeography and migration in the Late Cretaceous belemnite family Belemnitellidae

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The Late Cretaceous belemnite family Belemnitellidae Pavlow, 1914, which includes nine genera and two subgenera, occurs only in the Northern Hemisphere, that is in the North European and North American palaeobiogeographical Provinces of the North Temperate Realm, in addition to the northern margin of the Tethyan Realm in Europe. The North European Province is subdivided into the Central European, Central Russian and Baltoscandian Subprovinces. The centre of origin and dispersal of the belemnitellids lay in the North European Province and all known genera and subgenera occur there. The belemnitellids immigrated intermittently into the Tethyan Realm (at least nine times) and the North American Province (at least six times). The majority of the species occurring in the Tethyan Realm are conspecific with those from the North European Province, whereas the species occurring in the North American Province are endemic, with a few exceptions. The endemic species probably evolved by allopatric speciation from initial migrants. More than a score migrations have been recognized within the subprovinces of the North European Province. The palaeogeographical distribution and migration patterns of the belemnitellids were to a certain extent controlled by eustatic sea-level changes, cool or warm climatic phases and competition, although the cause of several migration events cannot be satisfactorily explained at present.

Key words: Belemnitellidae, Late Cretaceous, palaeobiogeography, migration, Northern Hemisphere.

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Introduction

During the Cenomanian, the earliest stage of the Late Cretaceous, belemnites had a tripartite distribution. The family Belemnitellidae Pavlow, 1914 inhabited the North Temperate Realm (Boreal Realm of authors), the family Dimitobelidae Whitehouse, 1924 inhabited the South Temperate Realm (Austral Realm) and the family Belemnopseidae Naef, 1922 inhabited the Tethyan Realm. The latter family became extinct in the

STAGES	BELEMNITE ZONES, NW EUROPE	ZONAL BELEMNITES, BALTO-SCANDIA	ZONAL BELEMNITES, RUSSIAN PLATFORM
L MAA E	<i>Bln. kazimiroviensis</i>		<i>Bln. kazimiroviensis</i> (E)
	<i>Blt. junior</i>		<i>Blt. junior</i> (W)
E MAASTRICHT	<i>Bln. fastigata</i>		<i>Belemnella</i> <i>B. sumensis</i> <i>B. lanceolata</i> <i>B. licharewi</i>
	<i>Bln. cimbrica</i>		
	<i>Bln. sumensis</i>		
	<i>Bln. obtusa</i>		
	<i>Bln. pseudoobtusa</i>		
	<i>Bln. lanceolata</i>	<i>Bln. lanceolata</i>	
L LATE CAMPAN.	<i>Blt. minor</i> II		<i>Blt. langei</i> <i>B.l. najdini</i> <i>B.l. langei</i> <i>B.l. minor</i>
	<i>Blt. minor</i> I		
E LATE CAMPAN.	<i>Blt. woodi</i>	<i>Blt. mucronata</i>	<i>Blt. mucronata</i>
	<i>Blt. mucronata</i>	<i>Blt. balsvikensis</i> / <i>Blt. mucronata</i>	
L EARLY CAMPANIAN	<i>Gt. q. gracilis</i> / <i>Blt. mucronata</i>	<i>Blt. mammillatus</i> / <i>Blt. mucronata</i> / <i>Gt. q. scaniensis</i>	<i>Blt. mucronata</i> / <i>Gt. q. gracilis</i> / <i>Blt. mammillatus</i>
	<i>Gt. q. gracilis</i>		<i>Blt. alpha</i> / <i>Blt. praecursor</i> / <i>Gt. q. quadrata</i>
	<i>Gt. q. quadrata</i> U Lo		
	<i>Gt. granulataquadrata</i>	<i>Gt. granulataquadrata</i> / <i>Blt. alpha</i>	<i>Blt. praecursor</i> / <i>A. laevigatus</i> / <i>Gt. granulataquadrata</i> (<i>Pteria</i> -beds)
L SANTONIAN	<i>Gt. granulata</i> U Lo	<i>Gt. granulata</i>	<i>Blt. praecursor</i> / <i>Gt. granulata</i>
	<i>Gt. westfalica</i> <i>granulata</i>	<i>Gt. westfalica</i> <i>granulata</i> / <i>Blt. propinqua</i>	
	<i>Gt. westfalica</i> U Lo	<i>Gt. westfalica</i> / <i>Blt. propinqua</i> U Lo	<i>Blt. propinqua</i>
	<i>Goniatolithis</i> extremely rare	<i>Gc. lundgreni</i> / <i>Gt. praewestfalica</i>	<i>Gc. lundgreni vilicus</i>
L CONIAC	<i>Gt. praewestfalica</i>	<i>Gc. lundgreni</i>	<i>Gc. lundgreni</i>
M CONIAC			
L TURON			
M TURON			<i>P. plenus triangulus</i>
L CENOMANIAN	<i>P. plenus</i>	<i>P. plenus</i>	<i>P. plenus</i>
	<i>P. primus</i>	<i>P. primus</i>	<i>P. primus</i> (NE)
E CENOMANIAN	<i>N. ultimus</i>		<i>N. ultimus</i> (SW)

Stolley, 1911 appeared in the Aptian and became extinct in the early and middle Cenomanian, respectively (Combémourel *et al.* 1981).

The belemnitellids were stenothermal shelf dwellers, but it seems that the breeding, spawning, hatching, and, possibly for the females at least, dying grounds, were inner neritic, shallow water environments (Christensen 1976, 1997). The dimitobelids were also stenothermal shelf dwellers (Doyle & Howlett 1989). Since both the belemnitellids and dimitobelids were stenothermal shallow-water dwellers, deep and warm water in the Tethyan Realm may have acted as a physical barrier and precluded spread of these families.

Species of *Neohibolites* and *Parahibolites* migrated away from the Tethyan Realm into both the North Temperate and South Temperate Realms during Aptian to Cenomanian time (Stevens 1973; Doyle 1988, 1992; Doyle & Howlett 1989). In the Cenomanian they are recorded as far north as northwest Germany and southern and eastern England, where they may be locally abundant. The two genera have been recorded from deep marine and continental slope deposits, as well as inner neritic sediments, and the habitat of these genera may therefore have been surface oceanic, but they probably spent their breeding season inshore (Doyle & Howlett 1989). They were thus eurythermal, adapted to life in warm temperate as well as tropical waters.

Christensen (1997) discussed the taxonomy and evolutionary history of the Belemnitellidae and recognized nine genera and two subgenera: *Praeactinocamax* Naidin, 1964, *Actinocamax* Miller, 1823, *Belemnocamax* Crick, 1910, *Gonioteuthis* Bayle, 1878, *Belemnelloamax* Naidin, 1964, *Goniocamax* Naidin, 1964, *Belemnitella* d'Orbigny, 1840, *Belemnella* (*Belemnella*) Nowak, 1913, *Belemnella* (*Pachybelemnella*) Schulz, 1979, *Belemnella* (*Neobelemnella*) Naidin, 1975, and *Fusiteuthis* Kongiel, 1962 (Fig. 1). He provided diagnoses for the genera and subgenera, figured representative species of the genera, and reviewed previous classifications by Naidin (1964b) and Jeletzky (unpublished manuscript 1972 for the *Treatise on Invertebrate Palaeontology*). *Belemnella* (*Neobelemnella*), *Belemnocamax*, and *Fusiteuthis* are monotypic, but the latter is most likely a *nomen dubium* (Christensen 1997).

The belemnitellids are of fundamental importance in biostratigraphy and correlation in Europe, especially during the Coniacian to Maastrichtian stages, because they were common, widely distributed and their fossilization potential is high (Christensen 1990b). Twenty six belemnite zones have been established in northwest Europe and a little less on the Russian Platform (Fig. 2). Some of the northwest European zones have been subdivided recently (Christensen 1995, 1996, 1997; Christensen & Schulz 1997). The first occurrence of a zonal index belemnite in a specific area is due either to an evolutionary event or a migration event. It has been assumed that the Late Cretaceous belemnite zones have isochronous boundaries, but Christensen (1996) showed that some of the Maastrichtian zones have slightly or highly diachronous boundaries, reflecting migrations. Nielsen (1995: p. 56), referring to trilobites, noted that: 'It is well-known that although biostratigraphy ideally correlates the appearance and extinction of taxa, it very often instead mirrors faunal migrations relating to palaeoenvironmental changes...'. It is, consequently, of great importance for biostratigraphy and correlation to unravel the cause of the first occurrences of index belemnites in various areas.

The aim of this paper is to discuss the migration of the belemnitellids within the palaeobiogeographical framework of Christensen (1975, 1976, 1988, 1993b, 1997).

Palaeobiogeographical framework

Kauffman (1973) established a quantitative scheme for defining Cretaceous biogeographical units on the basis of bivalve molluscan genera and subgenera. He recognized the following units, in decreasing order: realms (>75% endemic genera), regions (50–75% endemic genera), provinces (25–50% endemic genera), subprovinces (10–25% endemic genera) and endemic centres (5–10% endemic genera). It is obvious that this quantitative approach cannot be applied to animal groups high in the food-chain, as for example belemnites. However, the major biogeographical units of Kauffman are applicable to the Late Cretaceous belemnites, and Christensen (1975, 1976, 1988, 1990b, 1993b, 1997) recognized realms, provinces and subprovinces.

The North Temperate Realm comprises the North American and North European Provinces, and the latter includes the Central European, Central Russian and Baltoscandian Subprovinces. Christensen (1997) showed that the centre of evolution and dispersal of the belemnite families lay in the North European Province for the following reasons: (1) they are common and all known genera and subgenera occur there; (2) the earliest belemnite, *Praeactinocamax primus* (Arkhangelsky, 1912), appeared in the early Cenomanian, some way above the base of the substage, in this province; (3) the earliest species of the younger genera occurred either only there or appeared earlier there than elsewhere (Table 1). He also showed that the genera *Praeactinocamax* and *Belemnitella* are more widely distributed than the remaining genera, because they occur in both the North European and North American Provinces, in addition to the northern margin of the Tethyan Realm in Europe. He ranked the genera in the following way with respect to their palaeogeographical distribution, from the largest to the smallest areal extent (Table 1): (1) *Praeactinocamax* and *Belemnitella*; (2) *Gonioteuthis*, *Belemnelloamax* and *Belemnella*; (3) *Actinocamax*; (4) *Goniocamax*; and (5) *Belemnocamax*.

The Central European and Central Russian Subprovinces of Christensen (1975) are well-defined from the middle Coniacian to the boundary between the early and late Campanian, that is a period around 6–7 Ma (Mega annum = 10^6 years), and are characterized by independently evolving belemnite lineages. The *Gonioteuthis* stock inhabited the Central European Subprovince and the *Goniocamax*–*Belemnitella* stock inhabited the Central Russian Subprovince (Christensen 1975, 1976, 1988, 1990b, 1993c, 1997; Christensen & Schulz 1997).

The belemnite faunas of Baltoscandia show affinity to those of the Central Russian Subprovince at certain times, and to those of the Central European Subprovince at other times, as will be shown below. However, in the early Coniacian and latest early Campanian–early late Campanian the belemnite faunas of Baltoscandia are so distinct that it seems appropriate to regard them as belonging to a specific subprovince, which was called the Baltoscandian Subprovince by Christensen (1997). This subprovince is characterized by the species *Goniocamax lundgreni* (Stolley, 1897) in the early Coniacian and the genus *Belemnelloamax* in the latest early Campanian and early late Campanian.

At other times during the Late Cretaceous the subprovinces are less distinct and no subprovinces are recognized in the middle and late late Campanian and Maastrichtian.

Table 1. The occurrence of belemnitellid genera and subgenera in the North European and North American Provinces of the North Temperate Realm and the Tethyan Realm (after Christensen 1997). *Fusiteuthis* is most likely a *nomen dubium*. The genera and subgenera are ranked with respect to their palaeobiogeographical distribution. Nine genera and two subgenera occur in the North European Province, five genera and two subgenera in the Tethyan Realm and essentially two genera in the North American Province. The numbers 1–12 refer to the first appearances of the genera and subgenera in the various palaeobiogeographical units. Detailed data are not available for the subgenera of *Belemnella*. Abbreviations: 1 – early Cenomanian, 2 – late Cenomanian, 3 – middle Turonian, 4 – early Santonian, 5 – latest Santonian, 6 – latest Santonian–earliest Campanian, 7 – middle Coniacian, 8 – early Campanian, 9 – early Santonian, 10 – late Santonian, 11 – early Turonian, 12 – latest Santonian–earliest Campanian.

Genera and subgenera	North European Province	Tethyan Realm	North American Province
<i>Praeactinocamax</i>	+ ¹	+ ²	+ ³
<i>Belemnitella</i>	+ ⁴	+ ⁵	+ ⁶
<i>Belemnella</i> (<i>Belemnella</i>)	+	+	
<i>Belemnella</i> (<i>Pachybelemnella</i>)	+	+	
<i>Belemnella</i> (<i>Neobelemnella</i>)	+	+	
<i>Goniotеuthis</i>	+ ⁷	+ ⁸	
<i>Belemnelloamax</i>	+ ⁹	+ ¹⁰	
<i>Actinocamax</i>	+ ¹¹		(+) ¹²
<i>Gonicamax</i>	+		
<i>Belemnocamax</i>	+		
<i>Fusiteuthis</i>	+		

The middle Coniacian–middle early Campanian belemnite faunas of Baltoscandia are of great importance, because they include species of both the *Goniotеuthis* and *Gonicamax*–*Belemnitella* stocks, and thus provide a basis for correlation between the two subprovinces (Fig. 2).

England belongs to the Central European Subprovince as defined on belemnites, because the genus *Goniotеuthis* predominates in the Santonian and early Campanian. However, two loosely defined faunal provinces have been recognized in England (Wright & Wright 1951; Peake & Hancock 1961; Reid 1971, 1976; Wood & Smith 1978; Mortimore 1983; Mortimore & Wood 1986; Whitham 1993). The northern province includes Yorkshire, Lincolnshire and the northern part of Norfolk, and it shows faunal affinity to northern Germany and Poland. The southern province comprises Kent, Surrey, Sussex, Hampshire, Wiltshire and Dorset in southern England and belongs to the Anglo-Paris Basin. The two provinces are separated by the ‘transitional province’, which comprises the Chiltern Hills and East Anglia as far north as central Norfolk. The middle Cenomanian *Belemnocamax boweri* Crick, 1910 is recorded only from the northern province (Christensen 1993c), and Santonian and early Campanian species of *Goniotеuthis* are more common in the northern province than in the southern province (Mitchell 1994, 1995). *Goniotеuthis* is very common in the lower Campanian

near Ipswich in the 'transitional province' and also in northern Norfolk in the southern part of the northern province.

During the Late Cretaceous the belemnitellids immigrated intermittently into the North American Province and the northern European part of the Tethyan Realm. They migrated also within the subprovinces of the North European Province.

North European Province

This province extends from Ireland in the west to the Ural Mountains and beyond in the east (Fig. 3). In addition to the belemnitellids, Cenomanian species of the belemnopseid genera *Neohibolites* and *Parahibolites* are also known to occur there.

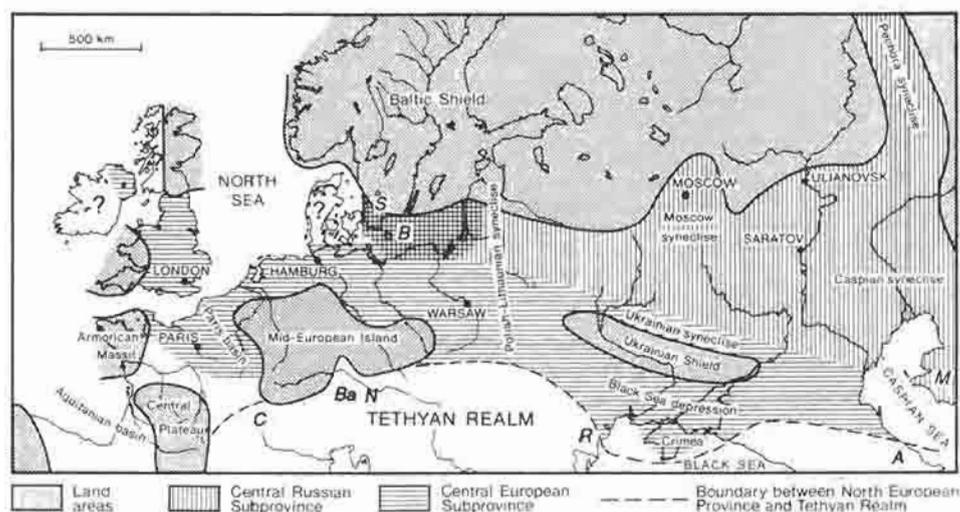


Fig. 3. Map showing the Central European and Central Russian Subprovinces of the North European palaeobiogeographical Province, as defined by the *Goniotentis* and *Goniocamax-Belemnitella* stocks, respectively (modified from Christensen 1976). The Baltoscandian Subprovince (indicated by crosshatching) is distinguished by *Goniocamax lundgreni* in the early Coniacian and the genus *Belemnelloamax* in the latest early and early late Campanian. Late Cretaceous land and sea areas represent maximum inundation for all stages. The boundaries are not reliable in detail and the biogeographic units are typically gradational in character. Abbreviations: A – Azerbaijan in the Caucasus, B – the island of Bornholm in the Baltic Sea, Ba – Bavaria in southern Germany, C – Chartreuse in the Subalpine Chain in France, M – Mangyshlak in Kazakhstan, N – Northern Calcareous Alps in Austria, R – Romania, S – Scania in southern Sweden. The Vocontian Basin in southeast France and the Corbières in the eastern part of the French Pyrénées are situated south of the map.

Cenomanian

The Cenomanian belemnite fauna of northwest Europe is diverse and includes four genera and five species: the belemnitellids *Praeactinocamax primus*, *P. plenus* (Blainville, 1825–1827) and *Belemnocamax boweri*, in addition to the belemnopseids *Neohibolites ultimus* (d'Orbigny, 1845) and 'cf. *Parahibolites tourtiaei*' (Weigner, 1909) (Christensen 1990a, 1993c; Christensen *et al.* 1992; Christensen, Juignet *et al.* 1993)

A1-51, B1-45, C1-46, D1-49 and E1-17 and provided an integrated stratigraphy for the Cenomanian, comprising ammonite, inoceramid and planktic foraminiferan biostratigraphy, sequence stratigraphy and cyclostratigraphy. Couplet C1 was deposited during the beginning of a transgression (TST = transgressive systems tract) following an eustatic sea-level lowstand (LST), some distance above a sequence boundary (Gale 1990; Paul *et al.* 1994; Mitchell *et al.* 1996). *Praeactinocamax primus* is accompanied by a pulse fauna of small bivalves, which consists of species that are identical or closely similar to species of Jefferies' (1962) North Boreal faunal group from beds 4-6 of the late Cenomanian Plenus Marls of the Anglo-Paris Basin. He interpreted these as migrants from the north and east, indicative of a cool climatic phase, which was called the Plenus Cold Event by Gale & Christensen (1996). The cool climatic phase in the early middle Cenomanian is here called the Primus Cold Event. The duration of this event was very short and less than 21 ky. Thus, *P. primus* abruptly invaded the Central European Subprovince coincidentally with a rapid rise of sea-level and a cool climatic phase in the early middle Cenomanian.

Christensen (1990a) described a little less than 100 specimens of *Praeactinocamax primus* from the *primus* bed of the Wunstorf pit near Hannover in northwest Germany, which equates with couplet C1 of the Anglo-Paris Basin (Gale 1995; Mitchell *et al.* 1996). This large number of specimens may falsely indicate that *P. primus* occurs commonly there compared with its occurrence in C1 couplets elsewhere. This is not the case, however, but relates to the facts that many private collectors have collected there for several years and the comparatively good exposure of the bed in question. The sample of *P. primus* from Wunstorf contains all growth stages. Christensen *et al.* (1992) recorded a juvenile specimen from the Münsterland Basin and I have seen another juvenile specimen from couplet C1 at Abbot's Cliff between Dover and Folkestone, southern England. It therefore seems that *P. primus* bred and spawned everywhere in the Central European Subprovince.

The stratigraphical ranges of *Neohibolites ultimus* and *Praeactinocamax primus* overlap, but, according to my knowledge, they have never been recorded from the same bed in the Central European Subprovince. The two species occur in the early middle Cenomanian of southern England, but *P. primus* occurs at a slightly higher stratigraphical level, i.e. couplet C1, than *N. ultimus*, which is from known only one specimen from the earliest middle Cenomanian (Christensen *et al.* 1992).

Praeactinocamax primus is followed upwards by *Praeactinocamax plenus* and the two species form an evolutionary lineage (Christensen 1974, 1990a). *P. plenus* is recorded from the middle Cenomanian to the earliest early Turonian on the Russian Platform (Naidin 1981). It occurs mainly in Beds 4-6 of the Plenus Marls of the Anglo-Paris Basin (Jefferies 1962, 1963) but a single specimen has also been found in Bed 8 (Gale & Christensen 1996). The Plenus Marls are of middle late Cenomanian age, *Metoicoceras geslinianum* Zone. *P. plenus* occurs also in the *geslinianum* Zone of northwest Germany (Christensen 1990a). Wood & Mortimore (1995) and Gale (1995) noted that it occurs in the top unit of the tripartite Plenus Bed in the Lower Saxony Basin, where it is an extreme rarity. This unit is inferred to correlate with Jefferies' Bed 4 of the Plenus Marls. *P. plenus* also occurs in the Plenus Bed in the Münsterland Basin. Marcinowski (1972) recorded *P. primus* and *P. plenus* from the late Cenomanian conglomerates at Glanów in the Polish Jura Chain. Christensen (1990a) suggested,

however, that the specimen referred to as *P. primus* by Marcinowski was either reworked or, more likely, a slender specimen of *P. plenus*.

Praeactinocamax plenus has thus a very limited stratigraphical distribution in northwest Europe, because the duration of the *M. geslinianum* Zone was estimated to be about 110 ky (Gale 1990). Beds 4–6 of the Plenus Marls or its correlatives were deposited during a significant fall of sea temperature, the Plenus Cold Event (see above), coincidentally with the beginning of a transgression (TST), following an eustatic sea-level lowstand, slightly above a major sequence boundary (Gale 1990, 1995; Mitchell *et al.* 1996). Thus, *P. plenus* invaded northwest Europe in the middle late Cenomanian during a cool climatic phase and a rapid rise of sea-level. In addition, lack of competition of the Tethyan belemnopseids, which became extinct in the middle Cenomanian may also have been of significance for this southwards migration. *P. plenus* even locally invaded the northern margin of the Tethyan Realm (see later discussion).

The very small and anomalous-looking *Belemnocamax boweri* has a very limited stratigraphical and geographical distribution. It occurs in the early middle Cenomanian, basal part of the *Turrilites costatus* Subzone, of the Lower Saxony and Münsterland Basins in northwest Germany, in addition to the Cleveland Basin and at Hunstanton, Norfolk, in eastern England (Christensen 1993c). *B. boweri* co-occurs with *Praeactinocamax primus* in the early middle Cenomanian. The highest record of *B. boweri* is from the base of the Nettleton Stone at South Ferriby in east England (Christensen *et al.* 1992), which is of late middle Cenomanian age, *Acanthoceras jukesbrownei* Zone (Mitchell *et al.* 1996).

Discussion. — *Belemnocamax boweri* and the last species of *Neohibolites* became extinct in the middle Cenomanian, and *Praeactinocamax plenus* of the *primus*–*plenus* lineage disappeared in the late Cenomanian in northwest Europe and in the earliest early Turonian on the Russian Platform (Fig. 4). This belemnite extinction, which lasted about 2.5 Ma, may be part of the well-known, global middle Cenomanian–early Turonian mass extinction, which was discussed at length by Kauffman & Hart (1996) and summarized by Barnes *et al.* (1996). It is associated with a near-peak Mesozoic eustatic sea-level highstand, a global warming peak, greenhouse climate reflecting elevated CO₂ and Oceanic Anoxic Event II. It is, however, difficult to imagine exactly which of these factors were responsible for the world-wide extinction of the eurythermal, surface oceanic belemnopseids and the extinction of some stenothermal, shelf dwelling belemnitellids in Europe.

Turonian–early Coniacian

Central European Subprovince. — After the belemnite extinction around the Cenomanian–Turonian boundary, belemnitellids are very rare or absent in the Turonian and Coniacian of the Central European Subprovince. They occur very rarely in England, Germany, the Czech Republic and southern Sweden and are not recorded from Northern Ireland, France, Poland and the Crimea. Neither are belemnites reported from the early Santonian of the Crimea (Naidin 1973) and Poland (Cieślowski 1963).

The small fauna from the Central European Subprovince and Baltoscandia, consisting of a little more than a dozen specimens, was revised by Christensen (1982), who recognized the following species: *Praeactinocamax bohemicus* (Stolley, 1916), *P. paderbornensis* (Schlüter, 1894), *P. strehlensis* (Fritsch & Schlönbach, 1872), and *Goniocamax esseniensis* (Christensen, 1982) (Fig. 4). The lectotype and paralectotype of the late Turonian *P. strehlensis* came from the Pläner limestone of Strehlen near Dresden. Christensen recorded five specimens of *P. bohemicus*: (1) the holotype which came from the Pläner limestone near Kostic in the Czech Republic; it is of late Turonian age; (2) two specimens from the Pläner limestone at Strehlen; these are of late Turonian age; (3) one specimen from the middle Coniacian of Yorkshire in England; and (4) one specimen of supposedly late Turonian age from Särödal in southern Sweden. Three granulated belemnite apical fragments of supposedly late Turonian age, from Särödal, were tentatively assigned to *P. bohemicus* by Christensen (1982). The holotype, by monotypy, of *P. paderbornensis*, from the Münsterland Basin, is of late early Coniacian age (Kaplan & Kennedy 1994). The holotype, by monotypy, of *G. esseniensis*, from the Münsterland Basin, is of early, but not earliest, early Coniacian age (Kaplan & Kennedy 1994).

Košťák (1996) described six specimens, including the holotype, of the late Turonian *Praeactinocamax bohemicus*, one specimen of the late Turonian *P. aff. bohemicus* and two specimens of *Goniocamax lundgreni* of late early Coniacian age from the Bohemian Basin in the Czech Republic.

The three species of *Praeactinocamax*, *P. bohemicus*, *P. paderbornensis* and *P. strehlensis*, differ from contemporaneous species of this genus from the Central Russian Subprovince and the North American Province (see below) and their origin is unknown (Christensen 1982). In contrast, the early Coniacian *Goniocamax esseniensis* is very closely allied to and may be conspecific with *G. lundgreni* (Christensen & Schulz 1997). The holotype of *G. esseniensis* is adult and may be regarded as an occasional migrant from the Baltoscandian Subprovince, as may the two specimens of *G. lundgreni* from the Bohemian Basin.

Central Russian Subprovince. — During Turonian and early Coniacian time belemnites are more common in the Central Russian Subprovince than in the Central European Subprovince, but they have a very limited area of distribution, occurring almost exclusively in the Volga district (Naidin 1981). The following species are recorded: *Praeactinocamax intermedius* (Arkhangelsky, 1912), *P. coronatus* (Makhlin, 1965), *P. planus* (Makhlin, 1965), *P. medwedivicus* (Naidin, 1964) and *P. matesovae* (Naidin, 1964), in addition to various subspecies of *Actinocamax verus* Miller, 1823 (Naidin 1964b; Makhlin 1965) (Fig. 4). However, only *P. intermedius* occurs commonly there. *P. plenus triangulus* Naidin, 1964 is used as an index species for the early early Turonian of the Central Russian Subprovince (Naidin 1981) (Fig. 2), but Christensen (1974) placed this subspecies in synonymy with the nominotypical subspecies.

Baltoscandia. — As shown above, Turonian belemnites are very rare in Baltoscandia, but it should be borne in mind that Turonian rocks have been recorded only from one outcrop in this area, the temporary exposure at Särödal on the Swedish west coast (Bergström *et al.* 1973). Since *Praeactinocamax bohemicus* occurs at this locality it seems that Baltoscandia was part of the Central European Subprovince in the Turonian.

Goniocamax lundgreni appeared at the base of the Coniacian of Bornholm and persisted into the early Santonian (Christensen & Schulz 1997) (Figs 4, 5). The early Coniacian of Baltoscandia is characterized by *G. lundgreni*, although it is rare. Christensen & Schulz (1997) recorded only about 60 specimens from the early Coniacian of Bornholm and these were collected over a period of about 100 years.

Actinocamax verus antefragilis Naidin, 1964 is early Turonian in age on the Russian Platform. Christensen & Schulz (1997) recorded two specimens of *A. verus* cf. *antefragilis* from the late early and middle Coniacian of Bornholm (Fig. 4). These were considered as stray specimens from an unknown area, where the subspecies survived from the early Turonian to the early early Coniacian.

One may get the impression that the belemnite species diversity is high in the Turonian and early Coniacian (Fig. 4). Christensen (1982: p. 77) noted, however, that some of the species of *Praeactinocamax* are distinguished on the basis of minor differences and may eventually prove to be in part conspecific. More material is necessary in order to solve this problem.

Middle Coniacian–early Campanian

During this period, which lasted about 6–7 Ma, the Central European Subprovince was characterized by the *Goniot euthis* lineage, whilst the Central Russian Subprovince was characterized by the *Goniocamax–Belemnitella* lineage. The middle Coniacian–middle early Campanian belemnite faunas of Baltoscandia include species of both the *Goniot euthis* and *Goniocamax–Belemnitella* stocks. *Belemnelloccamax* ex gr. *grossouvrei* (Janet, 1891) and *Actinocamax verus verus* are widely distributed in the Santonian and early Campanian of the North European Province. The first is very rare, and the latter is common.

Central European Subprovince.—The *Goniot euthis* lineage includes seven species and subspecies, in ascending order: *G. praewestfalica* Ernst & Schulz, 1974, *G. westfalica* (Schlüter, 1874), *G. westfalica granolata* (Stolley, 1897), *G. granolata* (Blainville, 1827), *G. granolata quadrata* (Stolley, 1897), *G. quadrata quadrata* (Blainville, 1827), and *G. quadrata gracilis* (Stolley, 1892) (Fig. 4).

The earliest member of this lineage is very rare. *Goniot euthis praewestfalica* occurs very rarely in the late middle and late Coniacian of Lägerdorf near Hamburg, northwest Germany (Ernst & Schulz 1974). A single specimen was recorded from the late Coniacian of Kent, southern England by Christensen (1991) and another specimen of supposedly late Coniacian age was reported from Helgoland by Wood & Schmid (1991). Kaplan & Kennedy (1994) recorded two specimens of late Coniacian age from Augustdorf and Paderborn–Elsen, respectively, in the Münsterland Basin. A single specimen has been collected from the late Coniacian chalk of northern France (C.J. Wood personal communication August 1997). The specimens of *G. praewestfalica* from Kent and northern France may be regarded as a stray specimens.

The early and middle Santonian belemnite fauna of southern England is diverse and includes species from both the Central European Subprovince, *Goniot euthis westfalica* and *G. westfalica granolata*, and the Central Russian Subprovince, *Goniocamax lundgreni* and *Belemnitella propinqua* (Moberg, 1885), in addition to the widespread *Belemnelloccamax* ex gr. *grossouvrei* and *Actinocamax verus verus* (Christensen 1991).

G. lundgreni, *B. propinqua*, and *B. ex gr. grossouvrei* are extremely rare, as is *G. lundgreni* in the early Santonian of the Münsterland Basin (Ernst 1964a; Christensen 1973, 1991). The specimens of *G. lundgreni* and *B. propinqua* from northwest Germany and southern England may be regarded as occasional migrants from the north.

The late Santonian belemnite faunas of the Central European Subprovince include *Goniot euthis granulata*, in addition to the widespread *Belemnello camax ex gr. grossouvrei* and *Actinocamax verus*. In contrast, the early and middle early Campanian faunas comprise species of *Goniot euthis* with subordinate species of *Belemnitella*, *A. verus* and *B. ex gr. grossouvrei*.

Mixed *Goniot euthis/Belemnitella* assemblages occur at three distinct horizons in the early Campanian of the Central European Subprovince and Baltoscandia, that is in earliest, middle and latest early Campanian time. In Scania, northern Germany and northeast Belgium, the two genera co-occur in the earliest early Campanian: *G. granulata quadrata* and *B. alpha* Naidin, 1964 in Scania (Christensen 1975, 1986, 1991); *G. granulata quadrata* and *B. praecursor* Stolley, 1897 at Braunschweig (Ernst 1964b, 1968; Christensen 1991); *G. q. quadrata*, *B. alpha*, '*B. aff. mucronata/praecursor*' or '*B. aff. senior/praecursor*' in the Bottrop Marl in the southwestern corner of the Münsterland Basin (Ernst 1964b; Christensen 1986, 1991); *G. granulata quadrata*, *G. q. quadrata* and *B. praecursor* in the Stromberg beds in the eastern part of the Münsterland Basin (Kaplan *et al.* 1996); and *G. q. quadrata* and *B. praecursor* at Hallembaye in northeast Belgium (Christensen & Schmid 1987; Christensen 1991).

The next mixed assemblages above consist of *Goniot euthis q. quadrata* and *Belemnitella praecursor* and occur in Northern Ireland (Fletcher & Wood 1978), Norfolk and Suffolk in eastern England, as well as in southern England (Christensen 1991) and northern France (Jarvis 1980). These are middle early Campanian in age, that is the traditional *Hagenowia blackmorei* Horizon of England, which equates with the German *Offaster pilula/Galeola senonensis* Zone and the lower part of the *G. senonensis* Zone (Christensen 1991). A single specimen of *B. praecursor* was recorded from the middle early Campanian *G. senonensis* Zone of Lägerdorf by Christensen & Schmid (1987).

The highest mixed assemblages, consisting of *Goniot euthis quadrata/Belemnitella mucronata* are latest early Campanian in age. At Lägerdorf near Hamburg and Misburg-Höver near Hannover in northwest Germany *G. quadrata gracilis* and *B. mucronata* (Schlotheim, 1813) occur in the so-called Overlap Zone of Schmid (1953), which equates with the *gracilis-mucronata* Zone of Ernst (1963a, 1963b). The assemblage comprises *G. quadrata scaniensis* Christensen, 1975 and *B. mucronata* in Scania (Christensen 1975, 1986). Mixed assemblages of this age occur also in England, Poland and the Subhercynian Cretaceous Basin.

Thus, it can be concluded that *Belemnitella alpha* invaded Baltoscandia and the Central European Subprovince in the earliest early Campanian. *B. praecursor* entered the Central European Subprovince twice in the early Campanian, in the earliest and middle early Campanian. *B. mucronata* immigrated into Baltoscandia and the Central European Subprovinces in the latest early Campanian.

The populations of *Belemnitella alpha* from Scania (Christensen 1986) and of *B. praecursor* from the early early Campanian *Inoceramus lingua/Goniot euthis quadrata* Zone of northeast Belgium (Christensen & Schmid 1987) and the middle early

Campanian of East Harnham in southern England (Christensen 1991) include all growth stages, indicating that these species bred there. On the contrary, populations of *B. praecursor* from Stiffkey in Norfolk and from Porchester and Shawford in southern England (Christensen 1991), as well as from localities in northern France (Christensen unpublished), consist only of adults, which may be considered as stray specimens. The populations of *B. mucronata* from the latest early Campanian of Scania and northwest Germany comprise all growth stages (Christensen 1975, 1986, 1995), implying that it bred there.

Belemnitella praecursor is more common at Hallembaye than elsewhere in the Central European Subprovince. Christensen & Schmid (1987) estimated that it accounts for about 40% of the belemnite fauna there. In contrast, *B. praecursor* comprises only 3–4% of the belemnite fauna from the middle early Campanian phosphatic chalk of Hardivillers and Ribemont in northern France (Jarvis 1980). Jarvis (1980) noted that *Actinocamax verus* does not occur in the phosphatic chalk and suggested that it was ousted by *Goniotoothis*. However, this suggestion is incorrect, because *Actinocamax* became extinct slightly earlier.

Central Russian Subprovince. — This subprovince is characterized by the *Goniotoothis*–*Belemnitella* lineage, which includes, in ascending order: *G. lundgreni*, *B. schmidi* Christensen & Schulz, 1997, *B. propinqua*, *B. praecursor*, *B. alpha*, and *B. mucronata* (Fig. 4).

As mentioned above, *G. lundgreni* appeared at the base of the Coniacian in the Baltoscandian Subprovince. It entered the Central Russian Subprovince in the middle Coniacian (Naidin 1964b).

Goniotoothis has not been recorded in this subprovince east of the Ukrainian Syneclise, with the exception of the doubtful reports of *G. prae-westfalica* and *G. ?prae-westfalica* from the Coniacian of Mangyshlak, Kazakhstan (Marcinowski *et al.* 1996). I suspect, however, that the specimens of these taxa should be placed in *Praeactinocamax aralensis* (Arkhangelsky, 1912) and/or *P. mujnakensis* (Naidin, 1964), two species occurring in the middle and late Coniacian of the Muinak Peninsula on the Aral Sea (Naidin 1964b). These species were considered as subspecies of *Goniotoothis* (*Goniotoothis* *westfalica*) by Naidin (1964b) and Makhlin (1965), but they were placed in *Praeactinocamax* by Christensen (1997), who noted, however, that they may be transitional forms between *Praeactinocamax* and *Goniotoothis*.

Naidin (1964a) recorded *Belemnitella praecursor* from the late Santonian of the Central Russian Subprovince and it thus appeared earlier there than in the Central European Subprovince. As discussed later, it entered the Tethyan Realm in the late Santonian.

Baltoscandia. — The middle and late Coniacian belemnite fauna of Bornholm includes *Goniotoothis lundgreni* with subordinate *G. birkelundae* Christensen & Schulz, 1997 (only known from Bornholm) and *Actinocamax verus* cf. *antefragilis* (see above) (Fig. 5). In the late Coniacian *G. lundgreni* accounts for about 95% of the belemnite fauna. *G. birkelundae* is closely allied to *G. lundgreni* and probably evolved from that species by allopatric speciation elsewhere; it immigrated later to Bornholm.

The early Santonian belemnite fauna of Bornholm is extraordinarily diverse and Christensen & Schulz (1997) recorded four genera and nine species: *Actinocamax*

STAGES	Ernst & Schulz (1974) Schulz <i>et al.</i> (1984) Schulz (1996)		Christensen & Schulz (1997)	
	Lägerdorf, NW Germany		Bornholm, Denmark	
	Faunal zones	<i>Gonoteuthis</i> Zones	Belemnite zones	Belemnite assemblage zones
M SANTONIAN	L <i>rogalae</i> / <i>westfalicagranulata</i>	<i>westfalicagranulata</i> (RI: 11.0-12.5)	not exposed	not exposed
	E <i>rogalae</i> / <i>westfalica</i>	<i>westfalica</i> (RI: 8.5-11.0)		
EARLY SANTONIAN	L <i>coranguinum</i> / <i>westfalica</i>	<i>westfalica</i> (RI < 8.5)	<i>Gonoteuthis</i> <i>westfalica</i> (RI < 8.5)	<i>Gt. westfalica</i> / <i>A. v. verus</i> / <i>Blt. propinqua</i> / <i>Gc. striatus</i> / <i>Gt. ernsti</i> / <i>Gt. westfalica</i> / <i>A. v. verus</i> / <i>Blt. propinqua</i> / <i>Gc. striatus</i>
	E <i>pachtii</i> / <i>undulotoplicatus</i>	<i>Gonoteuthis</i> extremely rare		<i>Gt. westfalica</i> / <i>Gc. lundgreni</i> / <i>Blt. propinqua</i>
CONIACIAN	L <i>bucaillii</i> / <i>praewestfalica</i>	<i>praewestfalica</i>	<i>Gonoteuthis</i> <i>praewestfalica</i>	<i>Gc. lundgreni</i> / <i>Gt. praewestfalica</i> / <i>Blt. propinqua</i>
	M <i>involutus</i> / <i>bucaillii</i>	no belemnites		<i>Gc. lundgreni</i> / <i>Gt. praewestfalica</i> / <i>Gc. birkelundae</i> / <i>Blt. schmidi</i>
	E <i>koeneni</i>	no belemnites		<i>Goniocamax lundgreni</i>
		not exposed		<i>Goniocamax lundgreni</i> <i>Goniocamax lundgreni</i> / <i>Actinocamax verus</i> cf. <i>antefragilis</i>
				<i>Goniocamax lundgreni</i>

Fig 5. Stratigraphical diagram, showing Coniacian–early Santonian belemnite zones and assemblage zones of Bornholm, in addition to middle Coniacian–middle Santonian faunal zones and *Gonoteuthis* Zones of Lägerdorf (modified from Christensen & Schulz 1997). Abbreviations: *A.* – *Actinocamax*, *Blt.* – *Belemnitella*, *Gc.* – *Goniocamax*, *Gt.* – *Gonoteuthis*, E – early, M – middle, L – late. RI is the Riedel Index of Ernst & Schulz (1974) indicating the depth of the pseudoalveolus as a percentage of the length of the guard. Full names of the non belemnite index-species are as follows: *Micraster rogalae*, *M. coranguinum*, *M. bucaillii*, *Sphenoceras pachtii*, *Cladoceras undulotoplicatus*, *Volviceras involutus*, *V. koeneni*. Vertical axis not to scale.

verus verus, *Gonoteuthis praewestfalica*, *G. westfalica*, *G. ernsti* Christensen & Schulz, 1997, *Goniocamax lundgreni lundgreni*, *G. birkelundae*, *G. striatus* Christensen & Schulz, 1997, *Belemnitella schmidi* and *B. propinqua* (Fig. 5). The genus *Belemnelloamax*, which occurs elsewhere in the early Santonian, is not recorded from Bornholm. It is in fact the only genus occurring in the early Santonian that does not occur on Bornholm.

Gonoteuthis praewestfalica is of early early Santonian age on Bornholm (Fig. 5), whereas it is of late middle and late Coniacian age in northwest Germany and of late Coniacian age in England and France (see above). It therefore spread northwards in the earliest Santonian. *G. westfalica* is, by and large, of late early Santonian age on Bornholm (Fig. 5). In the early early Santonian the genus *Gonoteuthis* is fairly common on Bornholm and extremely rare in northwest Germany. All growth stages of *G. praewestfalica* and *G. westfalica* occur on Bornholm, indicating that these taxa bred there. In contrast, the specimens of *G. praewestfalica* and *G. westfalica* from the chalk of Lägerdorf are adult.

Gonoteuthis ernsti occurs very rarely in the latest early Santonian of Bornholm and the Münsterland Basin in northwest Germany. It is a close ally of *G. westfalica* and may have evolved by allopatric speciation from this species elsewhere (Christensen & Schulz 1997). It later immigrated to Bornholm and the Münsterland Basin. The late early Santonian *Goniocamax striatus* is recorded only from Bornholm. It is closely allied to *G. birkelundae* and is considered as the lineal descendent of this species (Christensen & Schulz 1997). The earliest early Santonian *Belemnitella schmidi* occurs very rarely on Bornholm and in the Central Russian Subprovince. This species may have evolved from *Goniocamax lundgreni* by allopatric speciation in an unknown area; it later entered Bornholm and the Central Russian Subprovince (Christensen & Schulz 1997). *B. propinqua* is most likely the lineal descendent of *B. schmidi*.

Actinocamax verus verus appears in the early Coniacian of the Central Russian Subprovince (Naidin 1964b) (Fig. 4). On Bornholm it enters together with *Goniocamax striatus* in the latest early Santonian, above the extinction level of *Goniocamax lundgreni* and slightly later than *Gonoteuthis westfalica* (Fig. 5). *A. verus verus* appears also in the early Santonian of the Central European Subprovince. Thus, *A. verus verus* immigrated from the Central Russian Subprovince into the Central European Subprovince and Baltoscandia in early, but not earliest, Santonian time.

There is a major faunal turnover in the belemnite assemblages of Bornholm in the middle early Santonian (Christensen & Schulz 1997) (Fig. 5). Belemnite assemblages of middle Coniacian to early early Santonian age are characterized by *Goniocamax lundgreni*, which accounts for about 85–95% of the belemnite faunas, with subordinate *Actinocamax verus* cf. *antefragilis*, *Gonoteuthis praewestfalica*, *Goniocamax birkelundae*, *Belemnitella schmidi* and *B. propinqua*. Assemblages of late early Santonian age are characterized by *Gonoteuthis westfalica*, which comprises 90–95% of the belemnite faunas, with subordinate *Actinocamax verus verus*, *Gonoteuthis ernsti*, *Goniocamax lundgreni*, *G. striatus* and *Belemnitella propinqua*. Bornholm was thus part of the Central Russian Subprovince from middle Coniacian to early early Santonian time and became part of the Central European Subprovince in late early Santonian time. Baltoscandia remained part of the Central European Subprovince until latest early Campanian time, because *Gonoteuthis* predominates (Christensen 1973, 1975, 1986, 1993a).

The latest early Campanian and early late Campanian belemnite fauna of Scania are characterized by the genus *Belemnelloccamax*: *B. mammillatus* (Nilsson, 1826) in the latest early Campanian and *B. balsvikensis* (Brotzen, 1960) in the early late Campanian. Both species are extremely common in Scania and all growth stages occur, implying that the species bred there. *B. mammillatus* co-occurs with *Belemnitella mucronata*, *Gonoteuthis quadrata scaniensis* and *Belemnelloccamax* ex gr. *gros-souvrei*, and it comprises about 90–95% of the belemnite faunas (Christensen 1975: table 3). *Belemnelloccamax balsvikensis* co-occurs with *Belemnitella mucronata* and the former comprises about 95% of the belemnite faunas (Christensen 1976).

Belemnelloccamax mammillatus and *B. balsvikensis* are extremely rare outside Scania. A little more than 100 specimens of *B. mammillatus* are recorded from the Central Russian Subprovince, in addition to northwest Germany and northern Poland in the Central European Subprovince (Christensen 1975, 1986; Olszewska 1990). *B. balsvikensis* has not been recorded outside Scania, except for two specimens from

Misburg near Hannover in northwest Germany (Christensen & Schulz 1976). To my knowledge, the specimens of *B. mammillatus* occurring outside Scania are adult and they may be regarded as stray individuals buried outside their normal habitat, indicating belemnite migrations to the south and east. The two specimens of *B. balsvikensis* from northwest Germany include a juvenile and an adolescent individual. The presence of the juvenile specimen at Misburg is an enigma, since it is very unlikely that the distance from Scania to Misburg (about 500 km) could be covered by active swimming. Therefore, Christensen & Schulz (1976) suggested that it may have drifted to the Misburg area during heavy storms, either as a gas-filled carcass or clinging to driftwood or sea-weed.

Late Campanian

This substage is characterized by *Belemnitella*, because three genera became extinct at or near the boundary between the early and late Campanian. *Goniotethis* disappeared at the boundary, *Actinocamax* slightly below, and *Belemnelloccamax* slightly above (Fig. 1). The duration of this major belemnite extinction is estimated to be around 2.5 Ma. Kauffman & Hart (1996) did not record a regional or global faunal extinction event or turnover around the early and late Campanian boundary. However, there are significant microfaunal changes in the European chalks during this interval (Bailey *et al.* 1983). For the time being, this belemnite extinction is enigmatic.

As mentioned above the early late Campanian *Belemnelloccamax balsvikensis* is virtually restricted to the Baltoscandian Subprovince. Thus, only one species, *Belemnitella mucronata*, occurred in the earliest late Campanian of the remaining part of the North European Province (Fig. 4). The species diversity increased upwards and several large and small species of *Belemnitella* occurred in the middle and late late Campanian (Fig. 4).

The belemnite fauna of the late late Campanian Beeston Chalk of Norfolk is particularly diverse and includes five taxa of *Belemnitella*: the very large species *B. minor* I Jeletzky, 1951, the large species *B. pauli* Christensen, 1995, in addition to the small species *B. langei* Jeletzky, 1948, *B. najdini* Kongiel, 1962, and *B. sp. 1* (Christensen 1995) (Fig. 6). *B. minor* I predominates, while the others are rare. For instance, *B. minor* I constitutes about 60% of the fauna in the Caistor St. Edmunds pit (Christensen 1995; p. 15). *B. najdini* appeared slightly later than *B. langei* in the Beeston Chalk. In the latest Campanian Paramoudra₂ Chalk the very large species *B. minor* II Christensen, 1995 predominates and the small taxon *B. ex gr. langei/najdini* is rare. The Paramoudra₁ Chalk, which is sandwiched between the Beeston Chalk and Paramoudra₂ Chalk has yielded *B. minor* II and rare *B. pauli*. Thus, small species of *Belemnitella* entered Norfolk three times during the late late Campanian.

After the major belemnite extinction event around the early and late Campanian boundary, the genus *Belemnitella* expanded its area of distribution in late Campanian time and invaded the entire North European Province, where it occurs commonly. It even entered the Tethyan Realm (see later discussion). This extinction event differs, therefore, from that at the Cenomanian–Turonian boundary, when the belemnitellids retreated into refugia (see above).

SUB-STAGES	Belemnite zones, NW Europe		Norfolk	
			Belemnitella zones	Belemnitella subzones
E. MAASTRICHTIAN	L	<i>fastigata</i>	not exposed	
		<i>cimbrica</i>		
		<i>sumensis</i>		
	E	<i>obtusa</i>	minor II (= minor III of Christensen 1995)	
		<i>pseudobtusa</i>		
	<i>lanceolata</i>			
LATE CAMPANIAN	L	<i>langei</i>	minor II	minor II / ex gr. <i>langei</i> / <i>najdini</i>
		<i>minor</i>	minor I	minor II minor I / <i>langei</i> / <i>najdini</i> / <i>pauli</i> minor I / <i>langei</i> minor I
	E	<i>mucronata</i>	<i>woodi</i>	
			<i>mucronata</i>	
		not exposed		

Fig. 6. Stratigraphical correlation diagram, showing conventional late Campanian *Belemnitella* zones (Jeletzky 1951), early Maastrichtian *Belemnella* zones (Schulz 1979) and informal *Belemnitella* zones and subzones of Norfolk (Christensen 1995) (modified from Christensen 1995, 1996). The Beeston Chalk is placed in the zone of *B. minor* I, the Paramoudra₁ Chalk in the subzone of *B. minor* II, and the Paramoudra₂ Chalk in the subzone of *B. minor* II and *B. ex gr. langei/najdini*. Abbreviations: E – early, L – late. Vertical axis not to scale.

Maastrichtian

The genus *Belemnella* appeared suddenly at the base of this stage and continued to its end. It is widely distributed in the North European Province and has also been recorded from the northern part of the Tethyan Realm (see later discussion). *Belemnella* almost ousted *Belemnitella* and, consequently, the early Maastrichtian belemnite faunas of the North European Province consist of species of *Belemnella* with subordinate species of *Belemnitella*. The rarity of *Belemnitella* in the early Maastrichtian may be measured by the following observations. *Belemnella lanceolata* (Schlotheim, 1813) co-occurs with *Belemnitella minor* sensu Christensen (1975) and *B. mucronata* in the earliest Maastrichtian of the abandoned Balsvik pit in Scania, southern Sweden and *B. lanceolata* accounts for about 90% of the assemblage (Christensen 1975). *Belemnitella pulchra* Schulz, 1982 occurs together with species of *Belemnella* in the middle early Maastrichtian of Krons-moor near Hamburg in northwest Germany, and it accounts for about 0.3% of the assemblage (Schulz 1982). The early Maastrichtian belemnite fauna of the Maastricht, Liège and Aachen area consists of species of *Belemnitella* (about 20%) and *Belemnella* (about 80%) (compiled on the basis of data in Keutgen & van der Tuuk 1990).

Belemnella lanceolata appeared in the middle part of the *B. lanceolata* Zone in Denmark (Schulz 1979), probably reflecting a belemnite immigration into Denmark (Christensen 1996). The earliest Maastrichtian of Norfolk is not exposed and the early early Maastrichtian belemnite sequence of Norfolk is totally anomalous and not repeated elsewhere in Europe (Christensen 1996). It is in ascending order: (1) a mixed *Belemnella/Belemnitella minor* II assemblage; (2) only *Belemnitella*

minor II; (3) a mixed *Belemnella*/*Belemnitella minor* II assemblage; and (4) *Belemnella*. This belemnite sequence may be explained by two successive immigrations of *Belemnella* into the Norfolk area.

Christensen (1995) established *Belemnitella minor* III from the early early Maastrichtian of Norfolk and noted that this subspecies differs only from the latest Campanian *B. minor* II by its smaller guard. I have subsequently studied abundant material of *B. minor* from the early early Maastrichtian Craie Phosphatée de Cily of the Mons Basin in southern Belgium, and it is now known that this supposed dissimilarity is incorrect. Therefore, *B. minor* III is placed in synonymy with *B. minor* II.

It has been suggested that the cause of the nearly total replacement of *Belemnitella* by *Belemnella* at the base of the early Maastrichtian was due to a climatic cooling (Jeletzky 1951), and *Belemnella* has been envisaged as a genus adapted to life in cold water on the basis of its geographical distribution (Jeletzky 1951) and morphology (Kongiel 1962). However, palaeotemperatures of northwest Germany, registered by oxygen isotope data ($\delta^{18}\text{O}$), contradict this suggestion. The palaeotemperature was about 15°C in the early late Campanian, increased to about 17°C in the earliest Maastrichtian and decreased to about 15°C in the middle early Maastrichtian (Schönfeld & Schulz 1996). Moreover, if *Belemnella* was a cold water genus, one may assume that it was able to migrate northwards, but it has not been recorded north of Denmark and Northern Ireland, which lay about palaeolatitude 45°N in the Maastrichtian (Smith *et al.* 1994). As a matter of fact, *Belemnella* immigrated southwards into the northern Tethyan margin in Europe (see later discussion).

Belemnella (*Belemnella*?) *praearkhangelskii* Naidin, 1964 is an east European species, which is recorded from Ukraine and the Saratow district in Russia (Naidin 1975). In northwest Europe it occurs in a very narrow horizon, namely in the middle part of the middle early Maastrichtian *Belemnella sumensis* Zone at Hemmoor and Kronsmoor in northwest Germany (Schulz 1979) and at Altembroeck in northeast Belgium (Keutgen in Jagt *et al.* 1995; Keutgen 1997). Unhorizoned specimens from Møns Klint, Denmark probably came from the same stratigraphical level (Schulz 1979). Thus, its appearance in northwest Europe is probably due to a westwards migration (Schulz 1979: p. 53).

Belemnella disappeared slightly below the boundary between the early and late Maastrichtian at Kronsmoor in northwest Germany, whilst two specimens of *B. (Pachybelemnella) cf. cimbrica* Birkelund, 1957 have been recorded from the early late Maastrichtian *Belemnitella junior* Zone of Denmark (see Christensen 1996). *Belemnella* was replaced by *Belemnitella junior* Nowak, 1913, which ranged through the entire late Maastrichtian and occurs in northwest Europe, Poland, western Ukraine and Crimea in the North European Province, in addition to Azerbaijan in the Caucasus in the northern part of the Tethyan Realm. Christensen (1996: fig. 3) showed that it appeared distinctly later in Denmark (base of the late late Maastrichtian) than in northwest Germany and the Maastricht area (at or immediately above the base of the late Maastrichtian). He suggested, therefore, that the appearance of *B. junior* in Denmark was due to either a northwards migration of this species in the late late Maastrichtian or lack of suitable shallow-water habitats during the early late Maastrichtian. Belemnites are extremely rare in the early late Maastrichtian chalk of Denmark (Christensen 1996, 1997), which is known only from outcrops situated in the

basinal part of the Danish Subbasin. Belemnites are more common in the late late Maastrichtian chalk of Denmark, which is known mainly from outcrops located in the marginal part of the basin.

Belemnella (Neobelemnella) kazimiroviensis (Skolozdrówna, 1932) is an east European species, which ranged through the entire late Maastrichtian on the eastern part of the Russian Platform (Naidin 1973, 1975). Christensen (1996: fig. 4) showed that it appeared later in Denmark (late late Maastrichtian) and much later in the Maastricht area (latest late Maastrichtian), implying a westwards spread of this species. Machalski (1996) demonstrated that *B. (N.) kazimiroviensis* appeared earlier in Poland than in Denmark on ammonite evidence, that is in the upper part of the early late Maastrichtian. He thus provided supporting evidence for the westwards migration of this species.

The belemnitelids became extinct at the Cretaceous–Palaeogene boundary, as did many other fossil groups, including the ammonites. This major extinction event was discussed by Kauffman & Hart (1996) and summarized by Barnes *et al.* (1996). It is associated with a worldwide iridium anomaly, major $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ excursions and a global sea-level fall. The cause of the iridium anomaly has been discussed since 1980 and attributed to the impact of a major bolide or volcanism. It is beyond the scope of this paper to discuss the end Cretaceous mass extinctions in detail (see Keller 1996 and MacLeod *et al.* 1997 for two recent reviews).

Kennedy (1989) noted that the disappearance of the ammonites and belemnites at or close to the Maastrichtian–Danian boundary is a particular event in a general phenomenon. Kennedy (1993) suggested that the ammonite and belemnite extinction at the end of the Cretaceous may have been the result of the collapse of marine plankton and subsequent cut-off of food supply for the tiny ammonite and belemnite hatchlings. He noted, however, that equally small hatchlings of other coleoid groups survived the crisis.

Tethyan Realm

Belemnitelids invaded the northern European margin of the Tethyan Realm intermittently during the Late Cretaceous, and species of five genera and two subgenera have been recorded (Fig. 7): *Praeactinocamax*, *Goniotentis*, *Belemnelloamax*, *Belemnitella*, *Belemnella* (*Belemnella*), *B. (Pachybelemnella)* and *B. (Neobelemnella)* (Christensen 1997). The majority of the species occurring in the Tethyan Realm are conspecific with those from the North European Province and thus provide a basis for correlation. Endemic species of *Belemnitella* of late Campanian age occur in Austria, Azerbaijan, Bulgaria and Romania.

Praeactinocamax plenus was recorded recently from the middle late Cenomanian of les Lattes in the Vocontian Basin, Alpes-Maritime of southeast France (Gale & Christensen 1996), in a bed equivalent to Jefferies' Bed 4 of the Plenus Marls of the Anglo-Paris Basin. Thus, it was the first belemnitelid that invaded the Tethyan Realm. *P. plenus* occurs there together with elements of the North Boreal faunal group of Jefferies (1962) (see above). The small sample of *P. plenus*, consisting of nine specimens, includes all growth stages, indicating that the species bred there. The occurrence of *P. plenus* at les Lattes extends its distribution southwards by nearly 600 km from the southernmost locality in the Anglo-Paris Basin. This southwards

ex gr. *grossouvrei* occur in the earliest early Campanian at La Bastide. *B. praecursor* is recorded also from the late Santonian and earliest early Campanian of Azerbaijan (Ali-Zade 1972).

The early Campanian *Goniot euthis quadrata* and late Campanian *Belemnitella mucronata* were recorded from the Aquitaine Basin by previous authors (summarized by Séronie-Vivien 1972: pp. 135–136), but these records need to be confirmed. Previous records of *B. mucronata* from the northern margin of the Tethyan Realm, for instance the Balkans and Turkey, also need to be confirmed, because most previous authors lumped all *Belemnitella mucronata*-like forms, that is small and large species of *Belemnitella*, as well as species of *Belemnella*, in *B. mucronata*.

Late Campanian species and subspecies of *Belemnitella* from Romania were described by Neagu & Georgescu (1991), Bulgaria by Stoyanova-Vergilova & Jolkicev (1993) and Azerbaijan by Ali-Zade (1972). They recorded *B. mucronata*, *B. minor*, *B. langei* and *B. najdini*, as well as subspecies of these taxa, all known from the North European Province, in addition to some local species and subspecies. However, the descriptions of the species from Romania and Bulgaria leave much to be desired, because the internal characters are rarely studied or not studied at all, and the quality of the plates in the paper by Neagu & Georgescu (1991) is extremely poor.

Combémoré (1996) described a small sample of *Belemnitella* sp., consisting of five nearly-complete specimens and about 30 fragments, from the Sub-Alpine Chain at Chartreuse near Grenoble in the Savoie, southeast France (Fig. 3). This species is late late, but not latest, Campanian in age and may be conspecific with *B. hoeferi* (Schloenbach, 1867) (Christensen in press). However, a specific determination of *B. sp.* is not possible, because the internal characters are unknown. Combémoré figured only nearly-complete specimens, which are fully-grown, but all growth stages occur (R. Combémoré personal communication February 1997). *B. sp.* formed, therefore, a breeding population at Chartreuse.

The little known, but valid late late, but not latest, Campanian *Belemnitella hoeferi* was described by Christensen (in press) on the basis of material from the Gschliefgraben tectonic window of the northern Ultrahelvetic series and the Gosau Group of the Northern Calcareous Alps, Austria (Fig. 3). It belongs to the *B. mucronata* group of Christensen (1995), and can be distinguished from most species of this group on the basis of the slender guard. The sample of *B. hoeferi* from the Gschliefgraben includes all growth stages, indicating that the species bred there. Christensen suggested that *B. hoeferi* evolved by allopatric speciation from an initial migrant, which may have invaded the northern European margin of the Tethyan Realm coincidentally with the late late Campanian transgression of Hancock (1990, 1993). Christensen also described *B. cf. minor* II from the latest late Campanian of the Gosau Group. Thus, this species invaded the Tethyan Realm slightly later than *B. hoeferi*.

These records of species of *Belemnitella* indicate that this genus spread southwards into the Tethyan Realm several times during the late Campanian.

The genus *Belemnitella* has not been recorded from the early Maastrichtian of the Tethyan Realm, with one exception. Schulz & Schmid (1983) recorded a single, fully-grown specimen of *B. pulchra* from the middle early Maastrichtian, lower part of the *Belemnella sumensis* Zone, of Bavaria in southern Germany (Fig. 3), implying a southwards migration at that time.

Ali-Zade (1972) recorded *Belemnella lanceolata lanceolata* and *B. sumensis occidentalis* Birkelund, 1957 from the early Maastrichtian of Azerbaijan (Fig. 3). Schulz (1979) placed the first in synonymy with the early early Maastrichtian *B. (Pachybelemnella) inflata* (Arkhangelsky, 1912) and the latter in synonymy with the middle early Maastrichtian *B. (B.?) praearkhangelskii*. Moreover, Naidin (1975) and Schulz (1979) reported *B. (B.?) praearkhangelskii* from western Kazakhstan and Azerbaijan. *B. (B.) gracilis* (Arkhangelsky, 1912) occurs abundantly in the middle early Maastrichtian, lower part of the *Belemnella sumensis* Zone, of Bavaria in southern Germany (Schmid & Schulz 1979; Schulz & Schmid 1983). All growth stages are present, implying that the species bred there.

Therefore, the genus *Belemnella* immigrated into the Tethyan Realm twice in the early Maastrichtian, viz. in the earliest Maastrichtian and in the middle early Maastrichtian. The latter migration is coeval with the *B. pulchra* migration.

Belemnitella junior and *Belemnella (Neobelemnella) kazimiroviensis* are recorded from the entire late Maastrichtian of Azerbaijan in Caucasus (Ali-Zade 1972), implying a southwards immigration of these species into the Tethyan Realm at the base of the late Maastrichtian. Ali-Zade (1972) recorded *B. (N.) kazimiroviensis* as *B. arkhangelskii* (Naidin, 1951) and *B. pontica* (Russeau, 1842). Naidin (1975) placed *B. pontica* in synonymy with *B. kazimiroviensis* with a question mark and *B. arkhangelskii* in synonymy with *B. kazimiroviensis*.

Discussion. — Belemnitellids from the North European Province immigrated into the northern European margin of the Tethyan Realm at least nine times during the Late Cretaceous. These immigrations are in ascending order (Fig. 7):

- 1) *Praeactinocamax plenus* in the middle late Cenomanian.
- 2) *Belemnitella praecursor* and *Belemnelloccamax* ex gr. *grossouvrei* in the late Santonian.
- 3) *Gonioteuthis* sp., possibly *G. quadrata*, in the earliest early Campanian.
- 4) *Belemnitella* spp. in the late Campanian.
- 5) *Belemnitella hoeferi* in the late late Campanian.
- 6) *Belemnitella* cf. *minor* II in the latest late Campanian.
- 7) *Belemnella (Pachybelemnella) inflata* in the earliest Maastrichtian.
- 8) *Belemnitella pulchra*, *Belemnella (B.?) praearkhangelskii* and *Belemnella (B.) gracilis* in the middle early Maastrichtian.
- 9) *Belemnitella junior* and *Belemnella (Neobelemnella) kazimiroviensis* in the earliest late Maastrichtian.

In some areas, endemic late Campanian species of *Belemnitella* co-existed with species of *Belemnitella* from the North European Province. The endemic species probably evolved by allopatric speciation from initial migrants from the North European Province.

North American Province

This province includes Greenland, the Western Interior of North America, in addition to the Atlantic and Gulf coasts of the USA (Figs 8, 9). Belemnitellids are

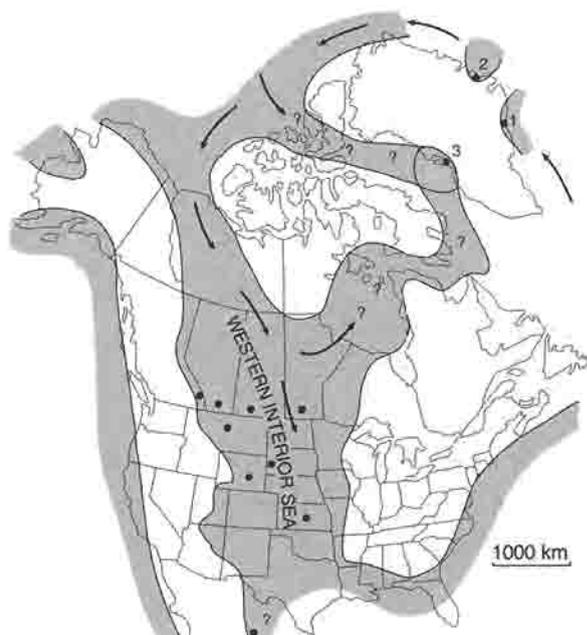


Fig. 8. Approximate distribution of land and sea in North America and Greenland during Turonian and Coniacian time. 1 – Kangerlussuaq area, central East Greenland; 2 – Geographical Society and Traill islands, central East Greenland; 3 – Svartenhuk and Nuussuaq peninsulas, central West Greenland. Dots show occurrences of Turonian to Santonian *Praeactinocamax*. Arrows show probably migration routes. The distribution of land and sea is based on Jeletzky (1971) and Williams & Stelck (1975) for North America and Christensen (1993b) for Greenland. Williams & Stelck (1975) postulated an extension of the Western Interior Sea to central West Greenland across the area of the Hudson Bay and Baffin Island. In contrast, Jeletzky (1971) suggested a marine link between the Western Interior and central West Greenland through the Canadian Arctic Archipelago.

generally very rare and belemnopseids have not been recorded. Christensen (1993b, 1997) showed that the belemnite faunas consist essentially of species of *Praeactinocamax* (Turonian to early Santonian) and *Belemnitella* (latest Santonian to Maastriichtian) (Fig. 10). The genus *Actinocamax* is represented only by one specimen of *A. verus?* from central East Greenland (Jeletzky in Donovan 1954) (see below) and two specimens of *A. aff. laevigatus* Arkhangelsky, 1912 from Kansas (Jeletzky 1961). However, Jeletzky (1961) noted that the two specimens from Kansas may be juveniles of one of the species of *Praeactinocamax*. The middle Turonian belemnite fauna seems to be rather diverse, but this is probably due to excessive subdivision (Christensen 1997).

Greenland

Belemnitellids are extremely rare in Greenland and about 30 specimens have been recorded. Twenty specimens have been described from central East Greenland: two adult specimens of the middle Turonian *Praeactinocamax* cf. *manitobensis* (Whiteaves, 1889) from the Kangerlussuaq area (Fig. 8) (Christensen & Hoch 1983), in

addition to one specimen of *Actinocamax verus?* and 13 specimens of *Belemnitella* ex gr. *alpha/praecursor* from the latest Santonian–earliest Campanian of the Geographical Society island (Fig. 8) (Jeletzky in Donovan 1954; Christensen 1993b, 1997). The small sample of *B.* ex gr. *alpha/praecursor* includes all growth stages, implying that the group bred there. The remaining material is undeterminable.

The small fauna of central West Greenland (Fig. 8), consisting of nine specimens, was described by Birkelund (1956). She recorded three specimens of the late early–middle Coniacian *Praeactinocamax* sp., four specimens of the early Santonian *P. groenlandicus* (Birkelund, 1956), one specimen of *P.* cf. *primus* and one specimen of *P.* aff. *groenlandicus* (= ?*P. manitobensis*, see below). The age of the two last-mentioned specimens is unknown (Birkelund 1956). *P. primus* occurs in the early and middle Cenomanian of the North European Province. The validity of Birkelund's determination of *P.* cf. *primus* was questioned by Christensen (1997), because the specimen is very poorly preserved and Cenomanian belemnites are not recorded elsewhere in the North American Province. Moreover, Dr H. Nøhr-Hansen, Copenhagen has kindly studied dinoflagellate cysts obtained from the matrix of this specimen, and these are most likely of Coniacian–Santonian age (personal communication 20 February 1997).

North America

The following species of *Praeactinocamax* have been recorded from North America: *P. manitobensis* and *P.* aff. *plenus* (described by Jeletzky 1950, 1961); *P. sternbergi* (Jeletzky, 1961) and *P. walkeri* (Jeletzky, 1961) (described by Jeletzky 1961); and *P. cobhani* (Christensen, 1993). *P. sternbergi* is probably a junior synonym of *P. manitobensis*, as is *P.* aff. *groenlandicus* (Christensen & Hoch 1982; Christensen 1997). Four species of *Belemnitella* have been reported from the United States. Jeletzky (1955) described a single, adult specimen of the European species *B. praecursor* from Kansas. Jeletzky (1960, 1962) recognized three late Campanian and Maastrichtian species: *B. americana* (Morton, 1830), *B. bulbosa* Meek, 1876, and '*B.* cf. *bulbosa*', the concept and stratigraphy of which are poorly known. They were discussed by Christensen (1997).

Praeactinocamax manitobensis is widely distributed in the middle Turonian of the Western Interior, from Manitoba, Saskatchewan, Alberta and British Columbia in Canada southwards to Kansas (Cobban 1991: fig. 1) (Fig. 8). *P.* aff. *plenus* was established on the basis of a single specimen from Manitoba (discussed by Christensen 1993b) and *P. walkeri* on the basis of two specimens from Kansas. Therefore, both taxa are poorly known.

Seibertz & Spaeth (1995) described *Praeactinocamax* cf. *manitobensis* from the early Turonian of northern Mexico (Fig. 8). Christensen (1997) regarded the validity of this determination as open to question for the following reasons: (1) the anterior end with the critical characters is missing in the specimens; (2) *P. manitobensis* has not been recorded previously south of Kansas (Cobban 1991); (3) *P. manitobensis* is of middle Turonian age elsewhere; and (4) belemnitellids have not been recorded so far south elsewhere; northern Mexico lay at palaeolatitude 15–20°N.

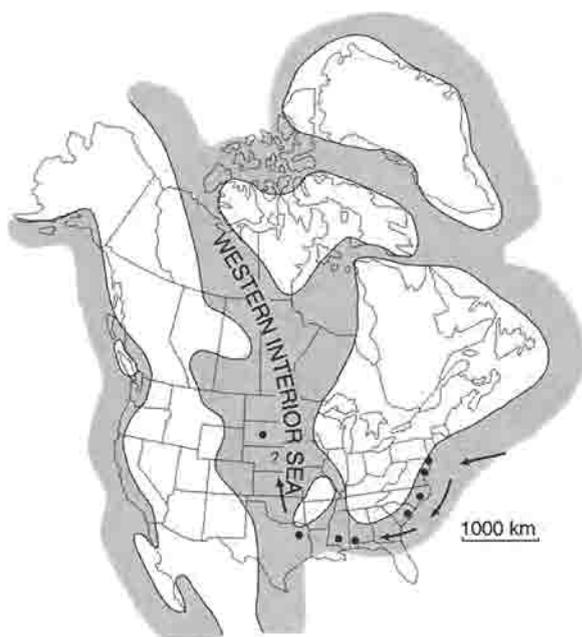


Fig. 9. Approximate distribution of land and sea in North America and Greenland during early Maastrichtian time. Dots show the occurrences of late Campanian and Maastrichtian *Belemnitella*. Arrows indicate migration routes. Modified after Williams & Stelck (1975).

Praeactinocamax cobbani occurs in the late early and middle Coniacian of Montana and Wyoming, and the sample from Montana, consisting of about 150 specimens, includes all growth stages, implying that the species bred there (Christensen 1993b).

Belemnitella americana has a flood occurrence in the Mound Laurel and lowest part of the Navesink Formations of the northern Atlantic Coastal Plain of New Jersey, Delaware and Maryland (Owens & Sohl 1973: fig. 4; Sohl 1987). This species is of late late Campanian and early Maastrichtian age (Christensen 1997). All growth stages are present, indicating that the species bred there. *B. americana* sensu Jeletzky (1962) is an extremely variable species, and the range of variation of both external and internal characters is, in fact, larger in this species than in any other species of *Belemnitella*. Jeletzky (1962) established seven varieties of *B. americana*, and var. *americana* is the most common variety; it constitutes 60–95% of the populations studied by him. He suggested that *B. americana* is derived from a species of the European late Campanian *Belemnitella* lineage.

Jeletzky (1960, 1962) recorded the younger late Maastrichtian '*Belemnitella* cf. *bulbosa*' from the southern Atlantic Coastal Plain and Gulf Coastal Plain of the Carolinas, Alabama, Mississippi and Texas. He failed to describe this taxon but noted that it has a larger Schatzky Distance than *B. americana*. I have studied two specimens of *Belemnitella* from the late Maastrichtian Prairie Bluff Formation of Alabama. These are closely similar to *B. americana* var. *americana* with regard to shape, slenderness and surface markings, but are slightly smaller and have a larger Schatzky Distance, a smaller fissure angle and a smaller alveolar angle.

The late Maastrichtian *Belemnitella bulbosa* is poorly known, because it was established on the basis of only a few specimens from the Fox Hills Formation of South Dakota and the internal characters are unknown. This species is small and extremely slender as interpreted on the basis of its types.

I have studied 10 specimens of *Belemnitella* sp. from the Pierre Shale of South Dakota, *Baculites baculus* and *B. clinolobatus* Zones (Christensen unpublished). These zones are of early, but not earliest, Maastrichtian age. *B.* sp. is closely similar to *B. bulbosa* with regard to size and slenderness and may be conspecific with this species. I have also studied a single specimen of *B.* cf. *bulbosa* from the *Jeletzkytes nebrascensis* Zone of the Pierre Shale of South Dakota. This zone is late late Maastrichtian in age and ranges into the highest Maastrichtian *Micula prinsii* Subzone CC26B of the nanofossil sequence. If *B.* sp. is conspecific with *B. bulbosa*, then the latter ranges through the Maastrichtian, except its basal and uppermost part. Thus, the stratigraphical range of *B. bulbosa* may overlap with that of *B. americana* in the early Maastrichtian and *B. bulbosa* may be partly coeval with '*B.* cf. *bulbosa*'.

Jeletzky (1960) suggested that '*B.* cf. *bulbosa*' and *B. bulbosa* are derived from *B. americana*. However, this suggestion is open to discussion, because the two taxa are poorly known.

Discussion. — It can be concluded that the majority of the belemnitellids of the North American Province are endemic. The endemic species include the Turonian–early Santonian species of *Praeactinocamax* and the late Campanian–Maastrichtian species of *Belemnitella*. Moreover, these have a punctuated, strongly discontinuous stratigraphical distribution and do not represent an evolutionary lineage (Christensen 1993b, 1997). They probably evolved from European species by allopatric speciation from initial migrants.

It might be worth emphasizing that, in contrast to Europe, the only Maastrichtian belemnitellids in North America are *Belemnitella*.

Three European taxa occur in the latest Santonian–earliest Campanian of the North American Province: *Belemnitella praecursor* in the Western Interior, and *Actinocamax verus?* and *Belemnitella* ex gr. *alpha/praecursor* in central East Greenland (see above).

Thus, the belemnitellids immigrated into the North American Province at least six times during the Late Cretaceous. These immigrations are in ascending order (Fig. 10):

- 1) *Praeactinocamax manitobensis* and other poorly known species of this genus in the middle Turonian.
- 2) *Praeactinocamax cobbani* and *P.* sp. in the late early Coniacian.
- 3) *Praeactinocamax groenlandicus* in the early Santonian.
- 4) *Actinocamax verus?*, *Belemnitella praecursor* and *B.* ex gr. *alpha/praecursor* in the latest Santonian–earliest Campanian.
- 5) *Belemnitella americana* in the late late Campanian.
- 6) *Belemnitella bulbosa* probably in the early, but not earliest, early Maastrichtian.

The earliest belemnitellids from the North American Province are of middle Turonian age, an unusual situation in view of the very limited area of distribution of belemnitellids in the Turonian of the North European Province (see above). The belemnitellids disappeared in the late Maastrichtian, some way below the Maastrichtian–Danian boundary.

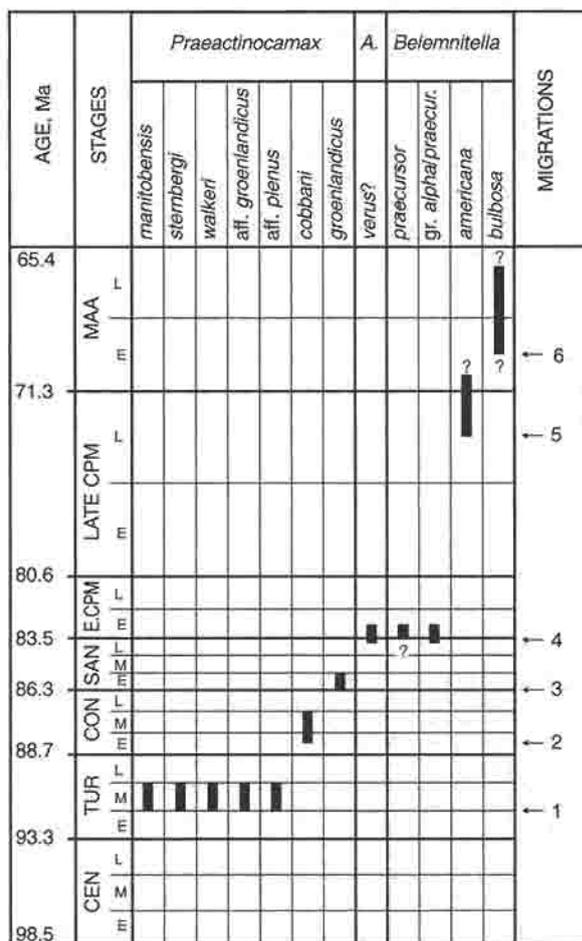


Fig. 10. Stratigraphical range diagram of Late Cretaceous belemnitellids of the North American Province (modified from Christensen 1997). Stage abbreviations as in Fig. 1; A. – *Actinocamax*. Ages in Ma after Obradovich (1994).

The endemic species of *Praeactinocamax* occur in central East Greenland, central West Greenland and the Western Interior Basin of Canada and the USA (Fig. 8). They probably immigrated into the North American Province by a northern route, from northwest Europe via Greenland and Arctic Canada to the Western Interior Seaway (Jeletzky 1950, 1971; Birkelund 1965; Christensen & Hoch 1983) (Fig. 8).

Belemnitella americana is recorded from the Atlantic Coastal Plain, from Maryland and northwards, and '*B. cf. bulbosa*' from the Atlantic Coastal Plain south of Maryland and the Gulf Coast Plain. These may have immigrated via a southern route (Fig. 9). *B. bulbosa* entered the Western Interior from the south.

The majority of the belemnitellid species of the North American Province are endemic, and, consequently, intercontinental correlation based on belemnites is not possible.

Synopsis and possible causes of belemnite migrations

The centre of belemnitellid evolution lay in the North European Province, because all known genera and subgenera occur there and the first members of the genera and subgenera appeared in this province. As shown above, species of five genera and two subgenera invaded the northern European margin of the Tethyan Realm at least nine times during the Late Cretaceous (Fig. 7). Species of essentially only two genera immigrated into the North American Province at least six times during the Late Cretaceous (Fig. 10). More than a score of migrations have been recognized within the subprovinces of the North European Province.

Praeactinocamax immigrated westwards into northwest Europe twice during the Cenomanian: *P. primus* in the earliest middle Cenomanian and *P. plenus* in the middle late Cenomanian. The duration of these immigration events was very shortlived and they took place coincidentally with a rapid rises of sea-level and cool climatic phases, the so-called Primus and Plenus Cold Events. *P. plenus* is more widely distributed in the North European Province than *P. primus* and it even entered the Tethyan Realm, probably due to lack of competition from the belemnopseids, which became extinct worldwide in the middle Cenomanian.

Since all growth stages of *Praeactinocamax primus* occur in the Central European Subprovince there were breeding populations of this species in this subprovince. All growth stages of *P. plenus* occur in the western part of the North European Province, as well as in the Tethyan Realm, implying that it bred there.

Belemnocamax boweri became extinct in the middle Cenomanian and *P. plenus* disappeared in the middle late Cenomanian in western Europe and in the earliest Turonian on the Russian Platform. This belemnite extinction, which included both belemnopseids and belemnitellids, lasted about 2.5 Ma and was probably part of the well-known, global middle Cenomanian to early Turonian mass extinction (see above).

After the crisis around the Cenomanian–Turonian boundary belemnitellids were extremely rare in the Central European Subprovince and had a very limited area of distribution in the Central Russian Subprovince during the Turonian and early Coniacian. Moreover, they did not invade the Tethyan Realm again until the late Santonian. It appears that the European belemnitellids retreated into refugia in the Turonian, which may have been situated in the Central Russian Subprovince.

While the belemnitellids retreated northwards in Europe during the Turonian, they entered, via a northern route, the North American Province for the first time. *Praeactinocamax* appeared in the middle Turonian of the Western Interior of Canada and the United States (*P. manitobensis* and other poorly known species of this genus) and central East Greenland (*P. cf. manitobensis*).

The northwards retreat of belemnitellids in Europe, the migration of belemnitellids into the North American Province via a northern route and the lack of belemnitellids in the Tethyan Realm in the Turonian may be causally related. Jenkyns *et al.* (1994) provided a palaeotemperature curve, derived from oxygen isotope data (δO^{18}), for the Cenomanian to Santonian of East Kent, which lay about palaeolatitude 40°N. They showed that the palaeotemperature reached a maximum of 27–28°C in the earliest Turonian. Moreover, they noted that this temperature compares well with a palaeotemperature of 32–33°C, obtained from fish teeth from Israel, which lay about palaeolati-

tude 10°N. This Late Cretaceous warming peak may be the cause of the northwards retreat of the belemnite stocks in the Turonian.

The Baltoscandian Subprovince was repopulated by *Goniocamax lundgreni* in the early Coniacian and this species spread to the Central Russian Subprovince in the middle Coniacian. The Central European Subprovince was repopulated by *Goniot euthis praewestfalica* in the late middle Coniacian.

Goniocamax esseniensis entered the Central European Subprovince in the early, but not earliest, Coniacian, *G. lundgreni* spread to this subprovince in the late early Coniacian and *Actinocamax verus* cf. *antefragilis* invaded the Baltoscandian Subprovince in the late early Coniacian. These may be considered as occasional immigrants. *Praeactinocamax* immigrated, via a northern route, into the North American Province in the late early Coniacian and persisted into the middle Coniacian: *P. cobbani* appeared in the Western Interior of the United States and *P. sp.* entered central West Greenland. The reasons for these colonization and migration events cannot be satisfactorily explained at present.

Christensen (1976: p. 125) suggested that the parallel evolution of the *Goniot euthis* and *Goniocamax-Belemnitella* stocks in the adjacent Central European and Central Russian Subprovinces during the middle Coniacian to early Campanian was due to mutual competition, because the two stocks are likely to have had the same general ecological requirements.

It seems that species of the *Goniocamax-Belemnitella* stock attempted to colonize the Central European Subprovince five times during the early Coniacian to early Campanian, namely in the early Coniacian (*G. lundgreni* and *G. esseniensis*), early Santonian (*G. lundgreni* and *B. propinqua*), earliest early Campanian (*B. alpha* and *B. praecursor*), middle early Campanian (*B. praecursor*) and latest early Campanian (*B. mucronata*). It was not until the late Campanian, however, that *B. mucronata* successfully colonized the entire North European Province, probably due to the cessation of competition of the genera *Actinocamax*, *Goniot euthis* and *Belemnelloamax*.

At the same time as *Goniocamax lundgreni* and *Belemnitella propinqua* invaded the Central European Subprovince in the early Santonian, *Praeactinocamax groenlandicus* entered central West Greenland, *Actinocamax verus verus* immigrated into the Central European Subprovince and Baltoscandia and *Goniot euthis praewestfalica* spread northwards to Bornholm. In addition, *Goniot euthis ernsti* appeared in the Münsterland Basin and Baltoscandia, and *Belemnitella schmidi* entered Baltoscandia and the Russian Platform from an unknown area. Thus, several southwards and northwards migrations occurred during early Santonian time. Some of the species were occasional immigrants, which did not form breeding populations, for instance *G. lundgreni* and *B. propinqua*. Other species formed breeding populations, among others *A. verus verus* and *G. praewestfalica*. In Baltoscandia there was a major faunal turnover in the middle early Santonian. Belemnite assemblages below are predominated by *Goniocamax* and above by *Goniot euthis*.

The cause of the migrations in the Santonian and the belemnite turnover in the early Santonian cannot be satisfactorily explained for the time being.

Belemnitella praecursor and *Belemnelloamax* ex gr. *grossouvrei* invaded the Tethyan Realm in the late Santonian and *Goniot euthis* entered this realm in the earliest early Campanian. *B. praecursor*, *B. ex gr. alpha/praecursor* and *Actinocamax verus*?

spread to the North American Province in the latest Santonian–earliest early Campanian. *B. alpha* and *B. praecursor* immigrated into Baltoscandia and the Central European Subprovince, respectively, in the earliest early Campanian. Thus, the genus *Belemnitella* migrated both northwards and southwards around the Santonian–Campanian boundary. Again, some of these taxa were occasional migrants, for instance *B. praecursor* in the United States and the Corbières, *B. ex gr. grossouvrei* in the Corbières and *A. verus?* in central East Greenland. In contrast, *B. alpha* and *B. praecursor* formed breeding populations in Baltoscandia and the Central European Subprovince. These migrations occurred during the time of relatively low sea-level (Schulz *et al.* 1984; Haq *et al.* 1987; Hancock 1990, 1993).

Belemnitella praecursor invaded the Central European Subprovince in the middle early Campanian and formed breeding populations. This migration occurred coincidentally with a rapid rise of sea-level (Hancock 1993). This is the *Offaster pilula* transgression of German workers (Niebuhr *et al.* 1997, among others).

Belemnitella mucronata invaded the Central European and Baltoscandian Subprovinces in the latest early Campanian, where it formed breeding populations. At the same time *Belemnellocamax mammillatus* migrated southwards into the Central European Subprovince and eastwards into the Central Russian Subprovince, but it did not breed there. These migrations occur coincidentally with a rapid rise of sea-level (Hancock 1993). This is the *Belemnitella mucronata* transgression of German workers, e.g. Niebuhr *et al.* (1997).

Three out of four genera disappeared at or near to the boundary between the early and late Campanian, namely *Actinocamax*, *Goniot euthis* and *Belemnellocamax*, and only *Belemnitella* survived. This genus spread southwards in the earliest late Campanian and occurred in the entire North European Province, probably due to lack of competition of the extant genera. It even invaded the Tethyan Realm.

It seems that small species of *Belemnitella*, that is *B. langei*, *B. najdini* and *B. ex gr. langei/najdini*, immigrated into the Norfolk three times during the late late Campanian.

Belemnitella americana entered the North American Province and *B. hoeferi* and *B. sp.* invaded the Tethyan Realm in the late late Campanian, where they formed breeding populations. These species may have evolved by allopatric speciation from initial migrants, which immigrated northwards and southwards during a rapid rise of sea-level (Hancock 1990, 1993). *B. cf. minor* II invaded Austria slightly later in the latest late Campanian.

The genus *Belemnella* almost ousted the genus *Belemnitella* in the early Maastrichtian. *Belemnella* is widely distributed in the North Europe Province and even invaded the Tethyan Realm. *Belemnitella* was virtually absent in the Tethyan Realm during early Maastrichtian time.

The anomalous early early Maastrichtian belemnite succession of Norfolk may be explained by two successive immigrations of *Belemnella*.

Belemnella immigrated into the Tethyan Realm twice during the early Maastrichtian, *B. (Pachybelemnella) inflata* near the base of the Maastrichtian, and *B. (B.) gracilis* and *B. (B.?) praearkhangelskii* in the middle early Maastrichtian. *B. gracilis* formed breeding populations. *B. praearkhangelskii* migrated also westwards into northwest Europe at the same time.

The faunal turnover at the base of the Maastrichtian, southwards migrations of early Maastrichtian species *Belemnella* into the Tethyan Realm and virtual absence of the genus *Belemnitella* in the early Maastrichtian of this realm, as well as other early Maastrichtian migrations events are apparently neither linked to palaeotemperature nor to sea-level changes. These faunal turnover and migration events remain to be solved.

Belemnitella junior and *Belemnella (Neobelemnella) kazimiroviensis* invaded the Tethyan Realm in the earliest late Maastrichtian. These migrations took place coincidentally with a rapid rise of sea-level (Hancock 1990, 1993). *B. junior* migrated northwards to Denmark in the late late Maastrichtian. *B. (N.) kazimiroviensis* spread westwards from the eastern part of the Russian Platform during the late Maastrichtian and arrived in Poland in the early late Maastrichtian, in Denmark in the late late Maastrichtian and in the Maastricht area in the latest late Maastrichtian.

Thus, it appears that the distribution pattern and migration events of the belemnitellids to a certain extent can be explained by sea-level changes, cool or warm climatic phases, and mutual competition, but the cause of several migrations cannot be satisfactorily explained at the present.

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Paleobiogeografia i migracje późnokredowych belemnitów z rodziny Belemnitellidae

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Streszczenie

Belemnitellidae Pavlow, 1914 to późnokredowa rodzina belemnitów, obejmująca dziewięć rodzajów i dwa podrodzaje. Przedstawiciele rodziny występowały wyłącznie na półkuli północnej, tj. w prowincjach paleobiogeograficznych północnoeuropejskiej i północnoamerykańskiej w obrębie północnego królestwa klimatu umiarkowanego (North Temperate Realm) oraz na północnych obrzeżach królestwa tetydzkiego (Tethyan Realm) w Europie. W obrębie prowincji północnoeuropejskiej można wyróżnić trzy podprowincje: środkowoeuropejską, środkoworosyjską oraz bałtoskandzką. Obszarem, na którym belemnitellidy powstawały i z którego się rozprzestrzeniały na inne obszary, była prowincja północnoeuropejska. Znane są stąd wszystkie rodzaje i podrodzaje wyróżnione w obrębie rodziny. Z prowincji północnoeuropejskiej belemnitellidy zapuszczały się na obszary królestwa tetydzkiego (co najmniej dziewięć razy) oraz prowincji północnoamerykańskiej (co najmniej sześć razy). Większość gatunków występujących na obszarze królestwa tetydzkiego znanych jest także z prowincji północnoeuropejskiej, natomiast większość gatunków prowincji północnoamerykańskiej to endemity. Te ostatnie powstawały zapewne na drodze specjacji allopatrycznej z imigrantów. W obrębie prowincji północnoeuropejskiej odnotowano łącznie ponad dwadzieścia wydarzeń migracyjnych między jej poszczególnymi subprowincjami. Niektóre zmiany w rozmieszczeniu belemnitellidów można wiązać z eustatycznymi oscylacjami poziomu oceanu światowego, wahaniami klimatycznymi, a także tłumaczyć oddziaływaniami konkurencyjnymi między poszczególnymi gatunkami. Przyczyny wielu wydarzeń migracyjnych pozostają jednak niejasne.