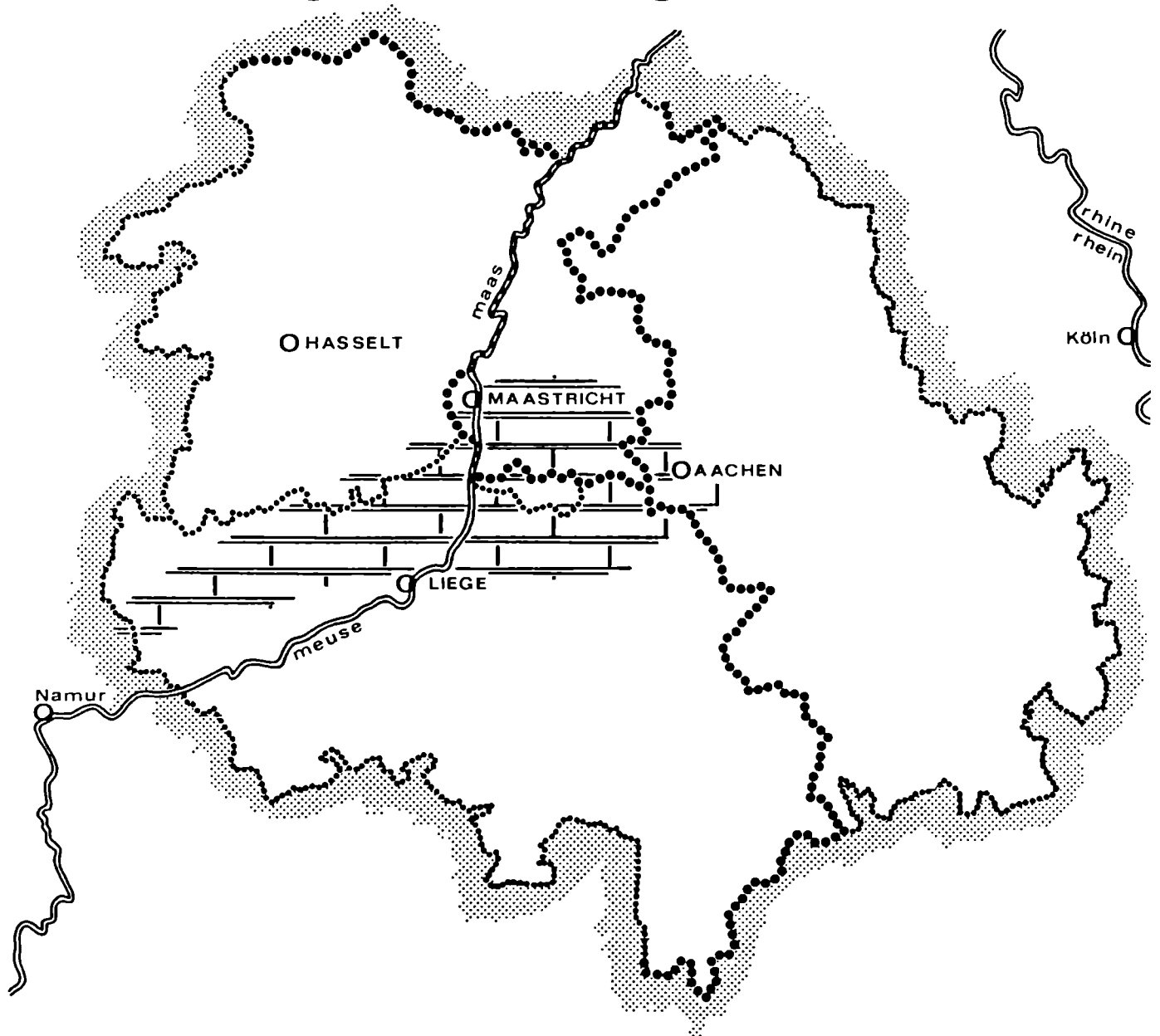


# THE CHALK DISTRICT OF THE EUREGIO MEUSE-RHINE



## SELECTED PAPERS ON UPPER CRETACEOUS DEPOSITS

EDITED BY: MAURICE STREEL & MARTIN J. M. BLESS

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## UPPER CRETACEOUS BELEMNITES OF EUROPE : STATE OF THE ART<sup>1</sup>

by

Walter Kegel CHRISTENSEN<sup>2</sup>

(4 figures)

**ABSTRACT.** - An outline survey of the current status of our knowledge of the Upper Cretaceous belemnites of Europe is given, including classification of Belemnitellidae, evolutionary patterns, biostratigraphy, and paleobiogeography.

**RESUME.** - Un examen des traits principaux de l'état de nos connaissances sur les Belemnites du Crétacé supérieur de l'Europe, y compris une classification des Belemnitellidae, leurs modes d'évolution, la biostratigraphie et la paléobiogéographie est proposé.

### INTRODUCTION

The Late Cretaceous North Temperate Realm, including the North American and North European Provinces, is characterized by Belemnitellidae Pavlov, and the South Temperate Realm by Dimitobelidae Whitehouse; Tethyan belemnites belonging to Belemnopseidae Naef disappeared in the Cenomanian (Christensen, 1976).

Belemnitellidae may have evolved from a northern endemic stock of the Tethyan belemnopseid *Hibolithes*, and the Dimitobelidae from a southern endemic stock of *Hibolithes* (Doyle, 1987a). A widespread Aptian-Albian migration away from Tethys by the belemnopseid *Neohibolites* Stolley and *Parahibolites* Stolley has been suggested by Doyle (1987b) (see also Mutterlose *et al.*, 1983). In the Cenomanian these genera have been recorded as far north as NW Germany

and southern England.

Belemnitellids are defined by having a conical depression, an alveolus, in the anterior part of the guard, which is connected with the surface of the guard through the ventral fissure. Moreover, belemnitellids have vascular imprints, dorso-lateral depressions, and dorso-lateral double furrows, in addition to granules and longitudinal striae.

The following genera of Belemnitellidae have received general recognition : *Actinocamax* Miller, *Gonioteuthis* Bayle, *Belemnelloamax* Naidin, *Belemnitella* d'Orbigny, *Belemnella* Nowak, *Belemnocamax* Crick, and *Fusiteuthis* Kongiel. The two last-mentioned genera are monotypic. These seven genera, in addition to *Neohibolites* and *Parahibolites*, occur in the North European Province, which extends from Ireland to the Ural Mountains (fig. 1). On the other hand, only two genera, *Actinocamax* and *Belemnitella*, are recorded from the North American Province, which includes Greenland, Canada, in addition to the Western Interior, the Atlantic Coast, and Gulf Coast of North America.

1 This paper was presented on June 12, 1987 in Maastricht, the Netherlands, at the field-meeting of the Working Group on the Coniacian to Maastrichtian Stages and the two Belgian Geological Societies.

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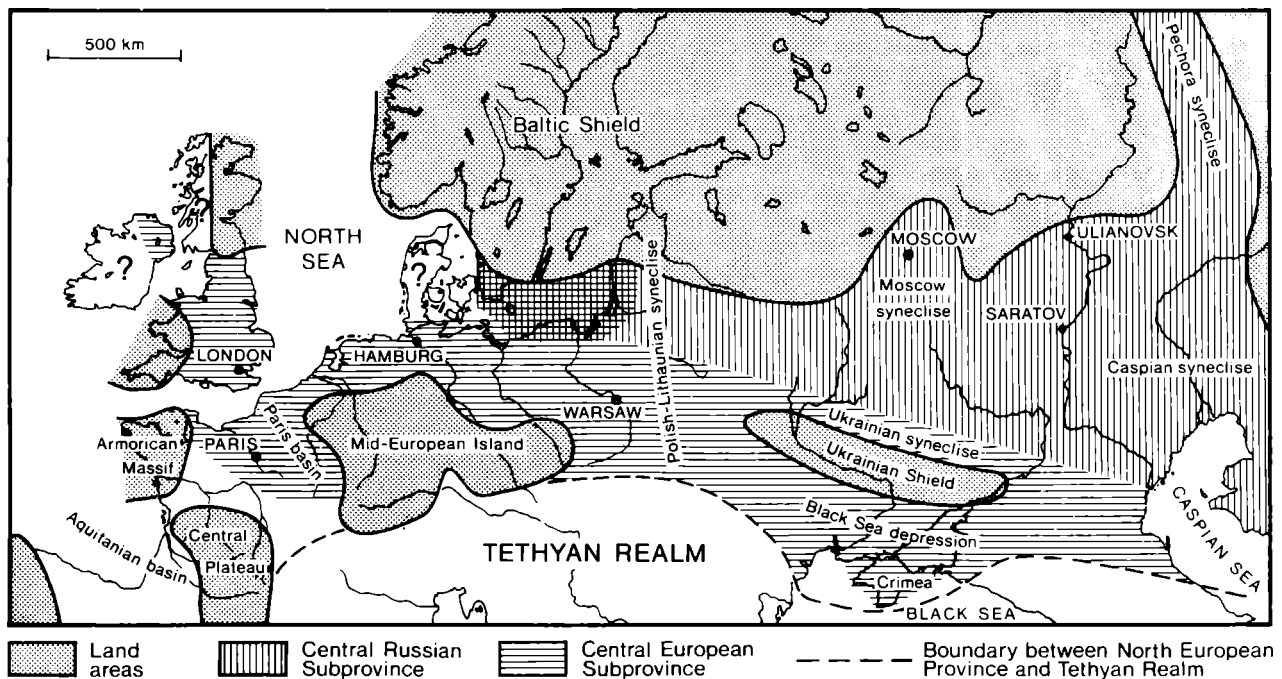


Fig. 1.- Distribution of Upper Cretaceous biogeographic units in Europe based on belemnites. Upper Cretaceous land and sea areas represent maximum inundation for all stages. The boundaries of land areas are not reliable in detail, and the biogeographic units are typically gradational in character. After Christensen (1976)

In the North American Province, *Actinocamax* is recorded from the Turonian-Santonian (possibly also the Lower Campanian) and *Belemnitella* from the Campanian-Maastrichtian (Jeletzky, 1950, 1955b, 1961, 1962; Birkelund, 1956; Christensen & Hoch, 1983). The belemnites from the North American Province are allied to those from the North European Province, and they probably migrated from this province via Greenland and Arctic Canada (Jeletzky, 1950, 1971; Birkelund, 1956; Christensen & Hoch, 1983), as did certain ammonites (Birkelund, 1965).

The North European Province includes the Central European Subprovince and the Central Russian Subprovince (Christensen, 1975a, 1976). These subprovinces are well-defined in the Coniacian-Lower Campanian and are characterized by independently evolving belemnite lineages: the *Goniotethis* stock inhabited the Central European Subprovince and the *Belemnitella* stock (including '*Actinocamax*' *lundgreni* Stolley) inhabited the Central Russian Subprovince.

The Balto-Scandian belemnite faunas can be considered as mixtures of the belemnite faunas from the two subprovinces and they provide a basis for correlation (fig. 2). Near the Lower-Upper Campanian boundary, the belemnite faunas of Balto-Scandian are characterized by the genus

*Belemnelloamax*: *B. mammillatus* (Nilsson) in the uppermost Lower Campanian and *B. balsvikensis* (Brotzen) in the lower Upper Campanian.

In other periods of the Upper Cretaceous the subprovinces are less distinct and may disappear completely. No subprovinces have been recognized during the Upper Campanian-Maastrichtian.

Christensen (1976) analysed the facies distribution of belemnitellids in NW Europe and concluded that they were neritic animals occurring commonly in a variety of nearshore sedimentary facies (biocalcarenes, greensands, and marls) and less commonly in offshore chalks. Since they occur in both nearshore and offshore rocks and their fossilisation potential is great, belemnitellids have been shown to be of fundamental importance in biostratigraphy and correlation in the Upper Cretaceous of Europe, especially during the Coniacian through Maastrichtian Stages.

## SEXUAL DIMORPHISM

Sexual dimorphism is well-known in ammonites (e.g. Kennedy & Wright, 1985) and in Recent cephalopods (see review by Westermann, 1969). Doyle (1985) has demonstrated sexual dimorphism in the Lower Jurassic belemnite *Youngibelus* Riegraf.

Belemnite zones, NW Europe		Zonal belemnites, Balto-Scandia		Zonal belemnites, Russian Platform		
U.Maastr. L   U	<i>B. casimirovensis</i>	U.Maastr. L   U		U.Maastr. L   U	<i>B. casimirovensis</i>	
	<i>B. junior</i>				<i>B. junior</i>	
L.Maastrichtian L   U	<i>B. fastigata</i>	L.Maastrichtian L   U		L.Maastrichtian L   U	<i>Belemnella</i> <i>B. sumensis</i> <i>B. lanceolata</i> <i>B. licharewi</i>	
	<i>B. cimbrica</i>					
	<i>B. sumensis</i>					
	<i>B. obtusa</i>					
	<i>B. pseudobtusa</i>					
	<i>B. lanceolata</i>		<i>B. lanceolata</i>			
	<i>B. lanceolata</i>					
Upper Campanian upper part   lower part	<i>B. 'langei'</i>	Upper Campanian		Upper Campanian U L	<i>B. langei</i> <i>B. l. najdini</i> <i>B. l. langei</i> <i>B. l. minor</i>	
	<i>B. 'minor'</i>					
	<i>B. mucronata</i>		<i>B. mucronata</i> <i>B. balsvikensis/B. mucronata</i>			<i>B. mucronata</i>
Lower Campanian upper part   lower part	<i>G. q. gracilis/B. mucronata</i>	Lower Campanian	<i>B. mammillatus/G. q. scaniensis</i> <i>B. mucronata</i>	Lower Campanian U M L	<i>B. mucronata/G. q. gracilis/</i> <i>B. mammillatus</i>	
	<i>G. q. gracilis</i>					
	<i>G. q. quadrata</i>				<i>B. alpha/B. praecursor/</i> <i>G. q. quadrata</i>	
	<i>G. granulataquadrata</i>		<i>G. granulataquadrata/</i> <i>B. alpha</i>		<i>B. praecursor/A. laevigatus/</i> <i>G. granulataquadrata</i> ( <i>Pteria</i> -beds')	
Santonian U M L   U	<i>G. granulata</i>	Santonian U M L   U	<i>G. granulata</i>	Santonian U L	<i>B. praecursor/G. granulata</i>	
	<i>G. westfalicagranulata</i>		<i>G. westfalicagranulata/</i> <i>B. propinqua</i>		<i>B. propinqua/</i> <i>A. lundgreni ulicus</i>	
	<i>G. w. westfalica</i>		<i>G. w. westfalica/B. propinqua/</i> <i>A. lundgreni</i>			
Coniacian L   M   U	<i>G. westfalica praewestfalica</i>	Coniacian L   M   U		Coniacian U L	<i>A. lundgreni</i>	
			<i>A. lundgreni</i>			
Turonian L   M   U		Turonian L   M   U		Turonian L   U	<i>A. plenus triangulus</i>	
	<i>A. plenus</i>		<i>A. plenus</i>		<i>A. plenus</i>	
Cenomanian L   M   U		Cenomanian L   M   U		Cenomanian U L	<i>A. primus/N. ultimus</i>	
	<i>A. primus</i>		<i>A. primus</i>			

Fig. 2.- Upper Cretaceous belemnite zones in western Europe, Balto-Scandia, and the Russian Platform. Modified from Christensen (1986)

In the case of Belemnitellidae no reliable criteria are available at present for determining either the ontogenetic age or the size at which the adult stage is reached. Large specimens with well-developed vascular imprints and an obtuse apical end are generally regarded as being adult, and small, often smooth, specimens with an acute anterior end as being juvenile. On the other hand, some species have a medium-sized to large, smooth, guard with an acute apex (e.g. *B. praecursor* Stolley and *B. mucronata postrema* Naidin).

Kongiel (1962) and Naidin (1971) have suggested that sexual dimorphism does occur in species of *Belemnitella*. The small and large forms regarded by Kongiel and Naidin to represent the two sexes, however, probably belong to different species (Schulz, 1979). Schulz (1979) showed that sexual dimorphism may occur in Lower Maastrichtian species of *Belemnella*.

#### VARIABILITY

The modern species concept in palaeontology is based on populations rather than a few specimens, including the type (the so-called typological-morphological species concept). Species are studied by analysing the variation of homogeneous samples from restricted stratigraphic intervals by means of biometric methods. This concept has only recently been applied to the Upper Cretaceous Belemnitellidae (e.g. Birkelund, 1957; Ernst, 1964 a, 1968; Christensen, 1971, 1973, 1974, 1975a, 1975b, 1986; Christensen *et al.*, 1975; Christensen & Schmid, 1987; Schulz, 1979; and Jarvis 1980), and biometric studies have shown that many species and subspecies established by earlier authors are nothing but morphological variants.

It is also very important to study the relative growth by bivariate analysis. In cases of isometric growth the ratio of the two variates will remain constant, whereas the ratio will change during growth in cases of allometric growth (see discussion by Christensen, 1973, 1975a). Ratios have been widely used in palaeontologic studies, but these have certain disadvantages, especially in cases where the growth is allometric (Christensen, 1973, 1974, 1975a). Naidin (1964) differentiated six subspecies of *A. plenus* (Blainville) and three subspecies of *A. primus* Arkhangelsky on the basis of various ratios. According to Naidin the ratio of length of guard to maximum lateral diameter varies from 7.0-12.5 in *A. primus* and 4.5-7.0 in *A. plenus*. Christensen (1974), however, showed that the relationship between the two variates in a large sample of *A. plenus* from the Plenus Marls of England is strongly allometric: juvenile specimens

are slender and adult specimens are stout. By using Naidin's classification juvenile specimens could be regarded as *A. primus* and adult specimens as *A. plenus*. Ratios, therefore, may only be used if the growth is isometric or when specimens of nearly the same size are compared.

#### GENUS *ACTINOCAMAX*

This genus includes a group of large species: *A. primus* and *A. plenus* from the Cenomanian; a group of small species: *A. verus* Miller from the Turonian-Lower Campanian and *A. laevigatus* Arkhangelsky from the basal Lower Campanian 'Pteria-beds' of the Russian Platform; and a third group of medium-sized to large species occurring in the Turonian-Lower Santonian (fig. 3). This latter group comprises *A. strehlensis* Fritsch & Schlönbach, *A. bohemicus* Stolley, *A. paderbornensis* Schlüter, and *A. essenensis* Christensen from the Central European Subprovince, *A. intermedius* Arkhangelsky, *A. coronatus* Makhlin, *A. planus* Makhlin, *A. medwedicus*, and *A. matesovae* from the Central Russian Subprovince, in addition to *A. manitobensis* Whiteaves, *A. sternbergi* Jeletzky, *A. walkeri* Jeletzky, and *A. groenlandicus* Birkelund from the North American Province.

Naidin (1964) assigned *A. primus* and *A. plenus* to *A. (Praeactinocamax)* Naidin and the small species to *A. (Actinocamax)*. The species of third group, in addition to the earliest members of the *Gonoteuthis* lineage, *G. westfalica* and *G. westfalica granulata*, and '*A.* *lundgreni*' were placed in *Gonoteuthis (Goniocamax)* Naidin by Naidin (1964) and Makhlin (1965). The subgenera were treated later as genera by Naidin & Kopaevich (1977) and Naidin (1981) among others. The classification of Naidin was discussed by Ernst & Schultz (1974) and Christensen (1982, 1986). It was not followed, however, because it is not logical from a phylogenetic point of view.

*A. primus* and *A. plenus* were discussed at length by Christensen (1974) (see also Christensen, 1976, 1982). *A. primus*, the earliest member of Belemnitellidae, appears in the Lower Cenomanian and continued into the Middle Cenomanian. It is mainly recorded from the northern part of the North European Province. *A. plenus*, which is closely allied to and probably evolved from *A. primus*, occurs in NW Europe in the Middle Upper Cenomanian. This taxon is widespread in the North European Province.

The last representatives of the Tethyan Belemnopseidae, species of *Neohibolites* and *Parahibolites*, became extinct in the Lower-Middle Cenomanian (Combémoré, Christensen, Naidin &

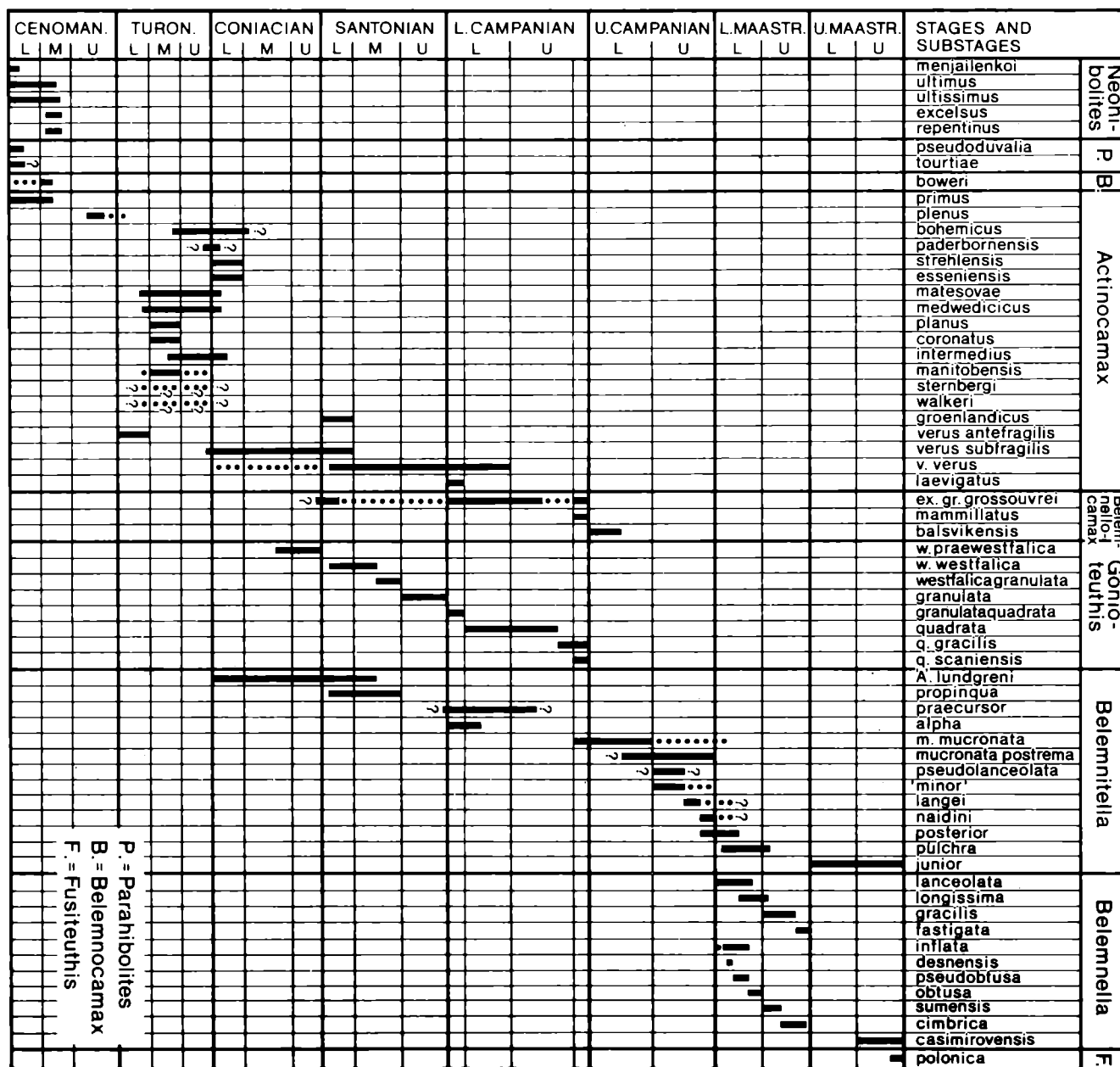


Fig. 3.- Diagram showing the stratigraphical distribution of Upper Cretaceous belemnites in the northern hemisphere. Sources : Kongiel (1962), Ernst (1964a), Christensen (1976, 1982, 1986) and Schulz *et al.*, (1984).

Spaeth, 1981), and it seems that the genus *Actinocamax*, exemplified by *A. plenus*, afterwards expanded its area of distribution to the south.

German authors have suggested an *A. primus* event in the Lower Middle Cenomanian *costatus* Zone and an *A. plenus* event in the Middle Upper Cenomanian *geslinianum* Zone (Ernst, Schmid & Seibertz, 1983; Kaplan & Best, 1985; Hilbrecht, 1986; Dahmer & Ernst, 1986).

According to Ernst *et al.* (1983) the *primus* eco-event was probably caused by a short-term influx of warm water. Since *A. primus* is mainly

recorded from the northern part of the North European Province the suggestion by Ernst *et al.* seems unlikely. On the other hand, Dahmer & Ernst (1986) reported that *A. primus* in NW Germany occurs together with a shallow water fauna. It seems likely, therefore, that *A. primus* may be confined to near-shore sedimentary rocks, as is *A. plenus* (Christensen, 1976 : 123).

The *A. plenus* event was considered to be an eustato-event related to a regression by Ernst *et al.* (1983). Kaplan & Best (1985) considered this event to be caused by an influx of warm water, while Hilbrecht (1986) suggested that deposition

during the *plenus* event took place under cooler conditions. According to Christensen (1976) *A. plenus* is fairly common in near-shore sedimentary rocks, whereas it is extremely rare in off-shore sediments.

*A. verus* is widespread in the North European Province. It is recorded from the Santonian-middle Lower Campanian in NW Europe, whereas it is also recorded from the Turonian and Coniacian of the Russian Platform (fig. 3). On the island of Bornholm (Denmark) *A. verus* has also been found in sediments from the Lower-Middle Coniacian. In the off-shore chalks of NW Europe *A. verus* is most common in the Upper Santonian, while in near-shore sedimentary deposits it occurs commonly also in the basal Campanian. Several subspecies of *A. verus* and *A. laevigatus* have been established (see Naidin, 1964) but, in the opinion of the author, the two species need revision.

Belemnites are virtually unknown in the Turonian-early Coniacian of the Central European Subprovince. The small fauna, consisting of less than a dozen specimens, was revised by Christensen (1982) who recognized four species: *A. strehlensis*, *A. bohemicus*, *A. paderbornensis*, and *A. essenensis*. The fauna was compared with coeval faunas from the Central Russian Subprovince and the North American Province.

Belemnites occur more commonly in the Central Russian Subprovince in the Turonia early Coniacian, but they have a very restricted distribution; they occur almost exclusively in the Volga region and adjacent areas (Naidin, 1981). The following taxa are recorded: *A. intermedius*, *A. matesovae*, *A. medwedicus*, *A. coronatus*, and *A. planus* in addition to various subspecies of *A. verus* (see above). Only *A. intermedius* is common, while other species occur infrequently.

The relationship of *A. strehlensis*, *A. bohemicus*, and *A. paderbornensis* to the coeval species from the Central Russian Subprovince is unknown, as is the relationship to the Cenomanian species of *Actinocamax* and the *Belemnitella* and *Goniotoothis* lineages. On the other hand, *A. bohemicus* and *A. paderbornensis* show resemblance to some specimens of *A. manitobensis* from the Turonian of the North American Province, especially with respect to size and shape of the guard. *A. essenensis* is somewhat similar to the Russian species and '*A. lundgreni*' with regard to size and shape of the guard and the structure of the anterior end.

It is worthy of note that in the North American Province belemnites are unknown in the Cenomanian and the first representatives are from the

Turonian (Jeletzky, 1950), an usual situation in view of the very restricted distribution of belemnites in the Turonian of the North European Province.

#### GENUS *BELEMNOCAMAX*

The peculiar small species, *B. boweri* Crick, was originally described from the Cenomanian of England (Crick, 1910; see also Wright & Wright, 1951; Peake & Hancock, 1970 : 339A). It has recently also been recorded from NW Germany, where it occurs together with *A. primus* in the Lower Middle Cenomanian (Ernst *et al.*, 1983; Dahmer & Ernst, 1986). The relationship of this genus to other genera of Belemnitellidae is unknown at present.

#### GENUS *BELEMNELLOCAMAX*

The evolutionary lineage of *Belemnello-camax*, in ascending order, *B. ex gr. grossouvrei* (Janet), *B. mammillatus* (Nilsson), and *B. balsvikensis* (Brotzen) was studied recently by Christensen (1975a, 1986). The general trend in evolution is the gradual calcification of the anterior end of the guard which also becomes more slender and less lanceolate through time.

Naidin (1964) placed species of the *grossouvrei* group in *Actinocamax* (*Paractinocamax*) Naidin. The subgenus *Paractinocamax* was discussed by Christensen (1986) and considered a junior synonym of *Belemnello-camax*. The *B. grossouvrei* group is widely distributed but rare in the North European Province and has been recorded from England, France, Germany, Sweden, and the Russian Platform. Eleven taxa have been established on the basis of relatively little material, and the group has been the subject of excessive subdivision. *B. ex gr. grossouvrei* occurs from the basal Santonian (possibly the uppermost Coniacian) to the boundary between the Lower and Upper Campanian.

*B. mammillatus* from the uppermost Lower Campanian and *B. balsvikensis* from the lower Upper Campanian are extremely common in Scania, southern Sweden, but rare to very rare outside this area. A little more than one hundred specimens of *B. mammillatus* are recorded from NW Germany, Poland, and the Russian Platform. *B. balsvikensis* is unknown outside Scania except for two specimens from NW Germany (Christensen & Schulz, 1976).

On the basis of size, overall morphology, and ontogeny the origin of *Belemnello-camax* possibly lay in the large Cenomanian-Turonian representatives of *Actinocamax*.

## GENUS GONIOTEUTHIS

During the Middle Coniacian-Lower Campanian the Central European Subprovince was characterized by members of the evolutionary lineage (in ascending order): *Goniotooth westfalica praewestfalica* Ernst & Schulz, *G. w. westfalica* (Schlüter), *G. westfalicagranulata* (Stolley), *G. granulata* (Blainville), *G. granulataquadrata* (Stolley), *G. quadrata* (Blainville), and *G. quadrata gracilis* (Stolley) (fig. 4).

The *Goniotooth* lineage was studied by G. Ernst in a series of papers (1963a, 1963b, 1964a,

1964b, 1966, 1968), and later by Ernst & Schulz (1974), Christensen (1975a, 1975b, 1986), Christensen & Schmid (1987), and Jarvis (1980). The lineage is an outstanding example of phyletic gradualism, viz. slow gradual transformation of a suite of characters within samples of *Goniotooth* through time. The lineage existed for about 10 Ma, and the general trend in evolution is (1) the gradual calcification of the anterior end of the guard, (2) the increasing size and stoutness of the guard, and (3) the gradual development of granulation. In the upper Lower Campanian the *Goniotooth* stock is characterized by a return of earlier features : reducing length of the guard, diminishing depth of

STAGES	ZONATION NW-GERMANY (1)	GONIOTEUTHIS ZONES (2)	SAMPLES OF GONIOTEUTHIS																	
			(3) LÄGER- DORF	(4) MISBURG /HÖVER	(5) OTHER AREAS	(6)	RIEDEL-QUOTIENT													
						20	18	16	14	12	10	8	6	4	2					
LOWER CAMPANIAN	gracilis/mucronata Zone	<i>G. quadrata gracilis</i> (RQ = ± 4.5)		RQ = 4.5																
	conica/gracilis Zone			RQ = 4.7 RQ = 4.5 RQ = 4.2	RQ = 4.5															
	papillosa Zone			RQ = 4.2 RQ = 3.8 RQ = 3.8 RQ = 3.9	RQ = 4.1															
	senonensis Zone	<i>G. quadrata quadrata</i> (RQ = ± 4.0)		RQ = 4.0 RQ = 3.9 RQ = 4.5	RQ = 3.7															
	----- pilula/senonensis Zone			RQ = 4.2 RQ = 4.2	RQ = 3.8															
	lower part pilula Zone			RQ = 4.2	RQ = 3.9															
	lingua/quadrata Zone		(RQ = 4.0-5.0)		RQ = 4.1 RQ = 3.9	RQ = 4.0														
	granulataquadrata Zone				RQ = 5.5															
	SANTONIAN	Marsupites/granulata Zone	<i>G. granulata</i> (RQ = 6.0-7.0)		RQ = 6.5															
Uintacrinus/granulata Zone				RQ = 6.9 RQ = 8.1																
westfalicagranulata Zone		<i>G. westfalica-granulata</i> (RQ = 8.0-9.5)		RQ = 8.8																
cordiformis/westfalica Zone			<i>G. westfalica westfalica</i> (RQ = 9.5-11.5)		RQ = 11.0															
undulatopicatus Zone					RQ = 13.0															
CONIACIAN	prae-westfalica Zone	<i>G. westfalica prae-westfalica</i>		RQ = 13.0																
	involutus Zone																			
	koeneni Zone																			
	deformis Zone																			

Fig. 4.- Diagram showing the zonation of the Coniacian-Lower Campanian of NW Germany, *Goniotooth* zones, and the mean value and observed range of the Riedel-Quotient (RQ). The Riedel-Quotient is the length of the guard divided by the depth of the pseudoalveolus.

Sources : column 1 is based on Schulz (1978, 1985), Ernst *et al.* (1979), and Schulz *et al.* (1984); and column 2-6 on Ernst (1963a, 1964a, 1968) and Ernst & Schulz (1974); column 3 shows the mean value of the Riedel-Quotient of small, closely spaced, samples from the chalk of Lägerdorf; column 4 the mean value of samples from broad stratigraphic horizons of the marls at Misburg/Höver near Hannover; and column 5 the mean value of samples from Braunschweig and Essen.



the pseudoalveolus, and increasing slenderness.

The *Gonoteuthis* lineage provides a good tool for biostratigraphy. It is, however, necessary to analyse homogeneous samples of a certain size in order to make a reliable specific determination, and limited material has only little stratigraphic value (see below).

Ernst defined the species of the *Gonoteuthis* lineage mainly on the basis of the mean Riedel-Quotient, which is length of guard to depth of pseudoalveolus (cf. fig. 4). I have analysed the relationship of these two variates by regression analysis of 24 samples of *Gonoteuthis* (Christensen in prep.). In 21 samples the relationship was found to be isometric. An allometric relationship was revealed in two samples of *G. quadrata gracilis* from the *conica/gracilis* and *mucronata/gracilis* Zones in addition to *G. q. quadrata* from the lower *lingua/quadrata* Zone. The *Gonoteuthis* zonation of Ernst based on the mean Riedel-Quotient is therefore workable, because the relationship of length of guard versus depth of pseudoalveolus is isometric in almost all analysed samples.

The *Gonoteuthis* zonation of the Upper Coniacian-Lower Campanian is shown in figure 4. Column 2 shows the mean Riedel-Quotient of typical samples, and column 3-5 the mean Riedel-Quotient of closely spaced samples from the offshore white chalk of Lägerdorf, the near-shore marls of Misburg/Höver, and other areas. It is evident that there is a discrepancy between the samples from Lägerdorf and Misburg/Höver in the lower and middle Lower Campanian. The samples from Misburg/Höver generally have a deeper pseudoalveolus.

Column 6 shows the mean value and observed range of the Riedel-Quotient. The earliest members have a relatively large variation and the variation gradually diminishes upwards. It can also be seen that there is a rapid change in the mean Riedel-Quotient from the upper

Coniacian to the basal Lower Campanian. There is virtually no change in stratigraphically younger material. Species with a very deep pseudoalveolus (Riedel-Quotient about 2.5) occur only in the middle Lower Campanian. The diagram shows that a single specimen, or few specimens, cannot be assigned safely to species. For instance, a specimen with a Riedel-Quotient of 7 might belong to either *G. w. westfalica*, *G. westfalica-granulata*, *G. granulata*, or *G. granulataquadrata*.

*Gonoteuthis* became extinct at the Lower-Upper Campanian boundary, and this horizon has

been proposed as boundary for the Lower and Upper Campanian (Jeletzky, 1958; Schulz *et al.* 1984, among others).

The earliest member of the *Gonoteuthis* lineage, *G. westfalica*, is closely allied to *Actinocamax* with respect to the structure of the anterior end. The genus probably evolved from Turonian representatives of the genus *Actinocamax* (see below).

## GENUS BELEMNITELLA

The Central Russian Subprovince is characterized by the *Belemnitella* stock in the Coniacian-Lower Campanian: '*Actinocamax*' *lundgreni* from the Coniacian-Middle Santonian, *B. propinqua* (Moberg) from the Lower-Middle Santonian, *B. alpha* Naidin and *B. praecursor* Stolley from the lower-middle Lower Campanian, in addition to *B. mucronata* (Schlothheim) which appears in the uppermost Lower Campanian (fig. 4).

The general trend in evolution is the gradual calcification of the anterior end, as in the genera *Gonoteuthis* and *Belemnelloamax*.

*B. propinqua* is generally considered to be the earliest representative of the genus *Belemnitella*. It is a well-defined species and was revised by Christensen (1971, 1973). It evolved from '*A.*' *lundgreni*, which appears in the basal Coniacian (Christensen, unpubl. inform). Christensen (1971) showed that the concept of *B. propinqua* has been misinterpreted by Russian palaeontologists.

Ernst & Schulz (1974) suggested that the subgenus *Gonoteuthis* (*Goniocamax*) Naidin (type species *A. lundgreni*) should be elevated to a genus or considered a subgenus of *Belemnitella*, and that only the *A. lundgreni* group and its ancestors should be assigned to *Goniocamax*. The suggestion must await further studies.

*B. praecursor*, *B. alpha*, and *B. mucronata* are closely allied. They were fully discussed and described (including biometric analyses) by Christensen (1975a, 1986), Christensen *et al.*, (1975) and Christensen & Schmid (1986). The two varieties of *B. praecursor* var. *media* and var. *mucronatiformis* established by Jeletzky (1955a) and later considered as subspecies by authors, were not recognized by Christensen (1986) and Christensen & Schmid (1987).

The neotype for *B. mucronata* proposed by Christensen *et al.* (1975, pl. 1 : 1) was designated as neotype by the International Commission on Zoological Nomenclature (see ICZN Opinion 1328, 1985, name n° 2979).

In the uppermost Lower Campanian the belemnite faunas of the subprovinces seem to intermingle. *B. mucronata* occurs together with *G. quadrata gracilis* in the Central European Subprovince; *G. quadrata gracilis* predominates and *B. mucronata* is relatively rare. *B. mammillatus* may also occur in some areas. In the eastern part of the Russian Platform *B. mammillatus* occurs together with *B. mucronata*, the latter form being predominant. In Scania *B. mammillatus*, *G. quadrata scaniensis*, and *B. mucronata* are found together, and in this area *B. mammillatus* comprises about 90-95 % of the belemnite faunas, whereas *G. quadrata scaniensis* and *B. mucronata* each account for 1-6% (Christensen; 1975a : table 3).

After the extinction of the genera *Actinocamax* in the middle Lower Campanian, *Gonioteuthis* at the Lower-Upper Campanian boundary, and *Belemnelloamax* in the lower Upper Campanian, the genus *Belemnitella* expanded its area of distribution in the Upper Campanian to cover the whole North European Province and has even been recorded from the northern part of the Tethyan Realm.

More than a score of species, subspecies, and varieties of *Belemnitella* from the Upper Campanian-Maastrichtian have been erected. The systematics of many of these taxa are in a state of flux, and they are poorly understood. Some of the taxa from the Upper Campanian-Lower Maastrichtian are discussed by Christensen (in Robaszynski & Christensen, in prep.). *B. junior* Nowak ranges throughout the Upper Maastrichtian in western Europe and Poland. It has not been recorded east of the Ukrainian syneclise.

The two independently evolving lineages, the *Gonioteuthis* stock and the *Belemnitella* stock, are considered to be sister groups with a common ancestor among the Turonian members of the genus *Actinocamax* from the Central Russian Subprovince (Christensen, 1976).

## GENUS BELEMNELLA

This genus appeared in the basal Maastrichtian and continued to the top of the Maastrichtian. It is widely distributed in the North European Province and has even been recorded from the northern part of the Tethyan Realm, the Helvetia and Ultra Helvetia of southern Germany, where *B. (B.) gracilis* Arkhangelsky occurs abundantly (Schmid & Schulz, 1979; Schulz & Schmid, 1983). The Lower Maastrichtian species were studied in great detail by Schulz (1979) who recognized two evolutionary lineages : a lineage with a slender guard, subgenus *B. (Belemnella)*,

and a lineage with a stout guard, subgenus *B. (Pachybelemnella)* Schulz. He subdivided the Lower Maastrichtian into six belemnite zones (fig. 2). According to Schulz, the subgenus *Pachybelemnella* is mainly found in off-shore chalks. It is worthy of note, however, that this subgenus also occurs commonly in near-shore sediments, such as the Craie de Ciplu of the Mons Basin (Robaszynski & Christensen, in prep.), at Beutenaken in the Maastricht area (Schulz, 1979), and at Nagorzany, USSR (Christensen, in press).

Naidin (1975) placed the last representatives of *Belemnella*, *B. ex gr. casimirovensis* (Skolozdrowna) from the Upper Upper Maastrichtian, in *B. (Neobelemnella)* Naidin. This subgenus shows characters typical for the genus *Belemnitella* : a short and cone-shaped juvenile guard, a relatively large Schatzky distance (up to about 4 mm), and strongly developed vascular imprints.

In the southeastern part of the Russian Platform, where *B. junior* does not occur, Naidin (1973, 1975) described transitional forms between *B. sumensis* Naidin non Birkelund and *B. casimirovensis*, which span the Lower-Upper Maastrichtian boundary. Schulz (1979), however, has suggested that Naidin placed the boundary between the Lower and Upper Maastrichtian at a lower level than he did.

Schulz (1979) discussed the origin of *Belemnella* and concluded that it may have evolved from an unknown species of *Belemnelloamax* or a closely allied genus.

## GENUS FUSITEUTHIS

Specimens belonging to *Fusiteuthis* are extremely rare. One specimen of *F. polonica* Kongiel was recorded from the uppermost Maastrichtian of Poland (Kongiel, 1962) and two specimens of *F. sp.* from the upper Maastrichtian of Crimea (Naidin, 1973, 1975). The origin of *Fusiteuthis* is unknown.

## CONCLUDING REMARKS

In my review I have relied mainly on recent belemnite studies by northwest-European workers in which the variation of species is studied by appropriate biometric methods (e. g. the studies on *Gonioteuthis* by G. Ernst, M.-G. Schulz *Belemnella* studies, and my own work).

It is worthy of note, however, that there is a long tradition for belemnite research in eastern Europe and it may be said that the cradle of belemnite research was in Russia. In this respect,

one may mention the names of A.D. Arkhangelsky, J. Nowak, I. Sinzow, J.A. Jeletzky, I.I. Nikitin, D.P. Naidin, and R. Kongiel. On the other hand, it should also be stressed that the species concept of the east-European workers often differs from that employed in western Europe. Species, subspecies, and varieties are frequently erected on the basis of relatively little material, and the variation of critical characters is very rarely studied.

Belemnitellids have been carefully studied during the last 30-40 years and important results have been achieved. Belemnites have been shown to be of fundamental importance in biostratigraphy and correlation, especially during the Coniacian through Maastrichtian stages. Nevertheless, much work is still needed in order to obtain a better understanding of the evolutionary patterns, biostratigraphy and palaeobiogeography of the Upper Cretaceous Belemnitellidae. In this context I would particularly stress that studies on the genus *Belemnitella* from the Upper Campanian-Lower Maastrichtian and the genus *Belemnella* from the Upper Maastrichtian are needed.

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